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Marine Ecosystem Assessment for the Southern Ocean: meeting the challenge for conserving earth ecosystems in the long term

Edited by
Andrew John Constable, Jess Melbourne-Thomas, Andrea Pinones, Anne Babcock Hollowed and Monica M. C. Muelbert

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Marine Ecosystem Assessment for the Southern Ocean: meeting the challenge for conserving earth ecosystems in the long term

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Table of contents

07 Editorial: Marine Ecosystem Assessment for the Southern Ocean: meeting the challenge for conserving earth ecosystems in the long term
Andrew J. Constable, Jess Melbourne-Thomas, Monica M. C. Muelbert and Anne B. Hollowed

11 Interaction of the Antarctic Circumpolar Current With Seamounts Fuels Moderate Blooms but Vast Foraging Grounds for Multiple Marine Predators
Sara Sergi, Alberto Baudena, Cédric Cotté, Mathieu Ardyna, Stéphane Blain and Francesco d'Ovidio

29 Changing Biogeochemistry of the Southern Ocean and Its Ecosystem Implications
Sian F. Henley, Emma L. Cavan, Sarah E. Fawcett, Rodrigo Kerr, Thiago Monteiro, Robert M. Sherrell, Andrew R. Bowie, Philip W. Boyd, David K. A. Barnes, Irene R. Schloss, Tanya Marshall, Raquel Flynn and Shantelle Smith

60 Subsurface Chlorophyll-a Maxima in the Southern Ocean
Kimberlee Baldry, Peter G. Strutton, Nicole A. Hill and Philip W. Boyd

79 Overcoming the Obstacles Faced by Early Career Researchers in Marine Science: Lessons From the Marine Ecosystem Assessment for the Southern Ocean
Madeleine J. Brasier, Stacey McCormack, Narissa Bax, Jilda A. Caccavo, Emma Cavan, Jessica A. Ericson, Blanca Figuerola, Alyce Hancock, Svenja Halfter, Nicole Hellessey, Juan Höfer, Peter S. Puskic, César Soares de Oliveira, Roshni C. Subramaniam, Jake Wallis and Christine K. Weldrick

88 Marine Ecosystem Assessment for the Southern Ocean: Birds and Marine Mammals in a Changing Climate
Sophie Bestley, Yan Ropert-Coudert, Susan Bengtson Nash, Cassandra M. Brooks, Cédric Cotté, Meagan Dewar, Ari S. Friedlaender, Jennifer A. Jackson, Sara Labrousse, Andrew D. Lowther, Clive R. McMahon, Richard A. Phillips, Pierre Pistorius, Peter S. Puskic, Ana Olivia de A. Reis, Ryan R. Reisinger, Mercedes Santos, Esther Tarszisz, Paul Tixier, Philip N. Trathan, Mia Wege and Barbara Wienecke

127 Global Drivers on Southern Ocean Ecosystems: Changing Physical Environments and Anthropogenic Pressures in an Earth System
Simon A. Morley, Doris Abele, David K. A. Barnes, César A. Cárdenas, Cedric Cotté, Julian Gutt, Sian F. Henley, Juan Höfer, Kevin A. Hughes, Stephanie M. Martin, Carlos Moffat, Marilyn Raphael, Sharon E. Stammerjohn, Coleen C. Suckling, Vivitskaia J. D. Tulloch, Cath L. Waller and Andrew J. Constable

151 Future Risk for Southern Ocean Ecosystem Services Under Climate Change
Rachel D. Cavanagh, Jess Melbourne-Thomas, Susie M. Grant, David K. A. Barnes, Kevin A. Hughes, Svenja Halfter, Michael P. Meredith, Eugene J. Murphy, Rowan Trebilco and Simeon L. Hill

172 A Review and Meta-Analysis of Potential Impacts of Ocean Acidification on Marine Calcifiers From the Southern Ocean
Blanca Figuerola, Alyce M. Hancock, Narissa Bax, Vonda J. Cummings, Rachel Downey, Huw J. Griffiths, Jodie Smith and Jonathan S. Stark

194 Science and Policy Interactions in Assessing and Managing Marine Ecosystems in the Southern Ocean
Anthony J. Press

200 Phenology and Environmental Control of Phytoplankton Blooms in the Kong Håkon VII Hav in the Southern Ocean
Hanna M. Kauko, Tore Hattermann, Thomas Ryan-Keogh, Asmita Singh, Laura de Steur, Agneta Fransson, Melissa Chierici, Tone Falkenhaug, Elvar H. Hallfredsson, Gunnar Bratbak, Tatiana Tsagaraki, Terje Berge, Qin Zhou and Sebastien Moreau

224 Stakeholder Engagement in Decision Making and Pathways of Influence for Southern Ocean Ecosystem Services
Josh Solomonsz, Jess Melbourne-Thomas, Andrew Constable, Rowan Trebilco, Ingrid van Putten and Lyn Goldsworthy

238 Responses of Southern Ocean Seafloor Habitats and Communities to Global and Local Drivers of Change
Madeleine J. Brasier, David Barnes, Narissa Bax, Angelika Brandt, Anne B. Christianson, Andrew J. Constable, Rachel Downey, Blanca Figuerola, Huw Griffiths, Julian Gutt, Susanne Lockhart, Simon A. Morley, Alexandra L. Post, Anton Van de Putte, Hanieh Saeedi, Jonathan S. Stark, Michael Sumner and Catherine L. Waller

268 Evidence for the Impact of Climate Change on Primary Producers in the Southern Ocean
Matthew H. Pinkerton, Philip W. Boyd, Stacy Deppeler, Alex Hayward, Juan Höfer and Sebastien Moreau

287 Enabling Enduring Evidence-Based Policy for the Southern Ocean Through Cultural Arts Practices
Lisa Roberts, Cat Kutay, Jess Melbourne-Thomas, Katherina Petrou, Tracey M. Benson, Danae Fiore, Paul Fletcher, Ellery Johnson, Melissa Silk, Stephen Taberner, Victor Vargas Filgueira and Andrew J. Constable

297 Local Drivers of Change in Southern Ocean Ecosystems: Human Activities and Policy Implications
Susie M. Grant, Cath L. Waller, Simon A. Morley, David K. A. Barnes, Madeleine J. Brasier, Mike C. Double, Huw J. Griffiths, Kevin A. Hughes, Jennifer A. Jackson, Claire M. Waluda and Andrew J. Constable

323 Productivity and Change in Fish and Squid in the Southern Ocean
Jilda Alicia Caccavo, Henrik Christiansen, Andrew J. Constable, Laura Ghigliotti, Rowan Trebilco, Cassandra M. Brooks, Cédric Cotte, Thomas Desvignes, Tracey Dornan, Christopher D. Jones, Philippe Koubbi, Ryan A. Saunders, Anneli Strobel, Marino Vacchi, Anton P. van de Putte, Andrea Walters, Claire M. Waluda, Briannyn L. Woods and José C. Xavier

348 Global Connectivity of Southern Ocean Ecosystems
Eugene J. Murphy, Nadine M. Johnston, Eileen E. Hofmann, Richard A. Phillips, Jennifer A. Jackson, Andrew J. Constable, Sian F. Henley, Jessica Melbourne-Thomas, Rowan Trebilco, Rachel D. Cavanagh, Geraint A. Tarling, Ryan A. Saunders, David K. A. Barnes, Daniel P. Costa, Stuart P. Corney, Ceridwen I. Fraser, Juan Höfer, Kevin A. Hughes, Chester J. Sands, Sally E. Thorpe, Philip N. Trathan and José C. Xavier

377 From Data to Marine Ecosystem Assessments of the Southern Ocean: Achievements, Challenges, and Lessons for the Future
Anton P. Van de Putte, Huw J. Griffiths, Cassandra Brooks, Pip Bricher, Maxime Sweetlove, Svenja Halfter and Ben Raymond

392 Southern Ocean Food Web Modelling: Progress, Prognoses, and Future Priorities for Research and Policy Makers
Stacey A. McCormack, Jessica Melbourne-Thomas, Rowan Trebilco, Gary Griffith, Simeon L. Hill, Carie Hoover, Nadine M. Johnston, Tomás I. Marina, Eugene J. Murphy, Evgeny A. Pakhomov, Matt Pinkerton, Éva Plagányi, Leonardo A. Saravia, Roshni C. Subramaniam, Anton P. Van de Putte and Andrew J. Constable

413 Status, Change, and Futures of Zooplankton in the Southern Ocean
Nadine M. Johnston, Eugene J. Murphy, Angus Atkinson, Andrew J. Constable, Cédric Cotté, Martin Cox, Kendra L. Daly, Ryan Driscoll, Hauke Flores, Svenja Halfter, Natasha Henschke, Simeon L. Hill, Juan Höfer, Brian P. V. Hunt, So Kawaguchi, Dhugal Lindsay, Cecilia Liszka, Valerie Loeb, Clara Manno, Bettina Meyer, Evgeny A. Pakhomov, Matthew H. Pinkerton, Christian S. Reiss, Kate Richerson, Walker O. Smith Jr., Deborah K. Steinberg, Kerrie M. Swadling, Geraint A. Tarling, Sally E. Thorpe, Devi Veytia, Peter Ward, Christine K. Weldrick and Guang Yang

454 Using a risk assessment framework to spatially and temporally spread the fishery catch limit for Antarctic krill in the west Antarctic Peninsula: A template for krill fisheries elsewhere
V. Warwick-Evans, A. Constable, L. Dalla Rosa, E. R. Secchi, E. Seyboth and P. N. Trathan

478 Biological responses to change in Antarctic sea ice habitats
Kerrie M. Swadling, Andrew J. Constable, Alexander D. Fraser, Robert A. Massom, Melanie D. Borup, Laura Ghigliotti, Antonia Granata, Letterio Guglielmo, Nadine M. Johnston, So Kawaguchi, Fraser Kennedy, Rainer Kiko, Philippe Koubbi, Ryosuke Makabe, Andrew Martin, Andrew McMinn, Masato Moteki, Evgeny A. Pakhomov, Ilka Peeken, Jody Reimer, Phillip Reid, Ken G. Ryan, Marino Vacchi, Patti Virtue, Christine K. Weldrick, Pat Wongpan and Simon J. Wotherspoon

503 A dynamic framework for assessing and managing risks to ecosystems from fisheries: demonstration for conserving the krill-based food web in Antarctica
Andrew J. Constable, So Kawaguchi, Michael Sumner, Philip N. Trathan and Victoria Warwick-Evans

523 Opportunities and limitations of large open biodiversity occurrence databases in the context of a Marine Ecosystem Assessment of the Southern Ocean
Anne-Sophie Bonnet-Lebrun, Maxime Sweetlove, Huw J. Griffiths, Michael Sumner, Pieter Provoost, Ben Raymond, Yan Ropert-Coudert and Anton P. Van de Putte

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Editorial: Marine Ecosystem Assessment for the Southern Ocean: meeting the challenge for conserving earth ecosystems in the long term

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Editorial on the Research Topic
Marine Ecosystem Assessment for the Southern Ocean: meeting the challenge for conserving earth ecosystems in the long term

Introduction and rationale

Southern Ocean ecosystems are unique, diverse, and globally valued (Stoeckl et al., 2024, Murphy et al., Roberts et al.) but are also very vulnerable to climate-driven habitat changes (Swadling et al., Cavanagh et al., Pinkerton et al., Morley et al.) and to other human impacts (Grant et al.). Indeed, recent years have seen rapid and dramatic changes, particularly in Antarctic sea ice environments (Purich and Doddridge, 2023), with implications for species and marine ecosystems. Managers of Southern Ocean ecosystems, together with national and international research agencies, need robust and regular assessments of the status and change of these systems in order to protect ecosystem services, to identify options for mitigating impacts, and to understand the likelihood of different future trajectories for these systems (Constable et al., 2014; Press). Regular assessments facilitate the setting and review of priority research activities to enhance future assessments and to provide science directed towards the needs of policy makers.

Our Research Topic *Marine Ecosystem Assessment for the Southern Ocean: Meeting the Challenge for Conserving Earth Ecosystems in the Long Term* addresses this need by providing the first circumpolar interdisciplinary assessment of Southern Ocean ecosystem status and trends. This first Marine Ecosystem Assessment for the Southern Ocean (MEASO) has been a core activity of Integrating Climate and Ecosystem Dynamics in the Southern Ocean (ICED; https://www.iced.ac.uk/). ICED is a regional program of Integrated Marine Biosphere Research (IMBeR, a joint program of the Scientific Committee on Oceanic Research [SCOR] and Future Earth), and co-sponsored by the

Scientific Committee on Antarctic Research (SCAR). MEASO was also supported by the Southern Ocean Observing System (SOOS), a joint program of SCAR and SCOR.

MEASO was a five-year inclusive international program, modelled on a working group of the Intergovernmental Panel on Climate Change (IPCC). It involved 203 scientists from across the Antarctic and Southern Ocean scientific community (19 countries, 51% female, 30% early career), contributing to 24 research articles published in this Research Topic.

Development of the first Marine Ecosystem Assessment for the Southern Ocean

MEASO has been a bridge across many science communities (Constable et al., 2014) including: working groups of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), SCAR and its science groups, the global program of IMBeR in which ICED is the regional Antarctic program, SCOR and the SOOS, and many different groups within the IPCC and Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES). It was formally initiated in 2018 at an International Conference in Hobart, Australia which included a one-day Policy Forum for framing the policy objectives of the assessment. A planning workshop to progress the first MEASO was held in Woking in the United Kingdom in 2019. At this workshop, MEASO participants agreed: to a systematic and integrated ecological, sociological, and policy framework for considering Southern Ocean ecosystems and supporting management advice (Figure 1A); to identify ecoregions that capture variation in ecosystem attributes around the Southern Ocean including their physical and topographical differences (Figure 1B); and to use these areas and frameworks to enable assessments of dynamics and change at ecologically relevant spatial scales within those areas.

MEASO areas were intended to reflect regions within which the dynamics of sea ice, ocean and benthic habitats remained similar across the region, from east to west. Connectivity arising from the large-scale currents and gyres makes it difficult to define more-or-less isolated marine regions. While the MEASO areas are similar to existing areas designed for particular disciplines and for management of fisheries in CCAMLR, they do not match because of the intention in MEASO to reflect ecological and ecosystem properties (i.e., across many disciplines) within an area. For this reason, they are often larger than areas designed to coordinate field research activities across nations operating in a given area, such as those adopted by the Southern Ocean Observing System (https://www.soos.aq/activities/rwg).

The activities and outputs of MEASO have been guided by an International Steering Committee and supported by research support staff (see Table 1). Information and knowledge synthesis and management for MEASO was undertaken through the Southern Ocean Knowledge and Information wiki (SOKI).

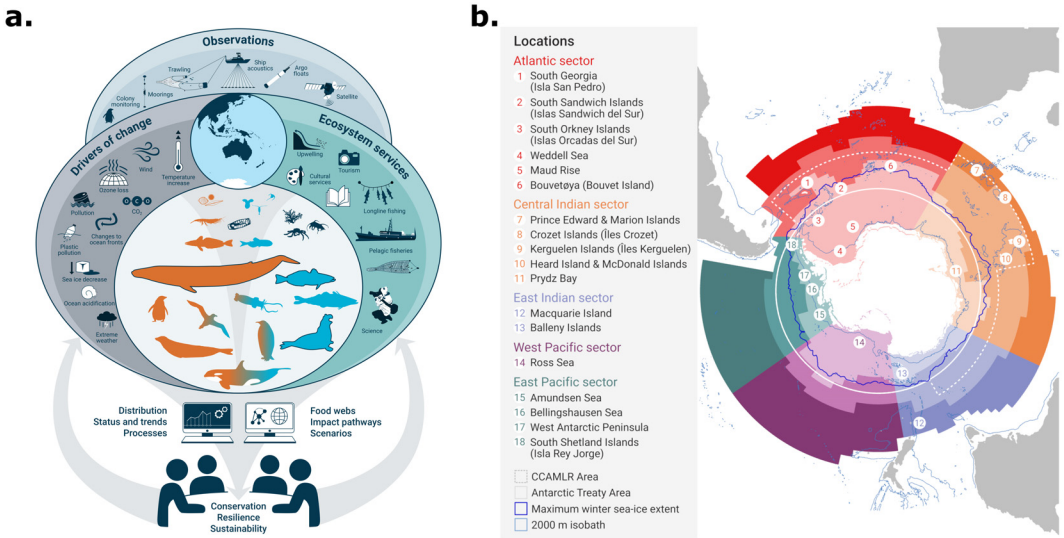

FIGURE 1
Systematic and integrated approach to the first Marine Ecosystem Assessment for the Southern Ocean. **(A)** Diagram showing the scope of MEASO (from Constable et al., 2023) – status and trends for habitats (drivers of habitat change shown as icons on the left), species and food webs (central icons with colours denoting the two main pathways of energy flow through krill in orange and through fish in blue; species icons with both colours are part of both pathways; icons with solid outlines show species recovering from past exploitation, including blue whales, groundfish and seals), and ecosystem services (icons on the right). Example observation platforms delivering data to underpin assessments are shown at the top. The assessment and modelling process is shown at the bottom, which in turn informs decision-making for conservation, resilience and sustainability. Decisions impact on the trajectories of drivers and the ecosystem (arrows looping back up to the central ellipse). **(B)** MEASO assessment areas formed from 5 meridional sectors (Atlantic, Central Indian, East Indian, West Pacific, and East Pacific) and 3 zones (Antarctic – extending from the coast to the Southern Antarctic Circumpolar Current Front [SACCF], Subantarctic extending from SACCF to the Subantarctic Front [SAF], Northern extending from SAF to the Subtropical Front). (adapted from McCormack et al.).

TABLE 1 Steering committee members and research support(*).

Andrew Constable	Huw Griffiths
Jess Melbourne-Thomas	Julian Gutt
Mônica Muelbert	Yan Ropert-Coudert
Anne Hollowed	Irene Schloss
Jilda Caccavo	Dan Costa
Sian Henley	Eileen Hofmann
Juan Hofer	Louise Newman
Nadine Johnston	Andrea Pinones
Eugene Murphy	Anton van de Putte
Madeleine Brasier*	Stacey McCormack*
Rowan Trebilco*	Christine Weldrick*

Framing and delivery of findings

The aim of the MEASO Steering Committee was to not only deliver a synthesis of the science (background, general understanding, the assessment of status, change and causes, and future science priorities) but also to make it accessible to non-scientists, including summaries for policymakers. Each of the papers in the MEASO Research Topic includes a summary infographic, designed by Stacey McCormack of VisualKnowledge, with a consistent theme and style. This Research Topic achieved its goal of providing a set of papers on all aspects of the integrated approach of Figure 1A.

Important context for this assessment was provided on the role of Southern Ocean ecosystems in the global system (Murphy et al.) and the provision of data underpinning the current and future assessments (van de Putte et al.; Bonnet-Lebrun et al.). Core assessments of status and change included: habitats (driven by global drivers – Morley et al.), biogeochemistry (Henley et al.) and primary productivity (Pinkerton et al.); several species groups (benthos – Brasier et al., krill and zooplankton – Johnston et al., fish and squid – Caccavo et al., marine mammals and birds – Bestley et al.); the sea ice system (Swadling et al.); and food webs generally (McCormack et al.). These were supplemented by contributions on subsurface chlorophyll maxima (Baldry et al.) and control of phytoplankton blooms (Kauko et al.), impacts of ocean acidification on marine calcifiers (Figuerola et al.), and food web effects of seamounts (Sergi et al.).

For policy- and decision-makers, core assessments evaluated historical and current pressures on the ecosystem from human activities in the region (local drivers – Grant et al.), global and local pressures on ecosystem services more generally (Cavanagh et al.), and pathways of influence and types of stakeholder engagement to manage for ecosystem services (Solomonsz et al.). These assessments were supplemented by outcomes from the MEASO conference and its Policy Forum on the importance of the interaction between science and policy (Press). Authors considered the great potential for cultural arts practices to enable enduring evidence-based policy in the region (Roberts et al.), and elaborated a framework, adopted by the Scientific Committee of CCAMLR, to assess spatial risks to ecosystems from krill fisheries (Constable et al.) and its implementation (Warwick-Evans et al.). Lastly, early career researchers developed their perspectives and strategies for ensuring future robust marine ecosystem science in the Southern Ocean (Brasier et al.).

A MEASO summary for policymakers (Constable et al., 2023) was developed by members of the Steering Committee and the lead authors of the core papers as a synthesis of key findings from papers in the Research Topic, in plain language and developed for policy- and decision-makers in managing Southern Ocean ecosystems. Assessment statements in the summary for policymakers are assigned confidence levels (as per the IPCC reporting process) and cross-referenced to the original source in the Research Topic. Infographics from the original papers were adapted and presented as part of the summary for policymakers. The text of the key findings is being translated to increase accessibility (https://soos.aq/partnerships/measo-2023/measo-2023-translations; at time of publication this included Dutch, French, Portuguese and Spanish).

Key messages

Key messages from the MEASO Research Topic and the summary for policymakers are:

- Southern Ocean ecosystems are an integral part of the Earth System, including being valued highly by people in many parts of the world.
- Changes in Southern Ocean ecosystems will impact ecosystem services, including cultural services, and have impacts throughout the world's oceans and climate system, and vice versa.
- Southern Ocean ecosystems are being impacted now by climate change. Moreover, sufficient evidence and tools are available for designing strategies to safeguard these ecosystems and to facilitate their resilience to future climate change and ocean acidification.
- Long-term maintenance of Southern Ocean ecosystems, particularly polar-adapted Antarctic species and coastal systems, can only be achieved by urgent global action to curb climate change and ocean acidification.

Meeting the challenge into the future

MEASO and the outcomes of this Research Topic provide an integrated framework, including a spatial partition at ecologically relevant scales, for assessing long term trends of Southern Ocean ecosystems. Regular updates and syntheses of status and prognoses for the future are needed for adjusting management strategies and, particularly, for providing advice globally on the future of this important region. Thus, their regularity would best align with, at least, the assessment review cycles of the IPCC. The outcomes of this first MEASO shows that a timely second assessment could be achieved by 2028, drawing on the research from the UN Decade of the Oceans

and integrating new initiatives in science, policy, management, and civil society.

While knowledge of physical and chemical systems is well advanced in the Southern Ocean, studies of the implications of physical-chemical change on ecological systems needs to be substantially enhanced to have equivalent coverage across all MEASO areas and to satisfy the global demand for prognoses for ecosystems as a whole, from protists to top predators, in this era of rapidly changing environments. This can be readily achieved by investing in (i) sustained, year-round and ocean-wide scientific monitoring and assessment of the health of these biological systems, and (ii) developing coupled bio-physical, end-to-end models of Southern Ocean ecosystems suitable for assessing what future habitat changes and human impacts will mean to different ecosystems, communities and species.

Author contributions

AC: Conceptualization, Project administration, Writing – original draft, Writing – review & editing. JM: Conceptualization, Project administration, Writing – original draft, Writing – review & editing. MM: Conceptualization, Project administration, Writing – original draft, Writing – review & editing. AH: Conceptualization, Project administration, Writing – original draft, Writing – review & editing.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Interaction of the Antarctic Circumpolar Current With Seamounts Fuels Moderate Blooms but Vast Foraging Grounds for Multiple Marine Predators

Sara Sergi[1], Alberto Baudena[1,2], Cédric Cotté[1], Mathieu Ardyna[2,3], Stéphane Blain[4] and Francesco d'Ovidio[1]*

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In the Antarctic Circumpolar Current region of the Southern Ocean, the massive phytoplankton blooms stemming from islands support large trophic chains. Contrary to islands, open ocean seamounts appear to sustain blooms of lesser intensity and, consequently, are expected to play a negligible role in the productivity of this area. Here we revisit this assumption by focusing on a region of the Antarctic Circumpolar Current zone which is massively targeted by marine predators, even if no island fertilizes this area. By combining high resolution bathymetric data, Lagrangian analyses of altimetry-derived velocities and chlorophyll *a* observations derived from BGC-Argo floats and ocean color images, we reveal that the oligotrophic nature of the study region considered in low chlorophyll *a* climatological maps hides in reality a much more complex environment. Significant (chlorophyll *a* in excess of 0.6 mg/m^3) phytoplankton blooms spread over thousands of kilometers and have bio-optical signatures similar to the ones stemming from island systems. By adopting a Lagrangian approach, we demonstrate that these moderate blooms (i) originate at specific sites where the Antarctic Circumpolar Current interacts with seamounts, and (ii) coincide with foraging areas of five megafauna species. These findings underline the ecological importance of the open ocean subantarctic waters and advocate for a connected vision of future conservation actions along the Antarctic Circumpolar Current.

Keywords: open ocean seamounts, phytoplankton blooms, Antarctic Circumpolar Current, Lagrangian approach, pelagic hotspots

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INTRODUCTION

Marine phytoplankton production drives ecosystem trophic structures (Iverson, 1990; Frederiksen et al., 2006; Boersma et al., 2009; Block et al., 2011) and ecosystem services, ranging from carbon export (Michaels and Silver, 1988; Legendre and Rassoulzadegan, 1995; Heinze et al., 2015) to fisheries production (Chassot et al., 2010). Consequently, understanding the factors underpinning phytoplankton productivity has major implications for process studies. These

include the parameterization of nutrient input adopted in biogeochemical models (Aumont and Bopp, 2006; Lancelot et al., 2009; Tagliabue et al., 2014) and the identification of biological hotspots for the management and conservation of marine living resources (Gove et al., 2016; Santora et al., 2017).

In the Atlantic and Indian sectors of the Antarctic Circumpolar Current (ACC) region (**Figure 1A**), iron limitation generates intense contrasts in the biological productivity (e.g., Martin, 1990; Sullivan et al., 1993; De Baar et al., 1995; Boyd et al., 2000) affecting the distribution of pelagic ecosystems, from primary producers to upper predators (De Broyer et al., 2014). The major source of iron for the shallow ocean is provided by the interaction of the eastward ACC flow with the shallow bathymetry around islands (Sullivan et al., 1993; Thomalla et al., 2011; Ardyna et al., 2017). The island mass effect stimulates dramatic phytoplankton blooms, such as the ones occurring downstream of South Georgia, Crozet, and the Kerguelen Plateau (Sohrin et al., 2000; Blain et al., 2001, 2007; Moore and Abbott, 2002; Lancelot et al., 2009; Pollard et al., 2009; Borrione et al., 2014; d'Ovidio et al., 2015; see also **Figure 1A**). This large phytoplankton biomass is at the basis of the pelagic food web which sustains numerous colonies of predators breeding in the subantarctic islands (De Broyer et al., 2014). Pinnipeds and seabirds intensively forage in the phytoplankton plumes extending in the Antarctic Polar Front (PF) region downstream of South Georgia (Barlow and Croxall, 2002; Staniland et al., 2004; Scheffer et al., 2010; Rogers et al., 2015) and the Kerguelen Plateau (Guinet et al., 2001; Lea et al., 2006; Cotté et al., 2015; O'Toole et al., 2017).

Away from the islands, the interaction of the ACC with large and deep (>2500 m) topographic features, as mid-ocean ridges, is recognized to generate intense upward movements (Sokolov and Rintoul, 2007; Rintoul, 2018). These vertical motions regularly sustain some phytoplankton productivity through the injection of iron into the euphotic layer (Sokolov and Rintoul, 2007). However, with the notable exception of isolated contributions from hydrothermal vents (Ardyna et al., 2019), these vast open ocean regions show a yearly averaged phytoplankton biomass much lower than the island systems. Thereby, their contribution to the primary production of the ACC region is considered comparatively negligible (Graham et al., 2015; Ardyna et al., 2017). Furthermore, these regionally contrasted quantitative assessments of primary production are accompanied by differences in phytoplankton community composition. Islands blooms are dominated by diatoms, while the open ocean low productive (low phytoplankton) regions are generally described by other lower size (nano-, pico-plankton) phytoplankton communities, like for instance *Phaeocystis* (Detmer and Bathmann, 1997; Gervais et al., 2002; Smetacek et al., 2004; Queguiner, 2013). These High Nutrient Low Chlorophyll (HNLC) communities are less likely to support pelagic ecosystems that include large predators as marine mammals or seabirds (Cushing, 1989; Moline et al., 2004; Pakhomov et al., 2019).

It is becoming therefore tempting to see the ACC as an (iron limited) HNLC phytoplankton-desert, punctuated by oases in the wake of islands or hydrothermal vents. However, this view is not consistent with megafauna observations. One of the supposedly low productive regions has been recently associated to intense foraging activity of five species of swimming predators breeding at the Prince Edward Islands: Antarctic Fur Seals (*Arctocephalus gazella*), Southern Elephants Seals (*Mirounga leonina*), King Penguins (*Aptenodytes patagonicus*), Macaroni Penguins (*Eudyptes chrysolophus*), and Southern Rockhopper Penguins (*Eudyptes chrysocome chrysocome*) (Arthur et al., 2017; Pistorius et al., 2017; Reisinger et al., 2018). Differently from the colonies of the South Georgia and Kerguelen Islands, penguins and seals, after moving to the PF region, travel upstream and explore an apparently oligotrophic area (**Figure 1A**). Although some of the animals focus on an area associated to intense phytoplankton blooms sustained by upwelled water masses enriched by hydrothermal iron (downstream of 30°E; Ardyna et al., 2019), some others travel and forage further upstream, in the supposedly HNLC biologically-desert area. These long trips are recurrent and energy-consuming and require to be balanced by profitable prey captures. But what is the origin of the phytoplankton production sustaining this prey field?

This paper addresses this question, reassessing from an ecological viewpoint the productivity and nutrient delivery of vast open ocean regions in the ACC area. In particular, our work proposes to extend the biogeochemical island mass effect to the numerous seamounts located upstream of the foraging grounds of marine high-level predators (**Figure 1C**). In respect to previous studies which assessed the seamounts effect as negligible compared with the island one (e.g., Graham et al., 2015; Ardyna et al., 2017), we propose to investigate it further through two new main datasets. First of all, we use the high resolution seamount inventory provided by Yesson et al. (2011) (an illustrative example is depicted in the bottom panels of **Figure 1**). Previous studies analyzed coarser bathymetric dataset, thus not allowing to identify most of the seamounts. Secondly, we assume a regional ecological perspective, while previous works had a large-scale biogeochemical focus (Graham et al., 2015; Ardyna et al., 2017). In this aim, we investigate the seamount effect over seasonal time scales and we complement the satellite images with profiling floats' observations, which allow us to infer the total phytoplankton biomass contained in the water column. Indeed, from a circumpolar biogeochemical viewpoint, moderate phytoplankton biomass may appear almost invisible on annual mean climatology when compared to the dramatic production occurring in the wake of the subantarctic islands. However, from an ecological perspective, seasonal secondary blooms may represent a critical input of biomass for local trophic chains. This is especially true when considering the possible effect of these blooms in sustaining foraging grounds of predators who are tied to a specific region for energetic or physiological purposes.

We stress that understanding the factors behind the foraging activity of land-breeding predators is of urgent concern, given the

Abbreviations: ACC, Antarctic Circumpolar Current; BGC-Argo, Biogeochemical Argo; CCAMLR, Commission for the Conservation of Antarctic Marine Living Resources; chl *a*, chlorophyll *a*; PF, Antarctic Polar Front; SRS, Shona Ridge System; SWIR, South-West Indian R.

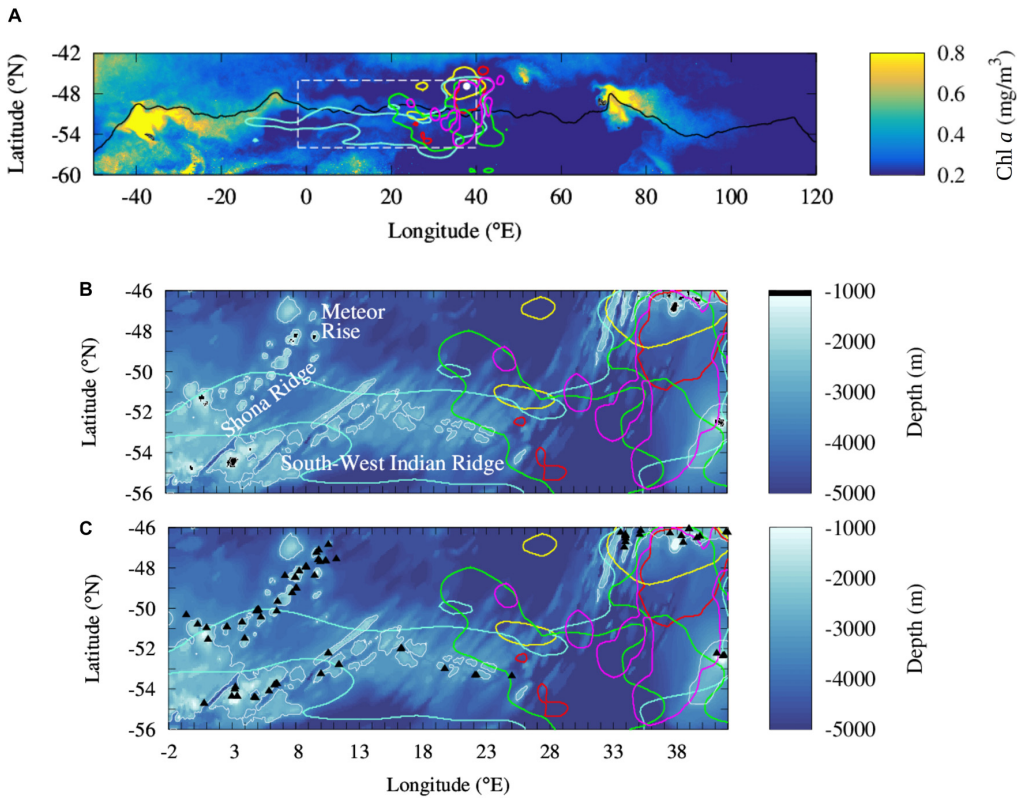

FIGURE 1 | Comparison of the at-sea distribution of five species of predators from the Prince Edward Islands to the distribution of regional phytoplankton biomass and shallow topographies in the southern Agulhas Basin. **(A)** Large scale climatology of concentration in chlorophyll *a* in the Atlantic and Indian sectors of the Southern Ocean during the bloom period (from November to January) between 2000 and 2015. Intense chlorophyll *a* blooms spread downstream of South Georgia (36 °W; 54 °S) and Kerguelen Plateau (70°E; 49°S) transported by the ACC. The solid black line locates an intense ACC core, the Polar Front. Dashed white box locates the study region shown in the bottom panels. **(B,C)** Comparison of shallow topography (<1000 m depth) identified in a global bathymetric product (**B**, black areas) and seamounts shallower of 1000 m located by Yesson et al. (2011) (**C**, black triangles) in the southern Agulhas Basin. Colored contour lines locate the at-sea habitat of Antarctic Fur Seals (*Arctocephalus gazella*; red), Southern Elephants Seals (*Mirounga leonina*; yellow), King Penguins (*Aptenodytes patagonicus*; cyan), Macaroni Penguins (*Eudyptes chrysolophus*; green) and Southern Rockhopper Penguins (*Eudyptes chrysocome chrysocome*; magenta) from the Prince Edward Islands (white dot in the **A**) [data are reproduced from Reisinger et al. (2018)].

increasing attention that the subantarctic open ocean is receiving within the Commission for the Conservation of Antarctic Marine Living Resources (e.g., Sc-Camlr-XXXVII (2018), Annex 7, para. 3.74; Ccamlr-XXXVII (2018), para. 6.60). A key step to that end is to improve our comprehension of the biophysical processes which sustain biological productivity up to megafauna species. Using a Lagrangian approach (Lehahn et al., 2018), we propose here to test how seamounts complement the island mass effect in fueling pelagic ecosystems within the ACC domain and how they affect the biological production inferred from land-based top predators.

MATERIALS AND METHODS

Predators Distribution

Predators distribution is estimated from tracking data of seabirds and seals from the Prince Edward Islands between 2003 and 2014 and collected from research programs supported by the National Research Foundation and the South African Department of Environmental Affairs (Reisinger et al., 2017)[1]. The animals' trajectories we use in this work have been analyzed in detail in Reisinger et al. (2018): here we report only the information relevant for our study, which is the large-scale geographical extension of their habitat utilization, i.e., the whole smoothed spatial range of predators. In this study we consider only the tracking data of seals and penguins, because they display a more selective habitat than flying seabirds (Reisinger et al., 2018). The Subantarctic Fur Seals (*Arctocephalus tropicalis*) are not considered because the at-sea distribution of this colony is mostly located north of the Subantarctic Front which bound our study region [see **Figure 2** in Reisinger et al. (2018)]. Kernel densities of Antarctic Fur Seals (*Arctocephalus gazella*), Southern Elephants Seals (*Mirounga leonina*), King Penguins (*Aptenodytes patagonicus*), Macaroni Penguins (*Eudyptes chrysolophus*) and Southern Rockhopper Penguins (*Eudyptes chrysocome chrysocome*) from the Prince Edward Islands were calculated using the "kde2d" function from

[1]https://figshare.com/articles/_/5613016

the R-package "MASS" on the observed tracks (Venables and Ripley, 2002). The habitat utilization for each colony is identified with a threshold of 95% of each predator density (complete kernel utilization distributions are available for each species in Reisinger et al., 2018; **Figure 2**). This allows us to identify the whole spatial range used by multiple subantarctic predators including different phases and behavior of their trajectories (usually traveling and foraging).

Seamounts

Seamounts are defined as geomorphological features having a vertical elevation of more than 1000 m from the seafloor with limited extent across the top summit region (Menard, 1964; Staudigel et al., 2010). The seamounts' summit location is extracted from Yesson et al. (2011). We retain here only the shallower structures having a maximal water depth of 1000 m, in order to compare them with the ocean upper layer horizontal velocity fields derived from altimetry. In the following, a seamount is defined by a disk centered in the seamount summit and with a 70 km radius. In the same way, the region under the influence of Bouvet Island is defined by a disk centered in the island (3.36°E; 54.42°S) with a 70 km radius.

Satellite Observations and Reanalysis Data

Geostrophic velocities, surface chlorophyll *a* (Chl *a*) and temperature reanalysis are evaluated between 2000 and 2015 from different products distributed by the European Copernicus Marine Environment Monitoring Service[2].

Geostrophic currents are quantified through an altimetry multi-satellite global product (product id: SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047) produced by SSALTO/DUACS. This product processes data from all altimeter missions (Jason-3, Sentinel-3A, HY-2A, Saral/AltiKa, CryoSat-2, Jason-2, Jason-1, T/P, ENVISAT, GFO, ERS1/2) and has temporal and spatial resolutions of, respectively, 1 day and 1/4°. Trajectories are derived by applying a Runge–Kutta fourth order scheme with a time step of 6 h. Velocity fields are linearly interpolated in both space and time.

Satellite surface Chl *a* concentration is analyzed with the Global Ocean Color product (product id: OCEANCOLOUR_GLO_CHL_L4_REP_OBSERVATIONS_009_082) produced by ACRI-ST. The product evaluated has a 1/24° spatial resolution. Here, we consider monthly-mean composites in order to reduce the cloud coverage and at the same time preserve the mesoscale variability of the Chl *a* blooms. Similarly to previous studies, the term "bloom" refers to regions of relative elevated Chl *a* compared to the background concentration (Sokolov and Rintoul, 2007). The statistical significance of the Chl *a* enhancement is evaluated with the bootstrap method (a detailed description of the method used for the identification of Chl *a* blooms is provided in the section "Seamount Mass Effect: Detection of the Lagrangian Plume Stemming From the Seamounts"). Chl *a* values are investigated in spring and summer (from October to February) ahead of the maximum feeding activities of higher trophic levels (Laws, 1985; Moline et al., 2004; De Broyer et al., 2014).

Phytoplankton dominance is evaluated from the PHYSAT observations (Alvain et al., 2005, 2008) between 2000 and 2011 from the month of December and January, when we expect a larger diatoms dominance (Smetacek et al., 1990; Alvain et al., 2008). The PHYSAT method has already been validated at the global and regional scale in the Southern Ocean (Alvain et al., 2005, 2008, 2013; see in particular

[2]http://marine.copernicus.eu/

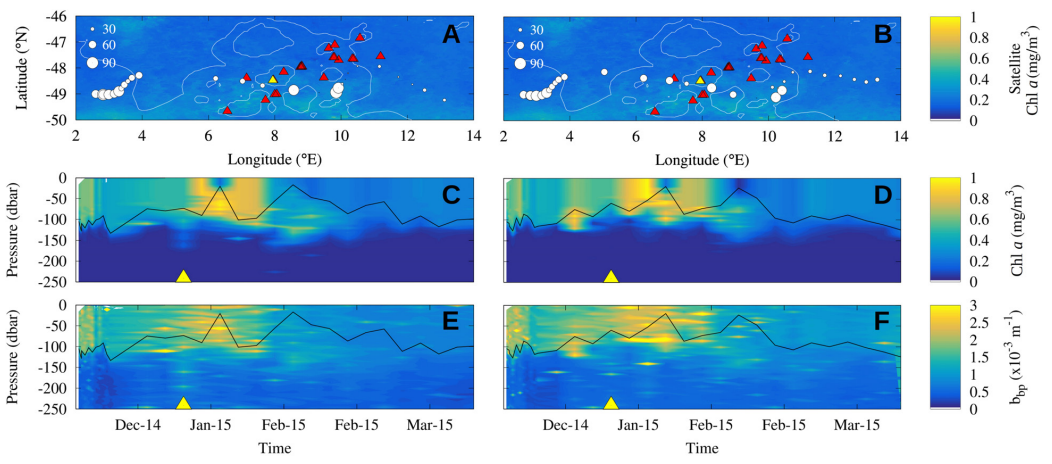

FIGURE 2 | Observed Chl *a* enhancement in the wake of seamounts by BGC-Argo WMO 6901688 **(A,C,E)** and WMO 6901585 **(B,D,F)** during the summer season 2014/2015. **(A,B)** Maps of the floats trajectory across the Shona Ridge System: each circle represents a vertical profile and its size is proportional to Chl *a* integrated over the mixed layer [the mixed layer depth is shown in the panels **(C–F)** with the solid black line]. Color scale shows the Chl *a* observed by satellite in January 2015 and red triangles the seamounts location. **(C,D)** Time series of the vertical distribution of Chl *a* concentration measured from the BGC-Argo floats along their trajectories. **(E,F)** Vertical profiles of backscattering measured from the BGC-Argo floats along their trajectories. Yellow triangles in the middle and bottom panels locate the time of the float closest position to the yellow seamount in the top panels. This may be interpreted as the contact of the BGC-Argo with the axis of the seamount chain.

d'Ovidio et al., 2010 **Supplementary Material** for a validation at the latitudes used here). The method identifies probable specific dominant phytoplankton groups based on the analysis of spectral measurements computed by ocean-color sensors. These are nano-eukaryotes, *Prochlorococcus*, *Synechococcus*, diatoms, *Phaeocystis*-like and coccolithophores. Note that a phytoplankton group is defined as dominant when it is a major contributor to the total pigment (Alvain et al., 2005). As demonstrated in Della Penna et al. (2018), a large number of pixels of PHYSAT daily maps are flagged as not classified in this oceanic region, so that composite maps must span very large periods in order to provide meaningful spatial patterns. For this reason, and because we study large scale features, in our analysis we have used multi-year PHYSAT composites, without resolving interannual variability.

Vertical distribution of temperatures is evaluated with the global ocean reanalysis GLORYS2V4 produced by Mercator Ocean for the Global Ocean and Sea Ice Physics (product id: GLOBAL_REANALYSIS_PHY_001_025). This product is performed with NEMOv3.1 ocean model in configuration ORCA025_LIM and has horizontal spatial resolution of 1/4° with 75 vertical levels. For the analyses we used the product version averaged by month. The water masses associated to the position of the Antarctic Polar Front (PF) are identified as the northern extent of the presence of the 2°C isotherm minimum in the subsurface (0–500 m depth) (Botnikov, 1963).

Biogeochemical Argo Floats

The vertical profiles of Chl *a* concentration and backscattering measured from the Biogeochemical Argo (thereafter BGC-Argo) floats have been extracted from the CORIOLIS Global Data Assembly Center[3]. Quality control tests have been achieved on the Chl *a* and backscattering data (Schmechtig et al., 2014, 2018). Non-photochemical quenching on daytime profiles are also corrected on the Chl *a* data following (Xing et al., 2012). In this aim, the maximal Chl *a* value above the mixed layer depth is extrapolated until the surface and corrected with a specific correction factor. In order to adapt the correction procedure to the study region, the non-photochemical quenching is corrected with the calibration factor of 3.3 used by Ardyna et al. (2019) in the same region. The mixed layer depth is evaluated in each profile as the depth of a density difference of 0.03 kg/m^3 in respect to the density at 10 m depth. The density is computed based on International Thermodynamic Equation of Seawater (Sérazin, 2011).

Seamount Mass Effect: Detection of the Lagrangian Plume Stemming From the Seamounts

In order to identify the effects of seamounts on phytoplanktonic blooms we analyze whether possible water parcels displaying enhanced Chl *a* have, or have not, been in contact with the seamounts. To achieve this, we compute a backward-in-time, altimetry-based Lagrangian calculation from the bloom periods. This calculation allows us to identify the water parcels that transited over a seamounts area, defined here as a disk of 70 km radius. This value is chosen considering that altimetry data are expected to resolve features on the order of 70 km or larger (Pascual et al., 2006). The aim is to compare the water dispersion pathways computed downstream of the seamounts, in the following referred to as the Lagrangian water plume, to the Chl *a* plume. This approach has already been validated for the island mass effect, to reproduce the Kerguelen bloom (d'Ovidio et al., 2015; Sanial et al., 2015) and the Crozet bloom (Sanial et al., 2014) at mesoscale precision.

For each studied period the analysis is conducted in two steps:

(1) Identification of the seamounts that are located within deep iron-enriched hydrographic regions. For each seamount we verify if, in the 4 months before the bloom, it was located within the PF. This current core of the ACC is associated to enhanced dissolved iron concentrations (De Baar et al., 1995; Löscher et al., 1997; Measures and Vink, 2001; Mengelt et al., 2001; Viljoen et al., 2018) presumably upwelled from the deep layer (Sokolov and Rintoul, 2007). The PF is identified for the whole period in the vertical temperature reanalysis as described in section "Satellite Observations and Reanalysis Data." We applied the same approach to the water parcels that have been in contact with Bouvet Island, which is also a potential source of iron to the environment (Perissinotto et al., 1992; Croot et al., 2004). The latter contact is estimated by detecting the water masses which transited over the island in the 4 months before the bloom.

(2) Identification of the Lagrangian water plume from the selected seamounts. Each water parcel of the study region is advected backward-in-time from the blooming period for 4 months. The parcels which are found to come from an area where a seamount is present are then given a timestamp with the time, in days, since they left that topographic features. The 4-month time window chosen for the integration assumes that the extension springtime bloom is pre-conditioned by the winter-time advection of iron rich waters (Mongin et al., 2009).

The enhancement of the Chl *a* concentration within the 100-day Lagrangian water plume is evaluated with the bootstrap method in order to obtain its statistical significance. The bootstrap is conducted on sub-sampled Chl *a* maps, selecting one pixel each five both in longitude and latitude directions. This is done to remove spatial correlations of the order of the typical size of a mesoscale eddy of this region (about 100 km). For the region under the influence of Bouvet, the Lagrangian water plume spreading downstream of the island is removed from the Lagrangian water plume reconstructed with the seamounts. This allows us to distinguish the plume from the seamounts in respect to the one induced by the island.

RESULTS

Chlorophyll *a* Enhancement Observed From BGC-Argo Downstream of Seamounts

Two BGC-Argo floats (WMO 6901585 and 6901688) sampled the Shona Ridge region. They crossed the seamount chain around 49°S between the end of December 2014 and January 2015 with a time lag of a few days (**Figure 2**). A local increase of the

[3]ftp://ftp.ifremer.fr/ifremer/argo/dac/coriolis/

depth-integrated biomass over the mixed layer downstream of seamounts (8–10°E) is recorded by the profiling floats: the Chl *a* content doubled in the float WMO 6901585 (**Figure 2A**) and increased by approximately one third in the float WMO 6801688 (**Figure 2B**). These observations contrast with the homogeneous low Chl *a* concentration (about 0.3 mg/m^3) observed by satellite in January 2015 in the near surface (background images in **Figures 2A,B**). When looking at the Chl *a* content in the water column, neglecting the variability of the mixed layer depth which is deeper than 100 m upstream of the seamounts and shallower than 40 m over them, the intensification of the Chl *a* signature downstream of the seamounts is evident in both floats (**Figures 2C,D**). The vertical profiles depict an increase in Chl *a* and backscattering values in the first 100 m depth downstream of the seamounts (respectively, about 1 mg/m^3 and 3.0×10^{-3} m^{-1}) compared to the water masses upstream (respectively, about 0.6 mg/m^3 and 2.0×10^{-3} m^{-1}). Note that the yellow triangles in **Figures 2C,E** (respectively, **Figures 2D,F**) locate the time of the closest position of the BGC Argos trajectories with the yellow seamount in **Figure 2A** (respectively, **Figure 2B**). They symbolize the crossing of the seamount chain. The phytoplankton enhancement downstream of seamounts is further investigate with satellite observations which have larger spatial and temporal covers.

Altimetry-Based Lagrangian Reconstruction of the Seamount Mass Effect

We assume here the hypothesis of a *seamount mass effect* on phytoplankton biomass, in analogy to the well known island mass effect. This hypothesis implies the formation of phytoplanktonic blooms induced by natural iron fertilization spreading downstream of the seamounts. We discuss the possible mechanisms of iron upwelling in section "Discussion".

Two seamount chains are susceptible to lift iron-laden deep waters to the surface layer and consequently enhance the phytoplankton biomass in the studied region: the Shona Ridge System (SRS), which is composed by the Shona Ridge and the Meteor Rise, and the South-West Indian Ridge (SWIR) (see **Figures 1B,C** for their localization). Yesson et al. (2011) identified 36 seamounts shallower than 1000 meters depth associated with the SRS, with one third of them shallower than 100 m depth, and 26 seamounts shallower than 1000 m associated to the SWIR in the study region (between 0 and 30°E). When looking at Chl *a* images not yearly averaged, but over time periods of 1 month during spring or summer, Chl *a* signatures significantly above the background (around 2-fold) do appear downstream of both the seamount chains (as illustrated in **Figures 3A,B**, **4A**).

In order to further sustain the hypothesis of a seamount mass effect, we study the morphology of the satellite-observed Chl *a* plumes detected in the vicinity of seamounts. In particular, we analyze whether the shape of these plumes is consistent with a dispersal pattern stemming from a seamount. In order to achieve this, we reproduce the Lagrangian plumes associated with the seamounts during the blooms event using altimetry-derived currents. The analysis consists in detecting the water parcels which transited above the seamounts in a certain time period with a Lagrangian approach. As explained in section (Seamount Mass Effect: Detection of the Lagrangian Plume Stemming From the Seamounts), for each bloom period the Lagrangian plumes are derived only from the subset of seamounts which were in contact with potentially deep iron-enriched hydrographic provinces. Here we consider two regions that have been identified in the literature for displaying higher iron concentration, the water masses downstream of Bouvet Island (Perissinotto et al., 1992; Croot et al., 2004) and the water masses located in the ACC along the jet associated with the PF (De Baar et al., 1995; Löscher et al., 1997; Measures and Vink, 2001; Mengelt et al., 2001; Viljoen et al., 2018). This hypothesis will be discussed in section "Drivers of the Seamount Mass Effect." We illustrate the analysis region by region.

Shona Ridge System

The ACC crosses longitudinally the SRS between 0 and 10°E. In both February and December 2004, a distinct Chl *a* plume topping at 0.6 mg/m^3 spreads downstream of the SRS aligned with the PF current core (**Figures 3A,B**). The monthly-mean composite images of Chl *a* are compared to the altimetry-derived Lagrangian reconstruction of the water plumes emanating from the seamounts of the SRS which have been in contact with iron-enriched water masses (**Figures 3C,D**). These plumes represent the water transported by the ACC which has transited over shallow seamounts in the 4 months before the blooms. The color of **Figures 3C,D** represents the number of days since last contact, i.e., a pixel color coded with "30 days" was on the top of a seamount 30 days before the date of the image. The 100-day Lagrangian water plumes (black contours in **Figures 3C,D**) are overlapped to the Chl *a* plumes (**Figures 3E,F**). The Lagrangian analysis reveals that, in both studied periods, the Chl *a* plume extending downstream of the seamounts matches up to fine details the reconstructed water masses that transited over the seamounts few months previous the bloom.

The good prediction of the extension and shape of Chl *a* gives us confidence about the role of the selected seamounts. Remarkable examples of the match between ocean-color and altimetry-derived features are the correspondence of meanders and mesoscale features between the two signatures, such as the distinct Chl *a* patch trapped by a mesoscale eddy around 17°E 48.5°S in February 2004 (**Figure 3A**). Note that even if the Chl *a* plume is aligned with the PF current core, particularly in December 2004 (**Figure 3D**), the complexity of the Chl *a* plume is captured just with the advection of water masses that surrounded the seamounts. This is the case for instance for the latitudinal extension of the plume close to the SRS, between 3 and 9°E, in December 2004 (**Figures 3D,F**) or the extension of the plume between 15 and 30°E in February 2004 (**Figures 3A,C**). We remark also that the selected seamounts are different in February and December 2004 and that similarly, the same seamounts may be located in different productivity regimes at the two periods. For instance, in December 2004 the shallow seamounts at 48 °S were not in contact with the current core of the ACC (they are not identified in **Figure 3D**) and seems to not display enhanced phytoplankton biomass (**Figure 3F**). Conversely, the

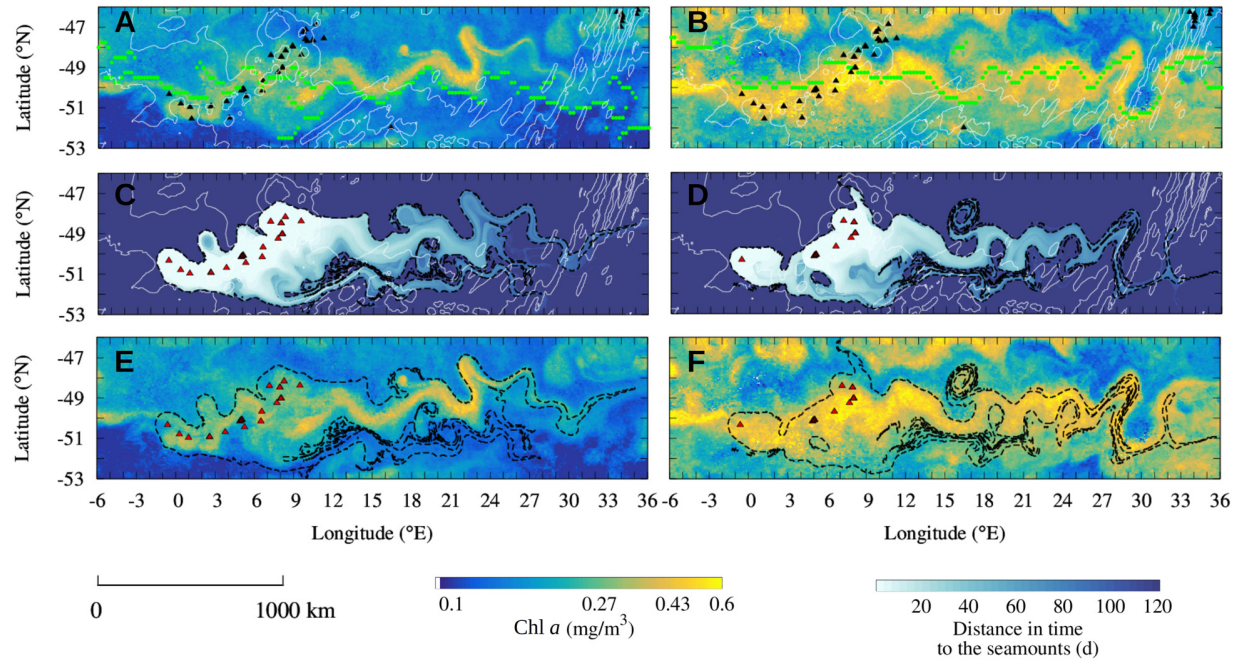

FIGURE 3 | Observation of the seamount mass effect on the Shona Ridge System in February 2004 **(A,C,E)** and in December 2004 **(B,D,F)**. **(A,B)** Observation of Chl *a* plumes downstream of the shallow seamounts of the SRS (black triangles) in February 2004 **(A)** and December 2004 **(B)**. The Chl *a* plumes spread over thousands of kilometers aligned with the PF current core (green dots). **(C,D)** Reconstruction of the Lagrangian plumes from the seamounts of the SRS selected for the study periods (red triangles). Black contours indicate the water masses that have been in contact in the 100 days before the blooms event with the selected seamounts. **(E,F)** Comparison of the Chl *a* plume observed in the monthly-mean composite images with the Lagrangian plumes estimated from altimetry [black contours extracted from panels **(C,D)**]. Shallow seamounts identified in each time period for the Lagrangian analysis are shown in red **(C–F)**. Isobaths of bottom topography of 3000 m and 4100 m depths are shown in white **(A–D)**. Note the logarithmic scale for the Chl *a* images.

same seamounts are associated by the Lagrangian analysis to the Chl *a* plume in February 2004 (**Figures 3C,E**). This different behavior suggests a temporal variability of the biological response associated to submerged topography features.

During the study periods, February 2004 and December 2004, the mean Chl *a* concentration in the water masses that transited in the last 100 days over seamounts in contact with the current core is, respectively, 49 and 40% higher than elsewhere in the region depicted in **Figure 3**. In order to test whether the observed differences in the Chl *a* content inside and outside of the Lagrangian plumes are significant, a bootstrap sampling is carried out for each studied period over the whole image size. The null hypothesis states that the observed difference in Chl *a* content inside and outside the Lagrangian plume is not significant. Standard deviation of the bootstrap distributions inside and outside the plumes are, respectively, 1.2×10^{-3} and 5.0×10^{-4} mg/m^3 for the year 2003/2004 and 2.1×10^{-3} and 7.1×10^{-4} mg/m^3 for the year 2004/2005. In all the study cases the null hypothesis is rejected with >99% confidence. These analyses provide observational evidence of a seamount mass effect associated to the SRS.

South-West Indian Ridge

Bouvet Island (3.36°E and 54.42°S, indicated by a square in **Figure 4**) lies on a volcanic system about 50 km west to the SWIR (Georgen et al., 2001) and represents a known iron input in the south-west of the study region (Croot et al., 2004). The island has been associated with enhanced Chl *a* concentrations and primary production compared to the surrounding areas. However, its effect seems to be locally restricted (e.g., Perissinotto et al., 1992; Croot et al., 2004, refers also to **Figure 1A**). Differently to what was found in previous studies, in October 2002 a Chl *a* plume spreads over almost 2000 km downstream of Bouvet Island (**Figure 4A**). However, the altimetry-derived Lagrangian plume stemming from Bouvet Island (green area in **Figure 4A**) overlaps only partially the Chl *a* plume observed from the satellite in this period. Indeed, the Chl *a* plume extended over a much larger area nearby 26 seamounts shallower than 1000 m (**Figure 4A**).

Similarly, to the analysis of the SRS, here we consider whether the seamounts of the SWIR may explain the Chl *a* enhancement which is not explained by the island alone. Specifically, we reproduce the altimetry-derived Lagrangian plume from the seamounts that have been in contact with the water masses enriched in iron at Bouvet Island in the few months before the bloom. Indeed, the few seamounts in the north edge of the SWIR that were not in contact with the iron-enriched water masses stemming from the island did not display enhanced Chl *a* concentrations. The Lagrangian water plume emanating from the selected seamounts allows us to reproduce the Chl *a* plume integrally (black contour in **Figure 4C**), differently to the island Lagrangian plume (green contour). As for the SRS, the Chl *a* plume and the Lagrangian plume stemming from

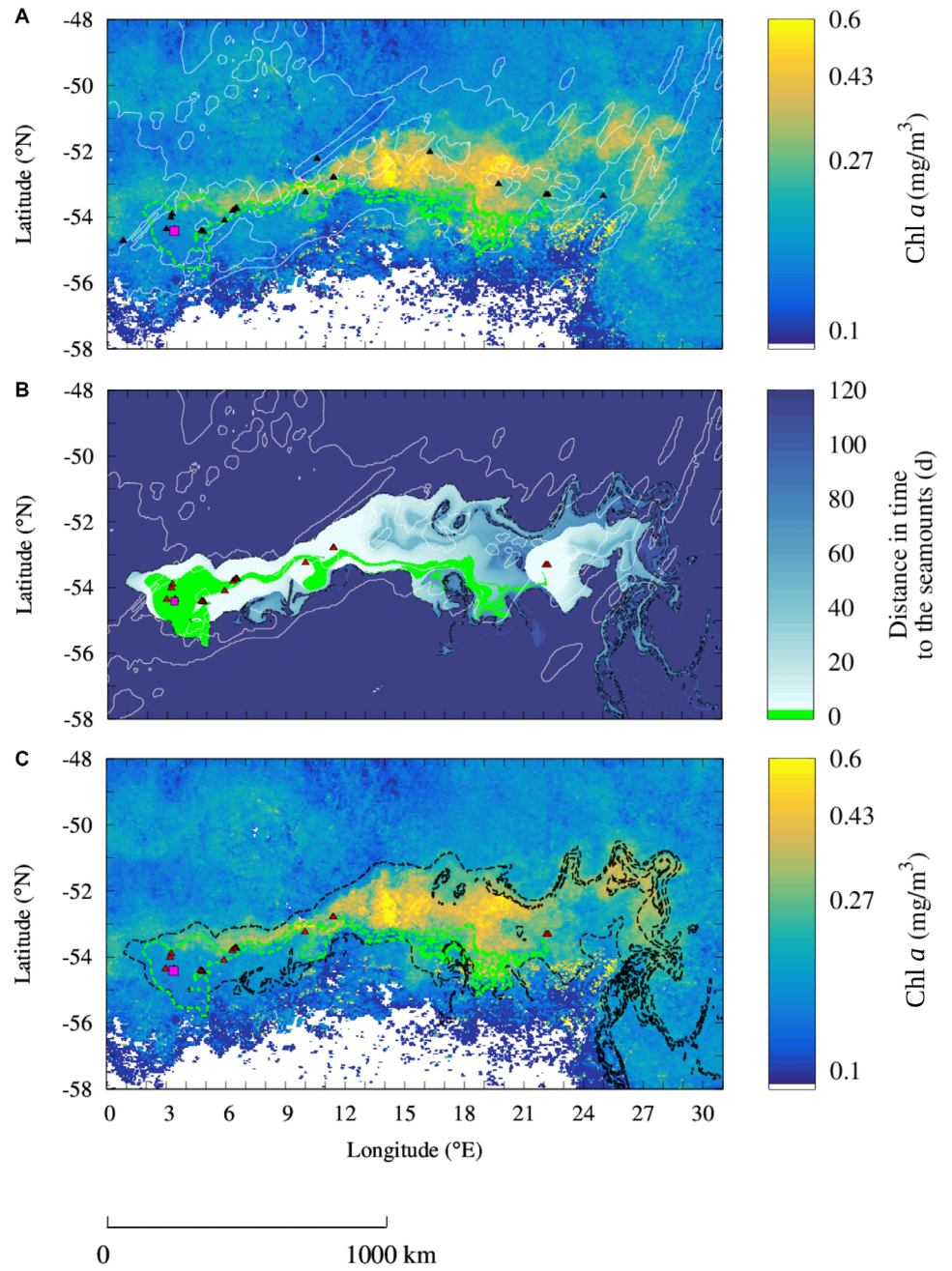

FIGURE 4 | Observation of seamount mass effect from the SWIR complex. **(A)** Observation of a Chl *a* plume downstream of the shallow seamounts of the SWIR (black triangles) in October 2002. **(B)** Reconstruction of the Lagrangian plume from the seamount of the SWIR selected for the study period (red triangles). Black contours indicate the water masses that have been in contact in the 100 days before the bloom event with the selected seamounts. **(C)** Comparison of the Chl *a* plume observed in the monthly-mean composite image with the Lagrangian plume estimated from altimetry [black contour extracted from panel **(B)**]. The Lagrangian plume stemming from Bouvet Island (magenta square) and computed over the 4 months before the bloom is overlapped in all the panels [green contours in panels **(A,C)** and green area in panel **(B)]**. Shallow seamounts identified at the study period for the Lagrangian analysis are shown in red **(B,C)**. Isobaths of bottom topography of 3000 and 4100 m depths are shown in white **(B,C)**. Note the logarithmic scale for the Chl *a* images. Whites areas in Chl *a* images **(A,C)** correspond to unidentified regions.

the seamounts are qualitatively very similar. In addition, the mean Chl *a* concentration inside the Lagrangian plume is two thirds higher than the mean concentration outside (respectively, 0.26 ± 0.098 mg/m^3 inside and 0.16 ± 0.071 mg/m^3 outside). Therefore, we infer that the region with highest Chl *a* values corresponds to water masses that transited, in the 100 days before the bloom, over the seamounts (black contours in **Figures 4B,C**). A bootstrap sampling carried out on the part of the SWIR

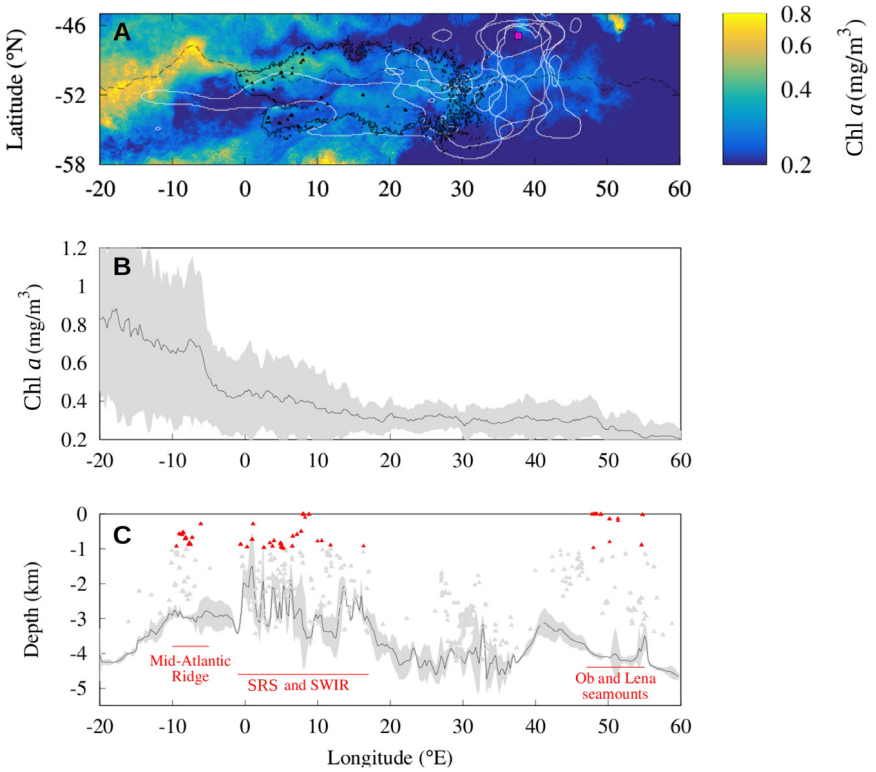

FIGURE 5 | Distribution of predators, Chl *a* concentration and seamount mass effect during December between 2000 and 2015 around the PF current core. **(A)** The distribution of top predators (white lines) from the Prince Edward Islands (magenta square) is compared to the distribution of the Lagrangian plumes (black solid line) constructed from the seamounts (black triangles) for every December between 2000 and 2015. Data are displayed with the Chl *a* climatology and the PF position (black dashed line) during December between 2000 and 2015. **(B,C)** Mean Chl *a* concentration **(B)** and mean shallowest depth **(C)** in a latitudinal band of 1° north and 1° south of the current core for every December from 2000 until 2015. Shaded areas show standard deviation associated with these lines. Gray and red triangles indicate the depth of the seamounts (respectively, deeper and shallower of 1000 m) identified by Yesson et al. (2011) in the same region **(C)**.

plume which is not superposed with the island's plume rejects the null hypothesis with >99% confidence. Standard deviation of the bootstrap distributions inside and outside the plumes are, respectively, 2.4×10^{-3} and 4.8×10^{-4} mg/m^3.

Comparison of Predators' Distribution, Phytoplankton Biomass and Seamounts Locations in the Southern Agulhas Basin

A 15-year climatology of the December Chl *a* concentration in the southern Agulhas Basin is shown in **Figure 5**, which corresponds to the time of Chl *a* peak in the region (Sokolov and Rintoul, 2007). A 15-year climatology of the Lagrangian water plume issued from the seamounts from the SHS and the SWIR (black triangles), computed as in section "Altimetry-Based Lagrangian Reconstruction of the Seamount Mass Effect," is overlapped to the Chl *a* map (black contour). The region covered by the Lagrangian water plume is upstream of the pinnipeds and penguins ranges (white contours). This indicates that the water masses targeted by the predators' colonies have been under the influence of the seamounts in the previous months (the Lagrangian water plume is represented with a 100-day threshold, as in the analyses of section "Altimetry-Based Lagrangian Reconstruction of the Seamount Mass Effect"). The similarity between the climatological Chl *a* and Lagrangian plumes is less evident compared to the monthly analyses previously considered. This is primarily due to the smoothed signal in the Chl *a* climatology. However, where the mean pigment distribution is more contrasted, as in the northern edge of the Lagrangian plume, the two signals appear to have qualitatively similar patterns.

In order to investigate the signal of the seamounts in the climatological phytoplankton biomass we compute the mean Chl *a* concentration in a 2° latitude narrow band centered on the current core of the ACC which we identify by the PF, between 2000 and 2015 (**Figure 5B**). **Figure 5B** shows that the highest values (mean Chl *a* about 0.7 mg/m^3) are observed upstream of the study region, between 20 and 5°W and decrease eastward. Intense Chl *a* concentrations extend downstream of South Georgia (36°W, 54°S) over wide distances due to the intense transport (e.g., Korb et al., 2004; Sokolov and Rintoul, 2007; De Jong et al., 2012; Borrione et al., 2014; Graham et al., 2015) and to the regular iron inputs linked to flow-topography interactions (Sokolov and Rintoul, 2007). The averaged Chl *a* level do not significantly increase

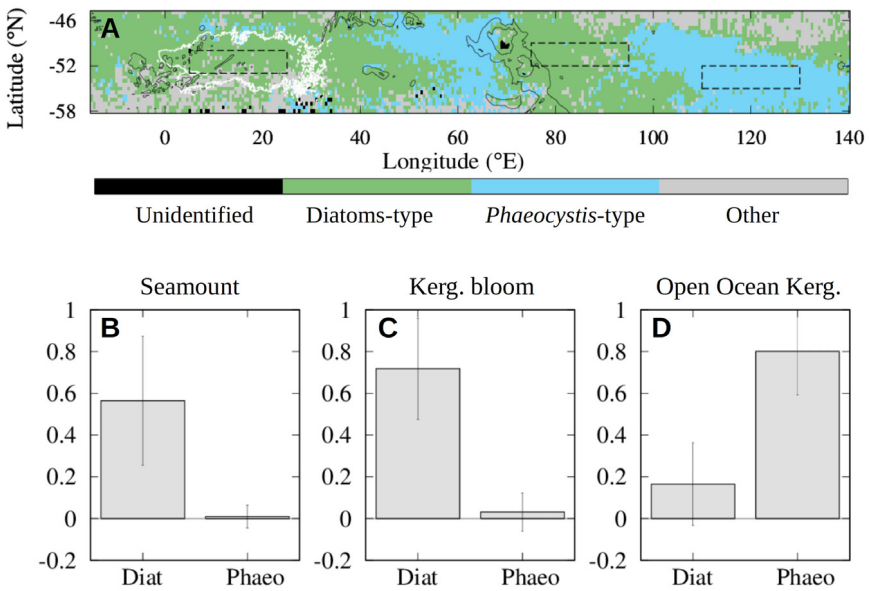

FIGURE 6 | Climatology maps (2000–2011) of dominant phytoplankton groups in December and January estimated using PHYSAT. **(A)** Most abundant phytoplankton type estimated from PHYSAT over the 2000–2011 time period. The distribution of the Lagrangian plumes from the seamounts (white solid line) is shown as in **Figure 5**. **(B–D)** Mean percentage of time that the seamount region **(B)**, Kerguelen (abbreviated Kerg. in the image) bloom region bloom region **(C)** and open ocean region downstream of it **(D)** are dominated by diatoms or *phaeocystis* types (respectively abbreviated Diat and Phaeo in the image) during December and January between 2000 and 2011. The three regions are located in the dashed black contours in the top panel. From left to the right these are: seamount region **(B)**, Kerguelen bloom region **(C)** and open ocean region downstream of it **(D)**. Error bars indicate the standard deviation over each region.

in correspondence of the interaction between the ACC and the shallow seamounts of the SRS (**Figure 5B**). However, we note the high standard deviation of the signal between 0 and 15°E compared to the downstream signal (respectively, $\sigma \approx 0.2$ mg/m^3 and $\sigma \approx$ and 0.1 mg/m^3) indicating an important interannual variability. Compared to the SHS, the Ob and Lena seamounts close to 50°E display a lower mean Chl *a* concentration ($\Delta\mu \approx 0.1$ mg/m^3) and a lower standard deviation ($\Delta\sigma \approx 0.1$ mg/m^3), indicating a lower phytoplankton biomass and a low temporal variability.

Phytoplankton Composition: Comparison of the Seamount Region, Kerguelen Bloom and Open Ocean Region

The possibility for primary production of sustaining the large trophic chain up to megafauna, is known to largely depend not only on its abundance but also on the phytoplankton composition (e.g., Moline et al., 2004). We thus analyze our study region with maps produced with the PHYSAT algorithm (Alvain et al., 2005, 2008). The latter cluster together the ocean color spectral signal into classes associated to typical phytoplanktonic types which are statistically dominant for those bio-optical anomalies.

PHYSAT patterns downstream of the SRS and SWIR seamounts (0–30°E, 50–53°S in **Figure 6**) mainly contain the same classes found in island-induced blooms (70–100°E, 50–53°S in **Figure 6**) and differ from the type classes found in the Australian-Antarctic Basin (i.e., downstream of the Kerguelen bloom about 100–130°E) (**Figure 6A**). According to the PHYSAT observations, during December and January between 2000 and 2011, the seamount region is dominated more than 55% of the time by diatoms (σ = 30%) and less than 1% of the time by *Phaeocystis* (σ = 5%). By comparison, the Kerguelen bloom (and respectively, the offshore region downstream of this bloom) is dominated 70% (respectively 16%) of the time by diatoms and 3% (respectively 80%) of the time by the small *Phaeocystis* (**Figures 6B–D**).

DISCUSSION

Enhanced primary production has been episodically reported in the past over some deep (>2000 m depth) submerged topographic features of the Southern Ocean, such as the Northwest Georgia Rise (Meredith et al., 2003) and the Maud Rise in the Weddell Gyre (Van Bennekom et al., 1988). At a circumpolar scale, Sokolov and Rintoul (2007) observed that blooms are initiated where the ACC crosses most of the deep bathymetric features and they persist for long distances. However, the biogeochemical focus of subsequent works has led to the conclusion that Chl *a* enhancements downstream of submerged features are negligible because on average they are much less intense than the ones in the wake of the subantarctic islands (e.g., Graham et al., 2015; Ardyna et al., 2017). These ideas have reinforced the view of the region in between the subantarctic islands as a HNLC phytoplankton-desert area. Here we revisit this apparently low chlorophyll region investigating its ecological

implications, in particular for land breeding marine predators for which the possibility of accessing a large islands' bloom far away from their colony may be associated to excessive energetic locomotion costs. This is the case for instance with several species of penguins and pinnipeds breeding at the Prince Edward Islands. A very limited island mass effect is observed around and downstream Prince Edward Islands because of its very narrow plateau (Perissinotto et al., 2000). Competition for food is thus expected to be high in this small productive area. Animals colonizing this island appear indeed to prefer the lower productive but extended inter-island waters than other targets, such as the small productive area around Prince Edward Islands (where competition may be high) or the larger blooms further away, costly to reach.

Our study targets two topographic systems of the southern Agulhas Basin: the Shona Ridge System and part of the South-West Indian Ridge, between 0° and 30°E. By focusing on shorter time scales and on higher bathymetric resolution than former studies, our results identify new phytoplankton blooms associated to the water masses that transited over these shallow topographic highs and provide a detailed description of them. Firstly, an increase in phytoplankton biomass is observed by BGC-Argo floats in the wake of the seamounts during the summer period, between the middle of January and the middle of February. This late Chl *a* enhancement suggests a possible positive biological effect linked to the presence of the topographic highs which is not simply linked to the seasonal bloom phenology (Sallée et al., 2015; Ardyna et al., 2017). Due to the important limitation of the primary production by iron in this region (e.g., Martin, 1990; Sullivan et al., 1993; De Baar et al., 1995), a relative enhancement of the Chl *a* values should be related to iron inputs in the surface waters. Secondly, the seamount effect is further investigated with satellite observations which have larger spatial and temporal covers. By identifying isolated Chl *a* plumes on monthly-mean maps and comparing them to the Lagrangian water plumes stemming from the topographic features we demonstrate the widespread influence of seamounts on the surface seasonal phytoplankton distribution. Therefore, the advection of water parcels from shallow topography can be considered as a powerful tool for identifying the effect of isolated submerged topography, similarly, to the analyses computed on islands (e.g., Mongin et al., 2009; Sanial et al., 2014, 2015; d'Ovidio et al., 2015; Ardyna et al., 2017). By comparison, Graham et al. (2015) investigated the spatial variability of the annual mean Chl *a* at the regional scale in the study area and concluded that, at this time scale, the phytoplankton biomass is not visibly enhanced over or downstream of the seamounts. However, we note that most of seamounts identified in our high resolution bathymetric data were not identified in this previous analysis (see for instance their **Figure 5A**), which could also influence their conclusions. Similarly, the Lagrangian pathways computed at the circumpolar scale using a bathymetric threshold also do not identify Chl *a* plumes in the southern Agulhas Basin, because no shallow topography was detected there with these data (Ardyna et al., 2017). These different outcomes highlight the need to consider both high resolution bathymetric data and short time scales for investigating a potential biological effect of seamounts.

In the following we firstly discuss the possible mechanisms at the origin of the seamount mass effect observed in the present study, the limits of the methods employed, and their applicability to other study cases. Secondly, we explore the ecological role of seamounts in the southern Agulhas Basin, from primary production to predators' distribution, as well as some implications of these new insights for conservation activities.

Drivers of the Seamount Mass Effect

What is the origin of the blooms observed in the wake of seamounts in the southern Agulhas Basin? In most of the previous studies, the Chl *a* anomalies observed over the seamounts and in the surrounding waters were linked to the shallow seamount depths. However, the spatial and temporal variability of biological effects were rarely understood due to the complex nature of the physical processes involved there (e.g., Venrick, 1991; Pitcher et al., 2007; Pauly et al., 2017). The process presented here is framed by the limiting effect of iron on primary production (Martin, 1990) and the preponderant structuring effect of the horizontal transport on biochemical properties and ecosystems in the ACC region. The two necessary conditions identified for the fertilization of water masses in the open ocean southern Agulhas Basin are thus: (i) the presence of hydrographic regions associated, according to the literature, to potential enhanced dissolved iron content at intermediate depth; and (ii) upwelling dynamics due to the interaction of seamounts shallower than 1000 m depth with an energetic branch of the ACC.

In terms of iron content, two possibly enriched regions are identified in the southern Agulhas Basin. The first one is composed by the water masses that have transited over Bouvet Island, which is a known iron source (Perissinotto et al., 1992; Croot et al., 2004). The second one, is composed by the water masses located in the ACC, along the jet associated with the PF. Numerous *in situ* observations have recorded enhanced iron concentrations in the surface waters close to this ACC front, both in the Atlantic sector (De Baar et al., 1995; Löscher et al., 1997; Viljoen et al., 2018) and elsewhere (Measures and Vink, 2001; Mengelt et al., 2001). In the deeper ocean, iron measurements are less frequent (e.g., Tagliabue et al., 2012). Nevertheless, enhanced iron concentrations appear to occur in the Circumpolar Deep Water close to the PF region in correspondence of the Mid-Atlantic Ridge (Löscher et al., 1997). Furthermore, the analysis of the global GEOTRACES database indicates a sharp ferricline in the Atlantic ACC region reflecting the signature of subsurface lateral transfer of dissolved iron from the subantarctic islands (Tagliabue et al., 2014). Indeed numerous studies have concluded that the intense velocities of the PF current core result in a strong transport of nutrients downstream of South Georgia (Korb et al., 2004; Venables and Meredith, 2009; Venables et al., 2012; Borrione et al., 2014) and in a regular iron supply to the surface water due to the ACC-bathymetry interactions (Sokolov and Rintoul, 2007).

In terms of upward dynamics, the interaction of the ACC with sharp topographic features is well known to generate upwelling hotspots carrying deep waters to the surface (Viglione and Thompson, 2016; Tamsitt et al., 2017) and enhancing surface Chl *a* concentrations (Sokolov and Rintoul, 2007). Three different mechanisms have been identified in the past for explaining upwelling in the presence of seamounts. The first mechanism is eddy fluxes which are intensified when the ACC encounters a rough topography due to an increase in baroclinicity. The eddy activity enhanced in this way at seamounts can vigorously drive upward northern-sourced deep water along steeply sloping isopycnals in the PF region (Tamsitt et al., 2017; Rintoul, 2018). The enhanced eddy activity at seamounts is also associated to intense flow shear, which in turn preconditions an ageostrophic submesoscale circulation characterized by deep reaching vertical motion (Lévy et al., 2018; Siegelman et al., 2019). A second possible mechanism for upwelling is the bottom pressure torque created when the ACC impinges over bathymetric obstacles. This process induces upwelling upstream of a seamount and downwelling downstream of it (Hughes, 2005; Sokolov and Rintoul, 2007; Thompson and Naveira Garabato, 2014; Rintoul, 2018). This situation has been described in the Atlantic sector of the ACC region, at the South and North Scotia Ridges, the South Orkney Islands and the South-West Indian Ridge (Sokolov and Rintoul, 2007). Finally, a third mechanism which is able to connect deep water to the surface layer is the generation of internal lee waves at seamounts. These waves propagate upward and break, enhancing diapycnal mixing (Watson et al., 2013) and fluorescence signature over the seamounts (Brink, 1995; Kunze and Sanford, 1997; Eriksen, 1998). This has been observed for instance at the seamounts of the SWIR, at the northeast of the southern Agulhas Basin (Read and Pollard, 2017).

The interaction of a strong current with a topographic sharp relief is also known to produce Taylor columns, that is, semi-permanent anticyclones on the top of the topographic obstacle which can trap water for periods of months or longer (Taylor, 1923; Meredith et al., 2015). These features can have a special ecological interest because they may retain over the seamounts aging trophic webs, thus providing predictable preying hotspots (e.g., Pitcher et al., 2007; Morato et al., 2010; Cascão et al., 2017). Such circulations, more intense at high latitudes due to the enhanced Coriolis force (Owens and Hogg, 1980; Chapman and Haidvogel, 1992), have been observed in the Southern Ocean at the Maud Rise (Van Bennekom et al., 1988) and conditions conducive to their formation have been found at the Georgia Rise, South Scotia Ridge and at the Prince Edward plateau (Perissinotto and Rae, 1990; Meredith et al., 2003, 2015).

All together, the mechanisms here proposed for the Atlantic ACC region are schematized in **Figure 7**. The iron content increases in the surface layer at the South Georgia Island and sinks to the subsurface along the flow direction, with regular upward movements due to the interactions between the ACC and the topography. The Chl *a* blooms identified in the study cases (**Figures 3**, **4**) and the important temporal variability of the climatological surface Chl *a* content close to the seamounts (**Figure 5**) are the surface expression of this topography-ACC interactions, usually hidden in the mean climatological Chl *a* signal when compared with subantarctic island-blooms (e.g., Graham et al., 2015; Ardyna et al., 2017). By highlighting the role of iron content of the upstream water masses, the mechanism here suggested could explain why seamounts seem to display re-enhanced phytoplankton biomass when they are close to rich systems, such as coastal margins (Van Bennekom et al., 1988; Perissinotto and Rae, 1990; Meredith et al., 2003; Graham et al., 2015; Oliveira et al., 2016; Lemos et al., 2018), or whether they are located in productive frontal zones (Djurhuus et al., 2017). On the other hand (and following Sokolov and Rintoul, 2007) our results identify processes extending at much larger spatial scales compared with the local phytoplankton enhancements described in previous studies which have focused on seamounts in other regions (e.g., Oliveira et al., 2016; Lemos et al., 2018). This larger extent is due to intense advection by the ACC, in analogy to the spread of non-consumed iron from the subantarctic islands in wintertime which preconditions the size of the islands' blooming area (Mongin et al., 2009; d'Ovidio et al., 2015; Graham et al., 2015).

Our approach does not explain all the patterns of primary production in the ACC region. The ACC core also interacts with a group of shallow seamounts (<1000 m depth) between 10°W and 6°E (**Figure 5C**) which corresponds to climatological Chl *a* concentrations topping at 0.7 mg/m^3 (**Figure 5B**). Differently from the analysis of the SHS and SWIR (black contour in **Figure 5A**) the Lagrangian plume spreading from the seamounts close to 10°W only partially explain the Chl *a* plume in this region (result not shown). Most of Chl *a* seems to be aggregated close to the current core, which, constrained by the Mid-Atlantic Ridge, shifts northward close to 10°W (Boehme et al., 2008). The specific regional circulation catalyzed by the topography may explain the Chl *a* distribution. On the other hand, our analysis leaves open the question concerning why seamounts of other regions do not seem to be associated to intense Chl *a* plumes, such as the shallow Ob and Lena seamounts (∼50°E in **Figure 5**). This could be explained by the mechanism schematized in **Figure 7**. The deep iron, primarily upwelled to the intermediate layer at the South Georgia Island (Korb et al., 2004; Borrione et al., 2014), is assumed to slowly decay along the flow direction from west to east. Following this hypothesis, it seems plausible that the seamount effect may be less intense for topography features located further downstream of the South Georgia Island (∼35°W), as the Ob and Lena seamounts (∼50°E), compared to the closer ones (as the SRS and SWIR). We note that the mechanism here proposed consider primarily external iron inputs, i.e., the upstream iron transport. However, some local processes have also been identified as sources of surface nutrient supply at seamounts. For instance, the interaction of the porewater with sandy sediment releases reduced metal species to the water column (Huettel et al., 1998) and leads to an enhanced erosion of the sediments due to the physical and chemical actions of potential benthic communities (Rhoads and Boyer, 1982). For all these reasons, more detailed studies should be done in order to unambiguously identify the mechanisms at the origin of the Chl *a* enhancements observed in this study.

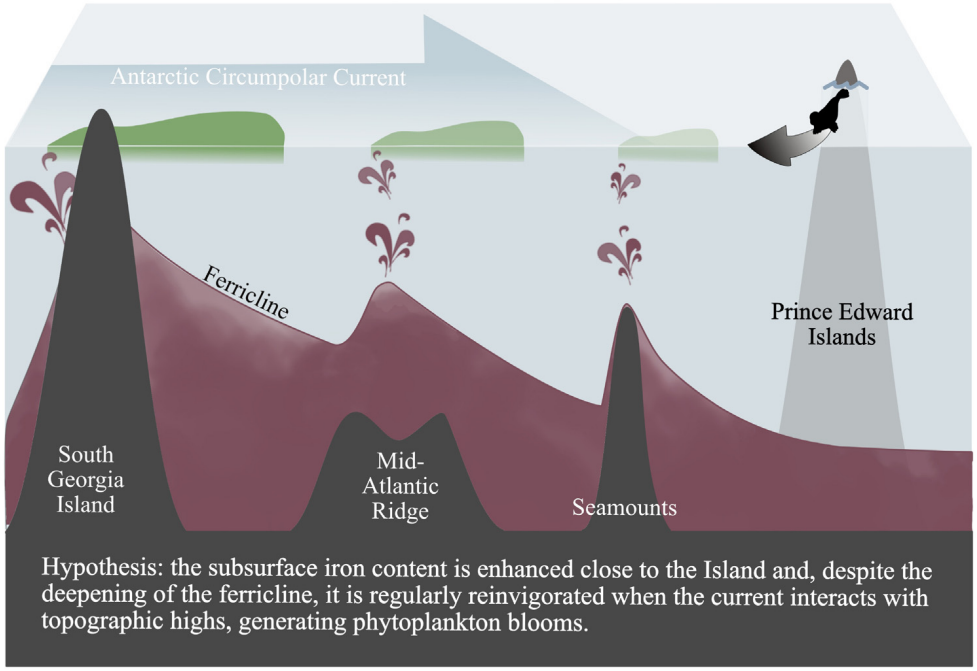

FIGURE 7 | Schematic summarizing of phytoplankton productivity in the Atlantic ACC region. The interaction of the ACC with topographic highs generates upward movements and facilitates the injection of iron in the euphotic layer (symbolized by the burgundy-colored jets). Lightening of the phytoplankton blooms (green) is an indication of the decreasing of the Chl *a* concentration. Subantarctic pinnipeds and penguins from Prince Edward Islands (symbolized by the gray arrow) are foraging on this complex biological system.

Ecological Significance of the Seamount Mass Effect in the Southern Agulhas Basin and Implications for Conservation

The surface Chl *a* concentrations observed in satellite images downstream of seamounts are minor compared to the ones occurring downstream of islands. For instance, in the Crozet bloom Chl *a* concentrations exceed 2 mg/m^3 (Bakker et al., 2007), four times the ones observed in our analysis. However, we stress that, to assess the total phytoplankton biomass of a given region, one must integrate Chl *a* concentration over the mixed layer (ML) (e.g., Ardyna et al., 2019). The ML in the seamount region is at least between 10 and 30% deeper of the ML in the Kerguelen bloom region during January and February and between 30 and 50% deeper during December (**Supplementary Figure S1**). When compared to the Crozet and the South Georgia blooming regions the seamount ML increases up to 60–100% (**Supplementary Figure S1**). Therefore, the phytoplankton biomass integrated over the ML may present less intense contrasts between the seamount open ocean and the island bloom regions than the surface signals. Furthermore, we note that a deeper ML may also induce a lower Chl *a* signal in the satellite images, intensifying the observed surface differences between the two regions.

The analysis of the phytoplankton composition of the seamount plumes provides further insights about the relevance of this biological production from an ecological perspective. The phytoplankton community identified in the Atlantic ACC shows a bio-optical signature similar to the ones found in diatom-dominated island blooms, such as the region downstream of Kerguelen, and different from the nearby oligotrophic waters, characterized by *Phaeocystis*-types (**Figure 6**). This nanophytoplankton is known to be rapidly consumed by the microbial food web (Detmer and Bathmann, 1997; Pakhomov et al., 2019) and therefore its occurrence is not associated with profitable foraging grounds for top predators (Cushing, 1989; Moline et al., 2004; Pakhomov et al., 2019). Conversely, diatom-dominated blooms are more likely to support large trophic webs which lead to fish and crustaceans and higher predators (Cushing, 1989; Moline et al., 2004; Pakhomov et al., 2019). Presence of a large and rich (in terms of diversity) megafauna in our study region is confirmed by biologging data (Arthur et al., 2017; Pistorius et al., 2017; Reisinger et al., 2018). The similarity between the seamounts region to the island blooms is supported also by *in situ* measurements showing diatom enhanced concentrations at the Atlantic PF region in the vicinity of the Islas Orcadas Rises and Mid-Atlantic Ridge (Laubscher et al., 1993; Froneman et al., 1995; Bathmann et al., 1997; Detmer and Bathmann, 1997; Smetacek et al., 1997). On the other hand, the contrasted phytoplankton community between the seamount region and the classic HNLC areas (as the one between 110 and 130°E in **Figure 6**) would emphasize the interest of regions downstream of topographic highs. However, the lack of *in situ* phytoplankton observations in this low chlorophyll region prevent us to conclude on the potential zonal differences in the circumpolar phytoplankton communities of

the PF region. Observation of mid trophic levels would also be valuable for linking the primary producers to the higher predators and verifying these hypotheses. Flynn and Williams (2012) showed that the topography-flow interaction over the Macquarie Ridge (160°E) seems to induce an increased biomass of the lanternfishes, a key prey for pinnipeds and seals (e.g., De Broyer et al., 2014). Further analyses of intermediate trophic levels should be done for explaining the biological productivity inferred from land-based top predators and assessing how each colony specifically relies on seamounts production. For instance, the distribution of surface and low trophic level foragers, such as Southern Rockhopper Penguin and Macaroni Penguin (Brown and Klages, 1987; Adams and Brown, 1989; Wilson et al., 1997; Crawford et al., 2003; Whitehead et al., 2016), might be more closely related to the surface productivity than the distribution of mesopelagic foragers.

Our analyses advocate for a connected vision of the biological productivity of the ACC region. Following the ACC, the high Chl *a* concentration decreases from west to east downstream of the South Georgia Island around the ACC core, but it is re-enhanced after the ACC interacts with submerged topographic features, in particular the SRS (as schematized in **Figure 7**). A more comprehensive view may have consequences especially in conservation policies. Currently, conservation planning in the ACC region is dominated by national programs and consequently displays important discontinuities constrained by the jurisdictional framework (e.g., exclusive economic zones). National Marine Protected Areas have been established around Heard and Mcdonald Islands, Kerguelen Islands, Crozet Islands, and Prince Edward Islands in order to conserve the rich and diverse ecosystems hosted in these oceanic waters. By comparison, the high seas of the southern Agulhas Basin, which are already managed for the fishing activities (**Supplementary Figure S2**), are currently not considered in conservation plans. However, our observations, along with the numerous foraging hotspots of numerous predators occurring in this latitudinal band, both from Bouvet Island and other subantarctic colonies (Biuw et al., 2010; Hindell et al., 2016; Arthur et al., 2017), highlight the need to consider the subantarctic range as a continuum. Current attempts made under the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) aim at characterizing the ecosystems structure and function in the subantarctic region and eventually identifying priority areas for conservation. Therefore, efforts shall address the continuity of this oceanic region and the biophysical processes across the high seas and the multiple economic exclusive zones.

SUMMARY AND CONCLUSION

In the Antarctic Circumpolar Current (ACC) region, island blooms stretch for hundreds of kilometers along the current. Island related production plays a primary role in the biogeochemical cycles of the Southern Ocean and sustains large trophic chains up to megafauna species. Conversely, submerged topography is also known to stimulate primary production in its interaction with the ACC, but this productivity is comparatively much less intense (e.g., Sokolov and Rintoul, 2007; Graham et al., 2015; Ardyna et al., 2017). As a consequence, its contribution has been considered negligible at the basin scale, and the ACC waters are often described as a high nutrient low phytoplankton desert, punctuated by massive blooms in the wake of the islands. Conservation efforts are in line with this description, with subantarctic marine protected areas only occurring in the economic exclusive zones around the islands.

Here we revisited the role of seamounts in this framework, focusing on a region of the Indo-Atlantic ACC zone. This area is massively targeted by marine predators, even if no islands fertilize it. By combining high resolution bathymetric data, multi-satellite data, and BGC-Argo observations, we found that the oligotrophic nature of the study region apparent in Chl *a* climatological maps hides a much more complex situation. Important production (in excess of 0.6 mg/m^3, **Figures 2**, **3**) occurs there and spreads over huge distances, comparable to the extension of the islands' blooms.

By applying a Lagrangian analysis to these lesser blooms we connected unambiguously these blooms to specific seamount systems. Our Lagrangian scheme was then depicted to track at mesoscale precision the thousands of kilometers long water plume influenced by each individual seamount system (**Figures 3**, **4**).

In order to estimate the type of phytoplankton present in these blooms, we used the PHYSAT product, which provides maps of putative planktonic functional types. The PHYSAT algorithm revealed that the signatures of seamounts' bloom are similar to the ones found in the islands' wake, and not nearby less productive waters (**Figure 6**). This is consistent with the presence in both systems of foraging grounds for megafauna species.

The ecological role of seamounts in sustaining large trophic chains was finally confirmed by comparing climatologies of Chl *a* to the predators' distributions (**Figure 5**). Our results allow us to conclude that, although temporally intermittent, less predictable, and less effective than the ones associated with the island mass effect, the blooms downstream of seamounts cannot be neglected. Our findings advocate for a connected vision of the ecosystems along the ACC and may support future conservation actions by providing the tools to track the areas under the seamount effect.

DATA AVAILABILITY STATEMENT

All the data used in this research are freely available and may be downloaded through the links detailed in the section "Materials and Methods."

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this study analyzed observations of vertebrate animals previously published by another study reviewed and approved by an animal ethics committee (doi: 10.1111/ddi.12702).

AUTHOR CONTRIBUTIONS

SS conducted the data analysis. SS and Fd'O wrote the manuscript. All authors contributed to the ideas and to the revision of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00416/full#supplementary-material

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Changing Biogeochemistry of the Southern Ocean and Its Ecosystem Implications

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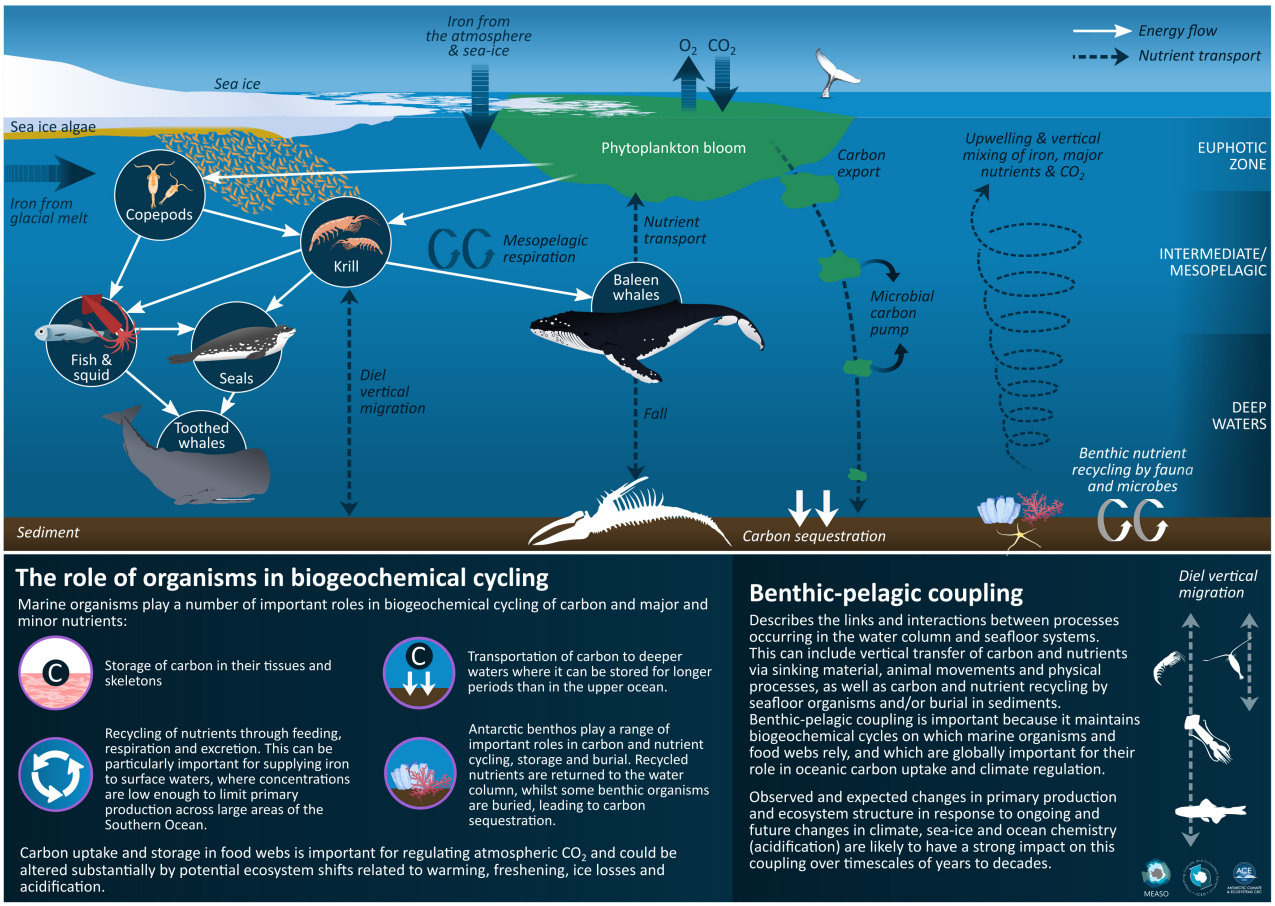
The Southern Ocean plays a critical role in regulating global climate as a major sink for atmospheric carbon dioxide (CO_2), and in global ocean biogeochemistry by supplying nutrients to the global thermocline, thereby influencing global primary production and carbon export. Biogeochemical processes within the Southern Ocean regulate regional primary production and biological carbon uptake, primarily through iron supply, and support ecosystem functioning over a range of spatial and temporal scales. Here, we assimilate existing knowledge and present new data to examine the biogeochemical cycles of iron, carbon and major nutrients, their key drivers and their responses to, and roles in, contemporary climate and environmental change. Projected increases in iron supply, coupled with increases in light availability to phytoplankton through increased near-surface stratification and longer ice-free periods, are very likely to increase primary production and carbon export around Antarctica. Biological carbon uptake is likely to increase for the Southern Ocean as a whole, whilst there is greater uncertainty around projections of primary production in the Sub-Antarctic and basin-wide changes in phytoplankton species composition, as well as their biogeochemical consequences. Phytoplankton, zooplankton, higher trophic level organisms and microbial communities are strongly influenced by Southern Ocean biogeochemistry, in particular through nutrient supply and ocean acidification. In turn, these organisms exert important controls on biogeochemistry through carbon storage and export, nutrient recycling and redistribution, and benthic-pelagic coupling. The key processes described in this paper are summarised in the **Graphical Abstract**. Climate-mediated changes in Southern Ocean biogeochemistry over the coming decades are very likely to impact primary production, sea-air CO_2 exchange and ecosystem functioning within and beyond this vast and critically important ocean region.

Keywords: Southern Ocean, biogeochemistry, primary production, iron, nutrients, carbon, ecosystem, ocean acidification



GRAPHICAL ABSTRACT | Infographic summarising the key processes described in this paper. Drawn by Dr. Stacey McCormack, University of Tasmania.

INTRODUCTION

Biogeochemistry refers to the cycling of chemical elements through living systems and their environments by physical, chemical, biological and geological processes, and is a fundamental component of the functioning of Planet Earth. Biogeochemical cycling of carbon, micronutrients and macronutrients in the Southern Ocean has strong implications for regional ecosystem functioning and sea-air gas exchange. The Southern Ocean plays a major role in modulating Earth's climate over seasonal-to-millennial timescales by taking up atmospheric carbon dioxide (CO_2) via biological and solubility pump processes and by releasing CO_2 from the deep ocean (e.g., Sarmiento and LeQuere, 1996; Gruber et al., 2009; Takahashi et al., 2009; Sigman et al., 2010). Ocean biogeochemistry exerts a critical control on primary production and phytoplankton species composition (Pinkerton et al., to be published in this research topic), which in turn have a strong impact on ocean biogeochemistry. Storage, transfer and transformation of carbon and nutrients in benthic (seafloor) and pelagic (water column) food webs regulate the degree to which these constituents are exported, sequestered or recycled and redistributed throughout the Southern Ocean system. Mode and intermediate water masses formed in the Sub-Antarctic influence primary production and carbon export throughout the world's oceans by setting the biogeochemistry of the global thermocline (subsurface layer characterised by a strong temperature gradient), from which nutrients are supplied to surface waters (Sarmiento et al., 2004; Marinov et al., 2006; Moore et al., 2018).

Anthropogenic climate change is affecting Southern Ocean biogeochemical cycling, directly through oceanic uptake of CO_2 and the resultant ocean acidification, and indirectly via its effect on sea ice dynamics, glacial meltwater inputs, winds and ocean physics (e.g., Le Quere et al., 2007; Midorikawa et al., 2012; Henley et al., 2017; Kerr et al., 2018; Gruber et al., 2019a; St-Laurent et al., 2019). Documented and projected climate-driven changes in biogeochemistry and primary production will impact ecosystem functioning and the transfer of carbon, energy and nutrients through benthic and pelagic food webs, with complex feedbacks on ocean biogeochemistry and climate. Biogeochemical and ecosystem responses to ongoing climate and environmental change may differ substantially in time and space, and in particular between shelf regions and the open Southern Ocean as a result of fundamental differences in phytoplankton dynamics, nutrient requirements and supply mechanisms, and

carbon export (Arrigo et al., 2008a,b, 2015; Tagliabue et al., 2009a; De Jong et al., 2015).

Within the framework of the Marine Ecosystem Assessment for the Southern Ocean (MEASO), we examine the status of and changes in Southern Ocean biogeochemistry in relation to its biological and physical drivers and its consequences for ecosystem functioning and sea-air CO_2 exchange. We consider the entire Southern Ocean south of 30°S, and focus on specific sectors, zones, regions and areas where appropriate. Zones are defined by the major circumpolar fronts, with the Antarctic Zone to the south of the Polar Front, the Polar Frontal Zone between the Polar Front and the Sub-Antarctic Front, the Sub-Antarctic Zone between the Sub-Antarctic Front and the Sub-Tropical Front, and the Northern Zone to the north of the Sub-Tropical Front (Deacon, 1982; Orsi et al., 1995).

We present new data and analyses to address outstanding questions regarding macronutrient cycling and carbon sink dynamics in the context of contemporary climate change. These analyses deepen our regional understanding of Southern Ocean biogeochemistry and reinforce its global-scale importance through modulation of atmospheric CO_2 concentrations and control of nutrient transport to the major ocean basins to the north. Finally, we highlight a number of current and future research priorities that will improve our understanding further, as well as a range of developments that are ongoing and anticipated in support of achieving these ambitions (**Box 1**). The biogeochemical phenomena and changes we describe for the Southern Ocean have strong implications for the marine organisms, food webs and ecosystem processes described throughout this research topic.

CHANGES IN PRIMARY PRODUCTION AND PHYTOPLANKTON SPECIES COMPOSITION

Phytoplankton Dynamics and Biogeochemistry

Southern Ocean biogeochemical cycles are influenced by phytoplankton through community-level processes (such as net primary production, NPP) and species composition. For example, carbon, nitrogen, phosphorus and iron are required to fuel primary production in euphotic (well-lit) surface waters, and in turn primary producers influence the cycling of these elements. In particular, the vertical export of organic matter produced by phytoplankton to the deep ocean (Section "Changes in the Biological Carbon Pump") is a key driver of temporal and spatial variability in Southern Ocean biogeochemistry, and this biological carbon pump exerts a strong control on oceanic CO_2 uptake and global climate (Section "Changes in the Southern Ocean Carbon Sink"). Different phytoplankton groups play multifaceted roles across a range of biogeochemical cycles (Boyd, 2019), with diatoms being major drivers of the biological carbon pump (Tréguer et al., 2018), as well as remineralisation and ecological stoichiometry (silicon and nitrogen cycles in particular). In addition, the small haptophyte *Phaeocystis antarctica* is important in the sulphur cycle (Kettle et al., 1999; Goto-Azuma et al., 2019) and coccolithophores are major modifiers of carbonate chemistry (Balch et al., 2011).

Current Status of Primary Production and Phytoplankton Species Composition

The Southern Ocean comprises the largest high nutrient low chlorophyll (HNLC) region globally, with primary production limited by iron, as well as silicon (as silicic acid) in summer north of the Polar Front and light during winter (e.g., de Baar et al., 1995; Boyd et al., 1999; Franck et al., 2000). Phytoplankton biomass and NPP are highest north of the Polar Front in the Atlantic sector, around the Sub-Tropical Front in the west Pacific sector, and over the Antarctic shelves in Prydz Bay and the Ross, Amundsen and Bellingshausen Seas (Pinkerton et al., to be published in this research topic). Biomass and NPP are lowest between the Polar Front and Southern Boundary of the Antarctic Circumpolar Current (ACC), particularly in the Indian sector within and just north of the open ocean sea ice zone (Pinkerton et al., to be published in this research topic). Despite sparse coverage of species composition data, HNLC waters in the Antarctic and Sub-Antarctic Zones where phytoplankton growth is limited by iron (Section "Changes in Micronutrient Biogeochemistry") tend to have mixed and seasonally changing assemblages of pico-, nano- and micro-phytoplankton (Gall et al., 2001; Eriksen et al., 2018). High-chlorophyll regions, such as island wakes and marginal ice zones (Boyd et al., 2012), tend to be dominated by blooms of diatoms, *Phaeocystis* or nanoplankton (Arrigo et al., 1999; Moreau et al., 2012; Quéguiner, 2013; Rembauville et al., 2015; Mangoni et al., 2017). One such region in the northern part of the west Antarctic Peninsula (WAP) experienced an intense diatom-dominated bloom with chlorophyll *a* concentrations >45 mg m^{-3} under favourable water column conditions (Costa et al., 2020). Diatoms also tend to dominate in silicic acid-rich waters south of the Polar Front (Wright et al., 2010; Petrou et al., 2016; Rembauville et al., 2017), whilst seasonally silicic acid-limited waters north of the Polar Front favour smaller phytoplankton (Freeman et al., 2018; Nissen et al., 2018; Trull et al., 2018). The Great Calcite Belt provides strong evidence for high coccolithophore abundance in the Sub-Antarctic (Balch et al., 2011).

Projected Changes in NPP and Drivers

Projected changes in primary production and phytoplankton species composition have been explored using model simulations (e.g., Bopp et al., 2013; Leung et al., 2015; Moore et al., 2018), manipulation experiments in polar and subpolar waters (e.g., Boyd et al., 2000, 2016; Hernando et al., 2015, 2018; Zhu et al., 2016; Petrou et al., 2019), and insights from paleoproxy records (Goto-Azuma et al., 2019) and contemporary natural variability such as the Southern Annular Mode (SAM) and El Niño Southern Oscillation (ENSO) (e.g., Saba et al., 2014; Schine et al., 2016). Projections of changes in NPP for the entire Southern Ocean based on model simulations within the coupled model intercomparison project 5 (CMIP5) show a good degree of agreement across models (Bopp et al., 2013;

Leung et al., 2015; Moore et al., 2018). Simulations point to increases in NPP of 50% or more above present-day rates across much of the Southern Ocean (Leung et al., 2015; Fu et al., 2016), driven by changes in environmental forcings including iron supply, surface mixed layer depth and its effect on underwater light climate, declining sea ice, and poleward shifts and increasing strength of westerly wind belts. Increases in temperature are expected, with medium confidence, to increase phytoplankton growth rates overall (Eppley, 1972; Steinacher et al., 2010; Sherman et al., 2016; Moore et al., 2018; Boyd, 2019), whilst changes in light attenuation by clouds may complicate the response (Meskhidze and Nenes, 2006). Increases in the partial pressure of CO_2 (pCO_2) are expected to have contrasting effects on different phytoplankton species, with the overall effect on primary production being uncertain (Section "Ocean Acidification and Its Effects on the Ecosystem").

Increasing NPP in the Southern Ocean is in contrast to the global trend of declining NPP (Moore et al., 2018). The models show that the dominant forcing of Southern Ocean NPP changes across latitudinal bands, corresponding to different circumpolar water masses separated by fronts (Leung et al., 2015). Increased iron supply and shallowing mixed layers play a key role in increasing NPP in the Northern Zone and sub-Antarctic waters north of 50°S, whilst factors controlling light availability are more influential in reducing NPP between 50 and 65°S. Increasing iron supply and a reduction in seasonal sea ice cover drive increases in NPP south of 65°S. Moore et al. (2018) report that the increase in wind-driven upwelling of nutrient-rich waters is the key driver of projected increases in NPP until 2150, after which increased surface stratification driven by ice melt becomes the dominant forcing. A more productive Southern Ocean would lead to greater nutrient uptake and potentially vertical export fluxes, thus retention of nutrients in this region, which would exacerbate declining NPP rates in low latitude waters to the north (Moore et al., 2018).

Projected Changes in Phytoplankton Species Composition and Drivers

Fewer model studies have provided projections of changes in phytoplankton species distributions (Bopp et al., 2005). Nevertheless, assessments of how species composition will be altered by ocean global change are possible by combining modelling, experimental and observational approaches. There is evidence that phytoplankton distributions are shifting southward as surface water temperatures increase, with sub-tropical waters and their warmer-water species incurring into the Sub-Antarctic Zone, and the poleward contraction of winter sea ice coverage extending southward the range of open ocean communities at the expense of sea ice zone communities (McLeod et al., 2012; Constable et al., 2014; Deppeler and Davidson, 2017). These southward shifts may increase the contribution of non-diatom phytoplankton overall, and this could be compounded in the Sub-Antarctic by the proposed favouring of small flagellates by projected increases in stratification (e.g., Petrou et al., 2016). Species shifts observed in response to sea ice changes at the WAP also suggest that phytoplankton communities in the seasonal ice zone may become less diatom-dominated as climate change proceeds (Montes-Hugo et al., 2008, 2009; Mendes et al., 2012, 2018; Hernando et al., 2015; Schofield et al., 2017). In contrast, it is well established from a range of *in situ* and laboratory studies that increased iron supply and ocean temperature have a beneficial effect on diatoms and other bloom-forming species, such that the projected increases in NPP may also lead to species shifts to diatoms, and in some regions *P. antarctica* (Gall et al., 2001; Hutchins and Boyd, 2016; Zhu et al., 2016; Boyd, 2019). Within diatom communities, species-specific responses to ocean acidification and other environmental factors are likely to alter species composition, primary productivity and biogeochemical cycles (Section "Ocean Acidification and Its Effects on the Ecosystem"). As such, the biogeographic provinces of phytoplankton assemblages in the Southern Ocean are likely to shift spatially or change fundamentally in the coming decades (Deppeler and Davidson, 2017). On longer timescales, a persistent new set of environmental conditions may drive evolutionary adaptation of existing species (Denman, 2017). Changes in NPP and phytoplankton species composition influence many biogeochemical processes, such as the magnitude and stoichiometry of nutrient uptake and recycling (Arrigo et al., 1999; Weber and Deutsch, 2010; Section "Changes in Macronutrient Biogeochemistry") and carbon transfer to higher trophic levels (Section "Carbon Transfer and Storage in Pelagic and Benthic Food Webs"). Changes in carbon export to the deep ocean will reflect changes in NPP to a varying extent, with important differences caused by phytoplankton species composition and other factors (e.g., Fu et al., 2016; Rembauville et al., 2017; Section "Changes in the Biological Carbon Pump").

CHANGES IN MICRONUTRIENT BIOGEOCHEMISTRY

Changes to Iron Supply and Availability in the Southern Ocean

The delivery and cycling of important trace elements that underpin all Southern Ocean productivity are being altered by shifts in physics, chemistry and biology in response to ongoing changes in Earth's climate (high confidence). Iron is required by phytoplankton for photosynthesis and nitrate assimilation, and is the primary limiting micronutrient in the HNLC region across large parts of the Southern Ocean (e.g., de Baar et al., 1990; Moore et al., 2013). Changes in the magnitude and pathways of iron supply to surface waters are being imposed from both the north and the south (**Figure 1** and **Table 1**). For example, the frequency and scale of iron-rich aerosol emissions from dust and wildfires are predicted to increase with trends in regional climate, such as drought and increased winds (IPCC, 2019). Strengthening western boundary currents are very likely to lead to greater eddy transport and thus advective inputs of iron-rich waters from the sub-tropics to the Sub-Antarctic (Bowie et al., 2009), whilst a weakening of the overturning circulation and

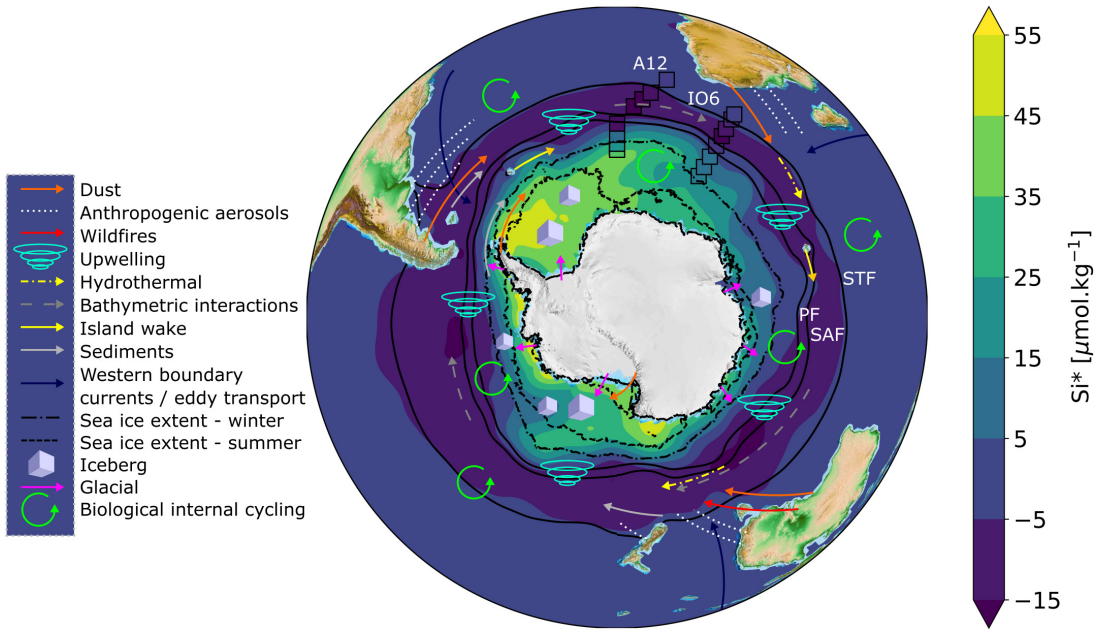


FIGURE 1 | Map of Si* with schematic representations of iron sources overlain. Annual climatological Si* concentrations (=[$Si(OH)_4$] – [NO_3^-]) for Southern Ocean surface waters (data source: WOA18, 1 degree grid resolution) are overlain by the measured Si* concentrations from A12 2019 and IO6 2017 winter cruises (open black boxes; this study). Solid black contours represent climatological frontal positions based on sea surface temperature; STF = Sub-Tropical Front at 11.5°C, SAF = Sub-Antarctic Front at 4°C, PF = Polar Front at 2°C (Deacon, 1982; Orsi et al., 1995) (data source: WOA18, 1/4 degree resolution). Dashed and dot-dashed black lines represent the mean climatological sea ice extent for summer (Dec/Jan/Feb) and winter (July/Aug/Sep), respectively, defined as 15% sea ice concentration (data source: NSIDC, 12.5 km resolution, Stroeve and Meier, 2018). Iron sources are represented according to the legend, and summarised in **Table 1**. The exact locations of some iron sources (e.g., hydrothermal vents, bathymetric interactions) are not well-defined, but are depicted schematically. The important processes of deep winter mixing and vertical diffusion occur throughout the Southern Ocean, but are not depicted.

TABLE 1 | Mechanisms of iron supply to the Southern Ocean, with estimates of geographical extent and projected trends under anthropogenic climate change.

Mode	Spatial scale	Temporal scale	Fe supply (μmol m^{-2} $year^{-1}$)	Geographical extent (km^2)	Future change	References
Aerosol mineral dust	Regional	Seasonal	19	6.1×10^6	?	Gabric et al., 2010; Boyd et al., 2012
Anthropogenic aerosols	Local	Seasonal	?	?	?	Sholkovitz et al., 2012
Wildfire emissions	Local	Seasonal	?	?	Increase	Ito et al., 2018
Deep winter mixing	Basin	Seasonal	100	4.2×10^7	?	Tagliabue et al., 2014
Vertical diffusion	Basin	Annual	3	4.2×10^7	Decrease	Tagliabue et al., 2014
Upwelling	Local	Annual	10	$<10^6$	?	Boyd et al., 2012; Tagliabue et al., 2014
Hydrothermal	Local	Annual	3	$\ll 10^6$	NC	Boyd et al., 2012; Ardyna et al., 2019
Bathymetric interactions	Local	Annual	55	$\ll 10^6$	NC	Boyd et al., 2012
Island wake	Local	Annual	11	$\ll 10^6$	NC	Blain et al., 2007; Boyd et al., 2012
Sediments	Regional	Annual	270	9.4×10^6	NC	Tagliabue et al., 2009a; Boyd et al., 2012
Western boundary currents/eddy transport	Local	Annual	15	$<10^6$	Increase	Bowie et al., 2009; Boyd et al., 2012
Sea-ice melt	Regional	Seasonal	120	1.4×10^7	Increase	Boyd et al., 2012; Lannuzel et al., 2016; Meehl et al., 2016
Iceberg	Local	Seasonal	363	$<10^6$	Increase	Lin et al., 2011; Boyd et al., 2012
Glacial	Local	Seasonal	?	$\ll 10^6$	Increase	Boyd et al., 2012; Herraiz-Borreguero et al., 2016
Biological internal recycling	Basin	Seasonal	10	4.2×10^7	?	Boyd et al., 2012

Table adapted and augmented from Hutchins and Boyd (2016). ? = unknown supply or extent; uncertain direction of change. NC = no change expected.

altered winds may result in changes in stratification patterns impacting delivery of nutrients from below (Tagliabue et al., 2009b; Rintoul, 2018). Warming waters surrounding Antarctica are virtually certain to drive glacial melt and increased calving of icebergs, releasing iron-rich terrigenous material (Lin et al., 2011; Sherrell et al., 2015; Herraiz-Borreguero et al., 2016;

Raiswell et al., 2016; Hopwood et al., 2017; Laufkötter et al., 2018; van der Merwe et al., 2019). Increasing iceberg scour in shallow coastal areas in response to ongoing glacial retreat and receding ice shelves is also likely to enhance the important sedimentary iron supply mechanisms to shelf surface waters (Marsay et al., 2014; McGillicuddy et al., 2015), and dust input from Antarctica itself may increase as ice loss exposes more glacial sediments to wind-driven transport (Winton et al., 2016; Duprat et al., 2019; Gao et al., 2020). Warming is very likely to reduce the extent and thickness of Antarctic sea ice (Lannuzel et al., 2016), which accumulates iron and other bioactive metals for subsequent release to surface waters in spring and early summer (Noble et al., 2013). Ocean acidification will alter the speciation (chemical form) and solubility of essential trace elements and nutrients in seawater, but it is unclear whether lowered pH will increase or decrease iron availability to phytoplankton (Shi et al., 2010; Hutchins and Boyd, 2016).

Predicting Ecosystem Responses to Changes in Iron Sources and Their Magnitude

Changes in environmental conditions can have complex and sometimes counterintuitive effects on iron sources and cycling. For instance, whilst increased dust input from Australasia, Patagonia and South Africa would be expected to increase surface iron concentrations and enhance productivity, a large proportion of the dust may remain undissolved and act as additional ballast for sinking particulate organic carbon (POC). This would deepen the mean iron remineralisation depth, and possibly supply new particle surfaces for adsorptive scavenging (i.e., removal) of dissolved iron, reinforcing a possible *reduction* in the subsurface iron pool (Ellwood et al., 2014; Bressac et al., 2019). The vertical iron gradient and upward iron flux would then be reduced, even in Southern Ocean regions that experience reduced stratification associated with declining sea ice and/or intensification of westerly winds (Rintoul, 2018). With reduced stratification, autotrophic cells are mixed over a greater depth range, thus spending more time under light limitation, which can increase iron demand unless physiological adaptation occurs (Strzepek et al., 2019). In contrast, closer to the Antarctic continent, stratification may be enhanced by increased atmospheric heat flux and freshwater delivery from icebergs, glaciers and ice shelves (e.g., Morley et al., to be published in this research topic). Shifts in phytoplankton species composition could alter cellular iron uptake and remineralisation, whilst changes in the chemical speciation of iron in the upper ocean, in response to altered iron sources, as well as changes in ocean pH, temperature and oxygen content, further complicate an accurate prediction of ecosystem response (Boyd, 2019).

Speciation, Internal Cycling and Remineralisation of Iron in the Southern Ocean

The relative availability of the myriad forms of dissolved (Blain and Tagliabue, 2016) and particulate (Planquette et al., 2013) iron in Southern Ocean surface waters is a key determinant of primary productivity, but remains poorly understood. Major uncertainties include the relative availability of iron bound to organic ligands (Buck et al., 2018; Bundy et al., 2018; Zhang et al., 2019), the interconversion of soluble and colloidal iron (Fitzsimmons et al., 2015; Santschi, 2018), the recycling rate of organic matter-bound iron in surface and subsurface waters (Bressac et al., 2019), and the adsorptive scavenging of regenerated iron in intermediate water masses (Tagliabue et al., 2019). There is a near-consensus that the largest flux of bioavailable iron to surface waters of the open Southern Ocean is currently delivered by wintertime deep vertical mixing from iron-enriched layers below (Tagliabue et al., 2012, 2014; Schallenberg et al., 2018). Except in regions proximal to, or downstream of, lateral sub-surface iron inputs from continental shelves and slopes (De Jong et al., 2012; Hatta et al., 2013; Annett et al., 2017; Sherrell et al., 2018), submerged plateaus (Blain et al., 2007; Bowie et al., 2015) or hydrothermal vents (Ardyna et al., 2019), the increase in iron below the surface mixed layer is ascribed to remineralisation from sinking particulate organic carbon, modulated by iron scavenging with depth (Sedwick et al., 2008; Middag et al., 2011; Abadie et al., 2017).

Effect of Multiple Stressors on Iron Availability and Phytoplankton Physiological Responses

Changes in iron availability in the future Southern Ocean will occur concurrent with, and as a function of, an array of other physical and chemical changes forced by climate change, that will impact the primary producers directly and indirectly by influencing iron dynamics (e.g., Boyd et al., 2014; Section "Changes in Primary Production and Phytoplankton Species Composition"). Although there is reasonable consensus among current models that Southern Ocean primary productivity will increase, largely as a function of increased iron supply, light availability and warming (Bopp et al., 2013; Leung et al., 2015; Moore et al., 2018; Boyd, 2019), no models capture mechanistically the myriad interactions among changing environmental variables and the physiological effects, adaptation strategies and evolutionary responses of the phytoplankton (Hutchins and Boyd, 2016; Strzepek et al., 2019). The magnitude and in most cases even the sense of these interactions remain insufficiently understood. Changes in phytoplankton species composition may also alter iron availability in surface waters by modifying the balance among biological uptake, chemical speciation, adsorptive scavenging, vertical export and organic matter recycling as controlling mechanisms. In addition, many cell types are surprisingly plastic in their iron requirements, and some have the ability, even in the short term, to adjust their iron assimilation mechanisms and maintain similar growth rates despite changes in iron availability (Andrew et al., 2019). Phytoplankton in a cold-core eddy with very low surface iron concentrations have been shown recently to upregulate iron uptake and utilise iron from enhanced microbially mediated recycling (Ellwood et al., 2020). Given the widespread distribution of eddies in the iron-limited Southern Ocean (Frenger et al., 2015), these mechanisms may have

large-scale importance in influencing phytoplankton dynamics under climate change.

Micronutrient-Limitation by Other Trace Elements

In addition to iron, phytoplankton require manganese and can be co-limited by manganese and iron in Southern Ocean regions where supplies of both metals to surface waters are restricted (Middag et al., 2011, 2013). Iron-manganese co-limitation of phytoplankton growth has been shown for *P. antarctica* in the Ross Sea in late summer (Wu et al., 2019) and in the Antarctic diatom *Chaetoceros debilis* (Pausch et al., 2019). The future status of iron-manganese co-limitation may depend in part on the poorly understood effects of ocean acidification on the availability of these metals (Koch et al., 2019). Cobalt in the form of cobalamin (vitamin B_{12}) can also co-limit, with iron, some Southern Ocean phytoplankton species (Moore et al., 2013; Bertrand et al., 2015). Because cobalamin can only be produced by bacteria and archaea, as is the case for some strong iron ligands, this points to a critical role for complex phytoplankton−bacteria interactions in regulating Southern Ocean primary productivity. Laboratory experiments investigating the interactions among all of these factors and their combined physiological and biogeochemical implications suggest that a complex and seasonally varying mosaic of limitation scenarios may apply in various subregions of the Southern Ocean and Antarctic shelf waters (Koch and Trimborn, 2019).

Differences Between Open Southern Ocean and Antarctic Shelf Regions

The open Southern Ocean and Antarctic shelves differ substantially in micronutrient dynamics due to large differences in circulation, bottom depth, productivity and biogeochemistry, and interactions with the atmosphere and cryosphere. Whilst vertical mixing and atmospheric dust inputs from more northerly continents are the main iron sources for much of the Southern Ocean, surface waters of the shelf regions are proximal to both continental and sedimentary iron sources. In regions bordered by ice shelves, ice-shelf melting by warmer oceanic waters at the ice-ocean interface can provide a glacial iron source to the adjacent surface ocean from iron-rich particulates within the ice shelf and from liquid water at the base of land-grounded ice (Gerringa et al., 2012; Sherrell et al., 2015; Raiswell et al., 2018). The buoyant plume transporting ice-derived iron also entrains iron from shelf sediments via the ice-shelf meltwater pump (St-Laurent et al., 2017, St-Laurent et al., 2019). Most evidence for these phenomena is from West Antarctica, where glacial meltwater input has been increasing for decades, adding iron that is potentially bioavailable for phytoplankton growth (Monien et al., 2017), but new evidence shows increased melting in East Antarctica (Rignot et al., 2019) that may be driving similar iron inputs. These glacial and sedimentary iron sources, in addition to oceanic sources, mean that surface waters are iron-replete in most shelf regions in spring (Marsay et al., 2014; Arrigo et al., 2017) and in coastal inner shelf regions in summer (Carvalho et al., 2019), although summertime iron limitation has been indicated off the WAP (Annett et al., 2017) and in the Amundsen and Ross Seas (Alderkamp et al., 2015, 2019). Whilst there is evidence for off-shelf export of shelf sediment-derived iron from the WAP and western Weddell Sea and transport to downstream open ocean regions (De Jong et al., 2012), much of the continental iron is retained within shelf systems by along-shelf circulation patterns and fronts (Rintoul, 2018), and by uptake in intense phytoplankton blooms that export iron to depth over the shelves (Annett et al., 2017). Contrasting physical and biogeochemical conditions between the shelf and open ocean regions dictate that future changes in iron dynamics and impacts on primary production are also likely to differ between these provinces. Given the expected increases in shelf-proximal glacial meltwater inputs and sedimentary iron delivery by the ice-shelf meltwater pump, and the effects on shelf sediment redox processes of enhanced carbon export from sea-ice-free surface waters, it is reasonable to speculate that larger increases in iron supply to primary producers will occur over the shelves than in the open Southern Ocean as climate change proceeds (Tagliabue et al., 2009a; Marsay et al., 2014; De Jong et al., 2015; St-Laurent et al., 2019; Dinniman et al., 2020).

CHANGES IN MACRONUTRIENT BIOGEOCHEMISTRY

Macronutrient Supply and Limitation of Phytoplankton Growth

Whilst iron is the primary limiting nutrient for phytoplankton growth in the Southern Ocean, macronutrients (nitrate, phosphate, silicic acid) sourced mainly from the Circumpolar Deep Water (CDW) mass in the ACC play an important role in regulating primary production and carbon export within and far beyond the Southern Ocean (Moore et al., 2013, 2018). Here, we present three new datasets to explore the seasonal changes in macronutrient concentrations and ratios in the Atlantic and Indian sectors of the open Southern Ocean south of South Africa (**Figure 2**) and in Marguerite Bay in the coastal zone of the central WAP region (**Figure 3**). Nitrogen and phosphorus do not limit Southern Ocean primary production in general, although short periods of nitrate limitation have been observed during peak-bloom conditions in high-productivity coastal and shelf areas (Henley et al., 2017, 2018; **Figures 2**, **3**). Additionally, diatoms under varying degrees of iron limitation deplete silicic acid in the Antarctic and Polar Frontal Zones to a far greater extent than nitrate (Pondaven et al., 2000; Smith et al., 2000), leading to summertime instances of silicic acid-limitation (Pollard et al., 2002). The preferential removal of silicic acid south of the Sub-Antarctic Front also yields northward-flowing surface waters that are silicic acid-deplete and nitrate- and phosphate-rich (**Figure 2**; Sarmiento et al., 2004). This condition, which favours the growth of non-siliceous phytoplankton (Balch et al., 2011; Quéguiner, 2013; Deppeler and Davidson, 2017 and references therein), could reduce carbon export since the dense siliceous shells of diatoms cause them to sink more rapidly than

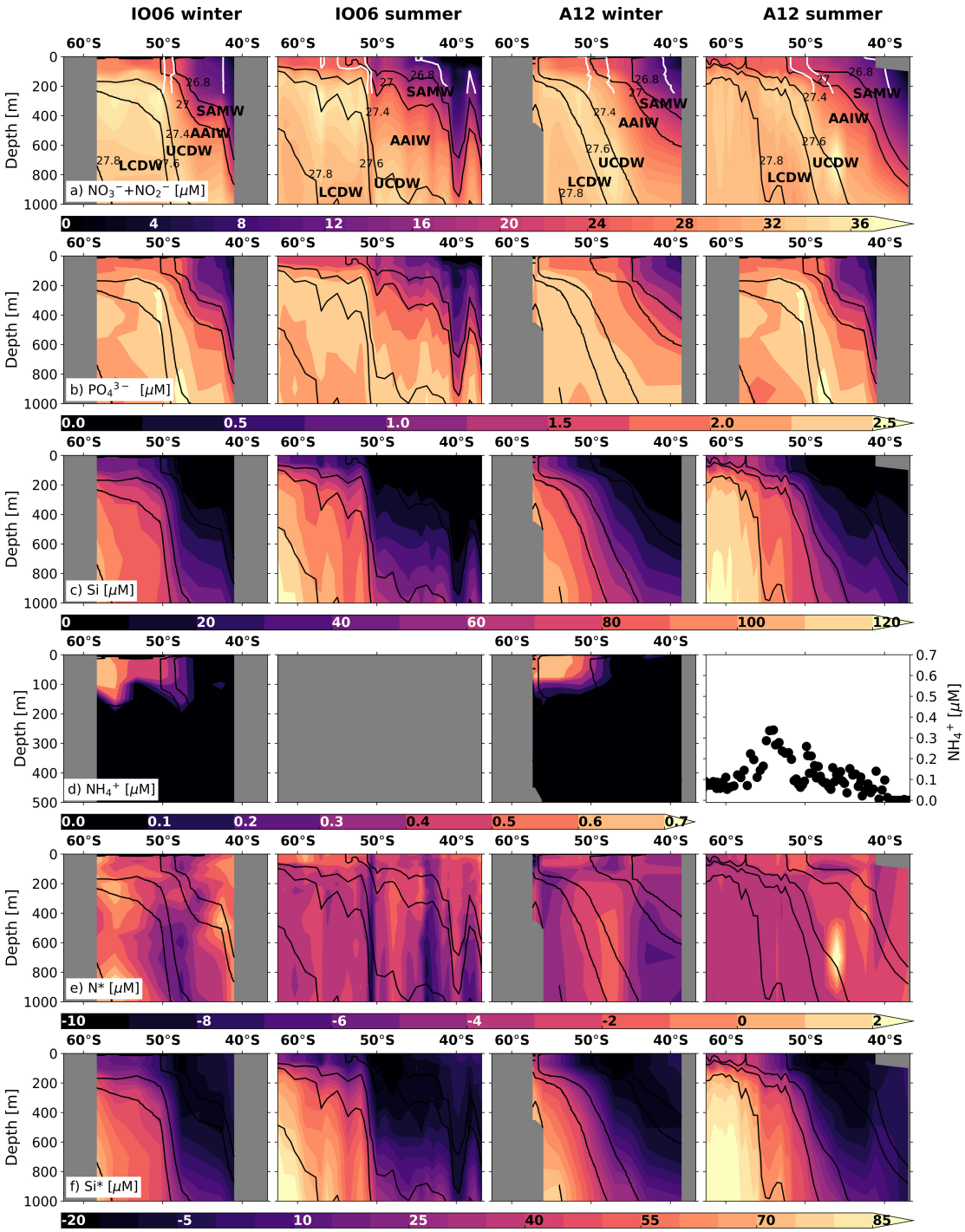


FIGURE 2 | Nutrient concentration and stoichiometry data across the Indian (WOCE IO6 line; left-hand columns) and Atlantic (WOCE A12 line; right-hand columns) sectors of the Southern Ocean in summer and winter (see **Figure 1** and **Supplementary Figure S1** for transect locations). Shown are the concentrations (0–1000 m, except for ammonium) of **(a)** nitrate + nitrite, **(b)** phosphate, **(c)** silicic acid, **(d)** ammonium (0–500 m), **(e)** N* (=[NO_3^- + NO_2^-] – 16 × [PO_4^{3-}]), and **(f)** Si* (=[$Si(OH)_4$] – [NO_3^-]). Winter measurements, which extend to the edge of the marginal ice zone, are for samples collected in 2017 (IO6) and 2019 (A12) (see **Supplementary Information 1** for details). Summer samples were collected in 1996 (IO6; WOCE 2018) and 2008 (A12; Schlitzer et al., 2018). No summer ammonium concentration data are available for IO6, whilst the summertime values shown for A12 are for samples collected at the surface along A12 in 2019. Where ammonium data are available, N* is calculated as N^*_{DIN} = [NO_3^- + NO_2^- + NH_4^+] – 16 × [PO_4^{3-}]. The major water masses defined according to Whitworth and Nowlin (1987), Park et al. (1993), Orsi et al. (1995), and Belkin and Gordon (1996) are labelled on panel a: SAMW, AAIW, Upper and Lower CDW (UCDW, LCDW). The positions of the major fronts at the time of sampling (after Deacon, 1982 and Orsi et al., 1995) are shown in white to 400 m on panel **(a)**: (from south to north) the Polar Front, Sub-Antarctic Front and Sub-Tropical Front. The new winter data presented here are available at https://doi.org/10.5281/zenodo.3883618.

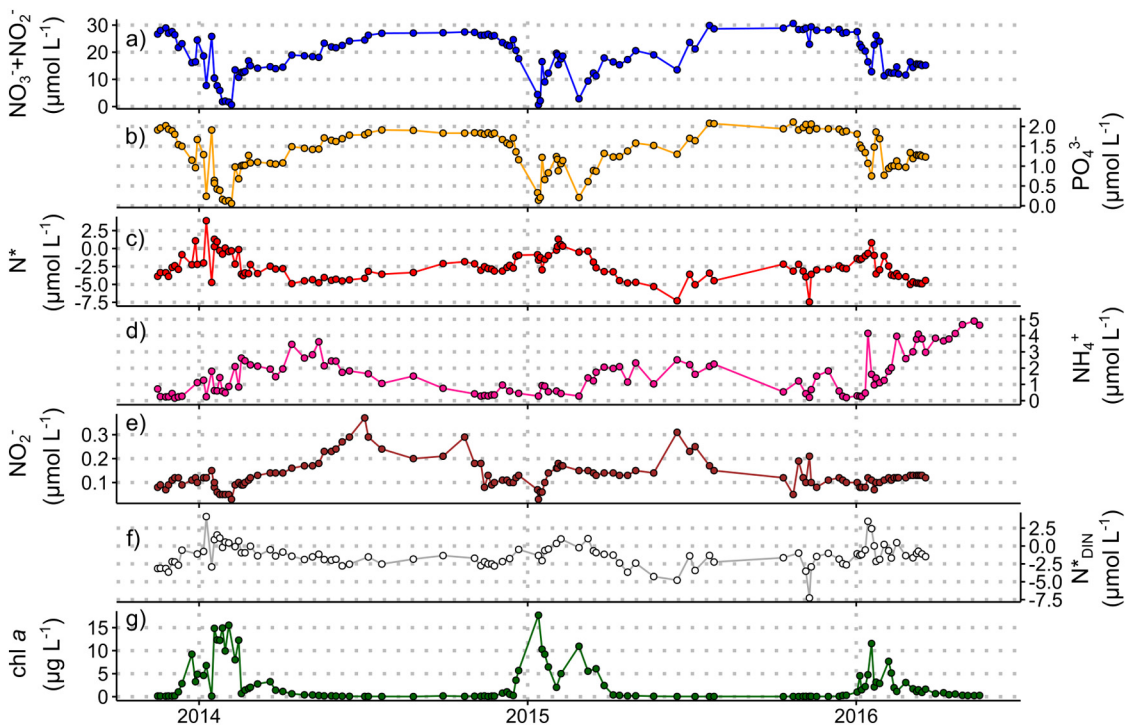


FIGURE 3 | Nutrient concentration and stoichiometry data from the Rothera Time Series, November 2013 to March 2016 (see **Supplementary Information 2** for details). Measured concentrations for samples taken at 15 m water depth of **(a)** nitrate + nitrite, **(b)** phosphate, **(c)** N*, **(d)** ammonium, **(e)** nitrite, and **(f)** N^*_{DIN}. Chlorophyll *a* concentrations **(g)** are included to indicate the timing and magnitude of summer phytoplankton blooms. Chlorophyll data courtesy of the British Antarctic Survey. These data are available through the British Oceanographic Data Centre (BODC) at https://www.bodc.ac.uk/data/published_data_library/catalogue/10.5285/98cc0722-e337-029c-e053-6c86abc02029/ (Henley and Venables, 2019).

other phytoplankton (Buesseler, 1998; Ducklow et al., 2001; Armstrong et al., 2009).

Seasonal Nutrient Dynamics in the Open Southern Ocean

The balance between wintertime nutrient supply and summertime nutrient drawdown is central to the Southern Ocean's role in setting atmospheric CO_2 (Sarmiento and Toggweiler, 1984; Section "Changes in the Southern Ocean Carbon Sink"). In general, Southern Ocean nutrient measurements are biased towards the spring and summer due in part to the challenges of sampling in winter. For the open Southern Ocean, two new winter datasets from the IO6 and A12 meridional transects (**Figures 2a–c** and **Supplementary Information 1**) show that surface nutrient concentrations as far south as the marginal ice zone, whilst higher in winter than summer, are still lower than in the underlying source waters despite vigorous mixing. This occurs because the seasonal incorporation of the relatively low-nutrient summer surface mixed layer into the winter mixed layer dilutes the nutrient concentrations of the latter (Smart et al., 2015). Biological uptake in summer thus affects mixed-layer nutrient concentrations year-round. In addition, nitrification (the chemoautotrophic oxidation of ammonium to nitrate via nitrite) occurs at high rates in the winter mixed layer across the Southern Ocean (Smart et al., 2015; Mdutyana et al., 2020), producing recycled nitrate subsequently available for consumption in spring. Nitrification is favoured in winter due to low light and reduced competition for ammonium (Olson, 1981; Ward, 2005; Smith et al., 2014). This effect may be augmented by enhanced iron availability (Shafiee et al., 2019) and, south of the Polar Front, by mixed-layer ammonium accumulation (**Figure 2d**) resulting from an enhanced microbial loop in late summer/autumn (Becquevort et al., 2000; Dennett et al., 2001; Lourey et al., 2003). Currently, the implications of nutrient (re)cycling within the seasonally varying mixed layer for Southern Ocean carbon production and export remain poorly understood.

Seasonal and Spatial Variability in Nutrient N:P Ratios

The ratios in which phytoplankton communities take up macronutrients exert important controls on carbon export, and are influenced by taxonomy, growth rate, resource allocation, equilibrium cellular nutrient ratios relative to supply ratios, and micronutrient limitation (Weber and Deutsch, 2010; Martiny et al., 2013). The nitrogen-to-phosphorus (N:P) uptake ratio varies broadly with latitude across the Southern Ocean, ranging from ∼20:1 in the Sub-Antarctic to 11−16:1 in the Antarctic Zone, corresponding with latitudinal gradients in phytoplankton species composition, light and temperature (Arrigo et al., 1999;

Finkel et al., 2006; Green and Sambrotto, 2006; Weber and Deutsch, 2010; Martiny et al., 2013). This produces the opposite trend in seawater nitrate-to-phosphate concentration ratios, as described by the stoichiometric parameter N* ($[NO_3^-] + NO_2^-]$–$16 \times [PO_4^{3-}]$; Gruber and Sarmiento, 1997). For the two new winter datasets (**Figure 2** and **Supplementary Information 1**), the previously observed summertime trend persists, with lower mixed-layer N* in the Sub-Antarctic and higher N* in the Antarctic Zone (**Figure 2e**). The meridional gradients are weaker in winter (average N* of -3.7 ± 0.7 μmol L^{-1} in the Sub-Antarctic and -2.3 ± 0.7 μmol L^{-1} in the Antarctic Zone), probably because they largely reflect the imprint of summertime uptake partially eroded by lateral and vertical mixing. Similarly, the wintertime surface-subsurface N* gradients are weaker because the rate of upward nutrient supply outpaces that of surface uptake and subsurface regeneration. Nonetheless, the data confirm that summertime phytoplankton N:P uptake ratios set surface and subsurface N* year-round in this open ocean region.

New year-round data from Marguerite Bay, in the coastal WAP, show distinct seasonal variations in upper ocean N* (**Figure 3**; **Supplementary Information 2**). Maximum N* in summer is driven by diatom-dominated phytoplankton blooms characterised by low N:P uptake ratios. Diatom-dominated ice algal production may also contribute to increasing N* in spring before sea ice retreats. Minimum N* in early winter (April—June), similar to deep-water values (-4.8 ± 0.6 μmol L^{-1} below 100 m), indicates a near-complete reset of surface nutrient stoichiometry due to vertical mixing of nutrient-rich modified CDW. This resupply, augmented by a minor contribution from remineralisation, drives a steady increase in surface nitrate and phosphate in a ratio close to the Redfield ratio (15.4 ± 0.9 in winter 2014; 16.2 ± 0.6 in winter 2015), although surface concentrations do not reach high CDW values. In mid-late winter, increases in N* coincident with decreasing ammonium concentrations, high and variable nitrite concentrations, and stable N^*_{DIN} ($[NO_3^-] + NO_2^-] + [NH_4^+]$–$16 \times [PO_4^{3-}]$; Gruber and Sarmiento, 1997) indicate *in situ* nitrification. Nitrification within the sea-ice matrix and ice-ocean nutrient exchange may also contribute to the observed signals. By contrast, phytoplankton nutrient uptake cannot account for the changes over winter when light is absent at these latitudes.

Taken together, the three new datasets presented here show that vertical mixing does not completely reset the surface macronutrient inventory over the Antarctic shelves or in the open Southern Ocean, at least in the regions examined here, such that summertime uptake influences surface and subsurface nutrient concentrations and stoichiometry year-round. We also highlight the importance of wintertime nitrification in shelf and open ocean settings.

Southern Ocean Nutrient Budgets and Silicic Acid-to-Nitrate Ratios in Global Biogeochemical Cycles

Southern Ocean macronutrient budgets are important for global nutrient distributions and carbon export in addition to regional processes and ecosystems (Sarmiento et al., 2004; Moore et al., 2018). In particular, surface nutrient concentrations and ratios in the formation regions of Sub-Antarctic Mode Water (SAMW) and Antarctic Intermediate Water (AAIW) are transported northward by these water masses and mixed through the thermocline into macronutrient-limited surface waters north of 30°S (Marinov et al., 2006). This is the case for low preformed silicic acid-to-nitrate ratios, quantified as Si* ($[Si(OH)_4]$–$[NO_3^-]$; Sarmiento et al., 2004). Although the Si* of upwelling CDW is high (∼10—55 μmol L^{-1}; **Figure 2f**), diatoms experiencing iron stress consume silicic acid and nitrate in a ratio higher than the 1:1 ratio expected for iron-replete diatoms (Hutchins and Bruland, 1998; Takeda, 1998). This decreases Si* south of the Polar Front and in northward-flowing surface waters, such that SAMW and AAIW form in the near-absence of silicic acid (i.e., Si* < -10 μmol L^{-1}) (**Figures 1**, **2**). The low Si* signal is transferred to the low-latitude thermocline, favouring non-silicifying phytoplankton species in the overlying surface waters.

Future Changes to Southern Ocean Nutrient Budgets and Global Consequences

Observed and anticipated changes in primary production and phytoplankton species composition across the Southern Ocean (Section "Changes in Primary Production and Phytoplankton Species Composition") influence the quantity and stoichiometry of nutrients transported in northward-flowing water masses. Increases in primary production would reduce total northward nutrient transport, and therefore primary production and carbon export throughout the lower latitudes (Moore et al., 2018). Southward shifts of phytoplankton communities as warming proceeds, and the resultant shift towards smaller species with higher N:P uptake ratios in each latitudinal band (Arrigo et al., 1999; Martiny et al., 2013), would increase the mean N:P uptake ratio at the basin scale (Weber and Deutsch, 2010), altering carbon export, which is more tightly coupled to nitrogen than phosphorus. The subsequent decrease of N* in mode and intermediate waters would lead to more intense nitrogen limitation relative to phosphorus in the low-latitudes, reducing carbon export and potentially influencing competition between nitrogen fixers and other autotrophs (Weber and Deutsch, 2010; Martiny et al., 2013). In contrast, a species shift to diatoms in the Sub-Antarctic could increase N* supply to the low latitudes, which could partially offset the reduction in low-latitude carbon export. Whilst such a shift could further reduce Si* in northward-transported water masses, the well-established silicic acid leakage hypothesis (Nozaki and Yamamoto, 2001; Brzezinski et al., 2002; Matsumoto et al., 2002) suggests that the projected increase in iron supply (Sections "Changes in Primary Production and Phytoplankton Species Composition" and "Changes in Micronutrient Biogeochemistry") would reduce the diatom silicon-to-nitrogen (Si:N) uptake ratio and thus increase Si* supply to the north. This increase in Si* could also be exacerbated by a reduction in diatom silica production under ocean acidification, which would further reduce the Si:N uptake ratio (Petrou et al., 2019; Section "Ocean Acidification and Its

Effects on the Ecosystem"). The extent to which changes in the stoichiometry of northward-transported nutrients compound or alleviate the impact of increased Southern Ocean nutrient retention on global-scale primary production and carbon export (Moore et al., 2018) requires further investigation.

CHANGES IN THE SOUTHERN OCEAN CARBON SINK

The Solubility Pump, Biological Pump and Upwelling

The Southern Ocean is a globally important region for ocean ventilation and the sea-air exchange of CO_2 and other climate-active gases, due to a complex interaction (sometimes counterintuitive) between physical-chemical and biological processes (Marinov et al., 2006). The solubility pump, whereby atmospheric CO_2 is taken up by dissolution into surface waters and subsequently subducted into the subsurface, exporting CO_2 into the ocean interior, is particularly strong in the high southern latitudes due to cold surface waters and deep and intermediate water mass formation (e.g., Sabine et al., 2004; Van Heuven et al., 2014; Gruber et al., 2019b). The Southern Ocean also has regions of strong upwelling linked to oceanographic fronts, which brings CO_2-rich deep waters to the surface, increasing pCO_2 in surface waters, altering the carbonate system equilibrium and driving CO_2 release to the atmosphere (e.g., Pardo et al., 2017; Chapman et al., 2020). The biological pump is also important in the Southern Ocean, particularly during spring and summer (e.g., Ducklow et al., 2001; DeVries et al., 2012; Cavan et al., 2019a). CO_2 is converted into organic carbon during photosynthesis by phytoplankton and other primary producers (Section "Changes in Primary Production and Phytoplankton Species Composition"), stored in plant and animal tissues (Section "Carbon Transfer and Storage in Pelagic and Benthic Food Webs") and subsequently exported to the deep ocean and seafloor when microalgae and other organisms die. The balance between solubility and biological pump processes and upwelling processes, and their combined effect on the difference between seawater and atmospheric pCO_2 (ΔpCO_2), determine whether the surface ocean behaves as a CO_2 sink or source. The magnitude of CO_2 fluxes depends mostly on wind speed, which strongly affects the sea–air gas transfer velocity (e.g., Fay et al., 2014; Wanninkhof, 2014).

Net CO_2 Sink Behaviour of the Southern Ocean

The Southern Ocean between 30°S and 50°S is currently a major net annual sink for atmospheric CO_2 since biological uptake during summer and solubility pump processes exceed CO_2 outgassing driven by upwelling and vertical mixing predominantly during winter (e.g., Takahashi et al., 2012; Roobaert et al., 2019). The Southern Ocean CO_2 sink has taken up approximately 40% of the total oceanic uptake of anthropogenic CO_2 (Orr et al., 2001; Fletcher et al., 2006; DeVries, 2014), increasing surface water pCO_2 and causing ocean acidification (Section "Ocean Acidification and Its Effects on the Ecosystem"). Export of CO_2 to the deep Southern Ocean occurs in specific locations and depends on the interactions between physical properties, such as mixed layer depth, ocean currents, fronts, eddies and winds, all of which are potentially sensitive to climate variability and change, and with bathymetric features (Sallee et al., 2012; Chapman et al., 2020). In addition to intense seasonality in sea–air CO_2 fluxes driven by the solubility and biological pumps, a high degree of interannual variability has been reported for particular regions, such as the WAP (Ito et al., 2018; Brown et al., 2019) and the Ross Sea (Dejong and Dunbar, 2017). Across the Southern Ocean, summertime conditions have been shown to drive sub-decadal variability in ΔpCO_2 whilst winter variability contributes to longer-term changes associated with the SAM (Lenton and Matear, 2007; Gregor et al., 2018).

Trends and Changes in Carbon Sink Strength

The strength of the Southern Ocean carbon sink declined between the 1980s and early 2000s, largely due to an increase in natural CO_2 release associated with stronger winds, which enhanced the advection and vertical mixing of dissolved inorganic carbon (DIC) into surface waters (Le Quere et al., 2007; Lovenduski et al., 2008; Lenton et al., 2013). Model simulations have shown that this increase in CO_2 outgassing was sustained from the late 1950s (Lovenduski et al., 2013). However, this trend reversed during the 2000s as the overturning circulation weakened (DeVries et al., 2017). The strength of the sink has increased again since around 2002, and by 2012 had recovered to its expected strength based on the increase in atmospheric CO_2 concentrations (Landschutzer et al., 2015). The Southern Ocean sea–air CO_2 flux was recently estimated to be -0.75 ± 0.22 Pg C year^{-1} by combining estimates of seawater pCO_2 from biogeochemical floats with shipboard measurements (Bushinsky et al., 2019). This estimate of CO_2 sink strength is reduced compared to that based on shipboard measurements alone (-1.14 ± 0.19 Pg C year^{-1}) because the use of floats increases substantially the data availability during winter when CO_2 outgassing is maximal.

Spatial and Temporal Variability in ΔpCO_2 and Its Physical and Biological Drivers

Here we use the Surface Ocean CO_2 Atlas (SOCAT) version 2019 (Bakker et al., 2016; **Figure 4**) to elucidate how carbon sink strength in the different sectors of the Southern Ocean south of 30°S has changed in recent decades (**Figure 5**). We also attempt to compare the proportional contributions of the solubility and biological pumps to the carbon sink (**Figure 6**). Analysis of ΔpCO_2 by season for 2002−2007 and 2012−2017 confirms the expected net CO_2 sink behaviour for both coastal and open-ocean regions where data are available (**Figure 5**). Net CO_2 uptake (negative ΔpCO_2) is observed overall in all seasons, with lower spatially-averaged ΔpCO_2 indicating higher CO_2 uptake during the summer seasons and particularly in the coastal regions (**Figures 5a,e**). However, variability is high within and

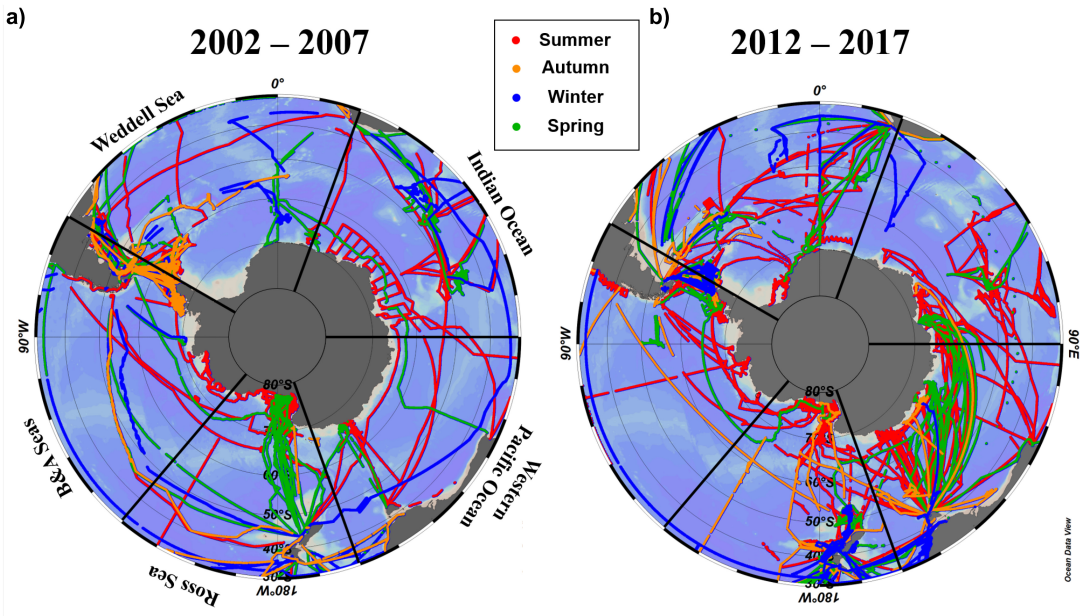


FIGURE 4 | Distribution of seasonal pCO_2 observational data used here from SOCAT version 2019 (Bakker et al., 2016) for **(a)** 2002–2007 and **(b)** 2012–2017. The seasonal periods computed were austral summer (JFM; red trajectories), autumn (AMJ; orange trajectories), winter (JAS; blue trajectories) and spring (OND; green trajectories).

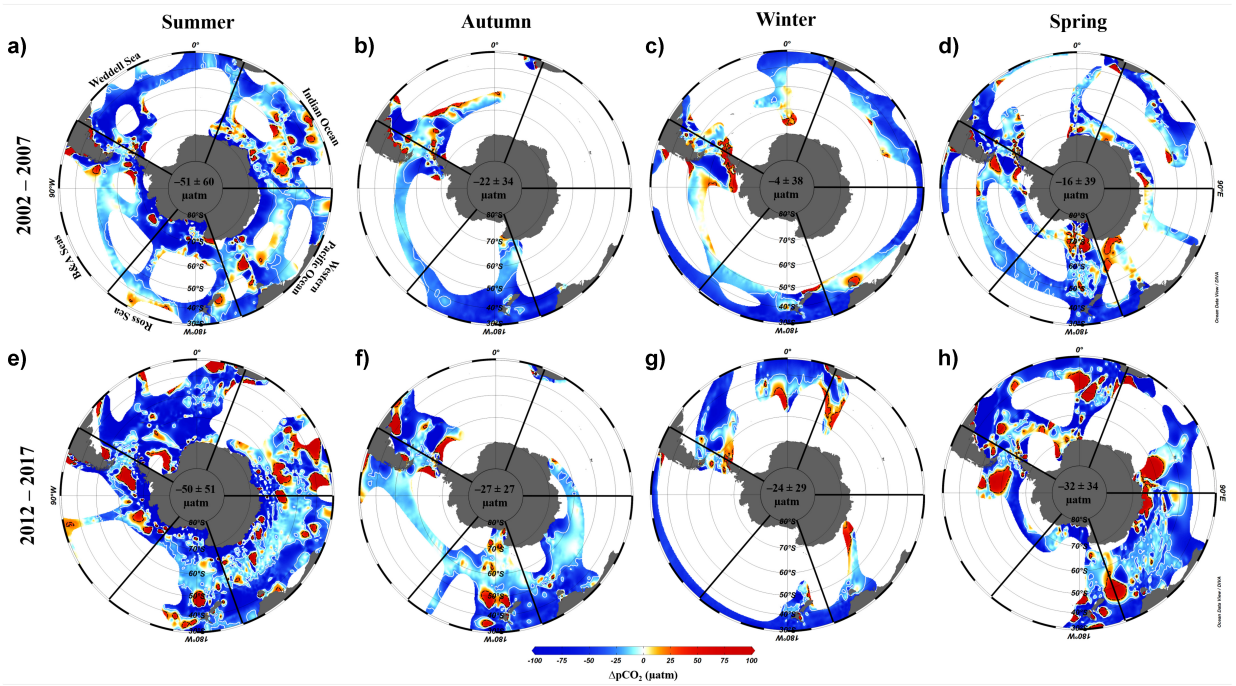


FIGURE 5 | Difference between the pCO_2 of the ocean and atmosphere (ΔpCO_2, µatm) by season for two composited periods: **(a–d)** 2002–2007 and **(e–h)** 2012–2017. The maps were produced using Data-Interpolating Variational Analysis (DIVA; 10 × 10 per mille) in the Ocean Data View software (Schlitzer, 2018). Seasonal ΔpCO_2 was computed using publicly available data from SOCAT version 2019 (Bakker et al., 2016). Atmospheric pCO_2 was determined using monthly averaged values obtained by Palmer, Halley, Syowa and South Pole meteorological stations on Antarctica (https://www.esrl.noaa.gov/gmd/dv/site/?stacode=none). The white and black isolines depict the ΔpCO_2 values of –25 and +25 µatm, respectively. The mean and standard deviation of ΔpCO_2 for the entire area for each season is shown in the centre of each map. The Southern Ocean sectors are named as: Weddell Sea, Indian Ocean, Western Pacific Ocean, Ross Sea, and Bellingshausen and Amundsen Seas. The seasonal periods computed were austral summer (JFM), autumn (AMJ), winter (JAS), and spring (OND).

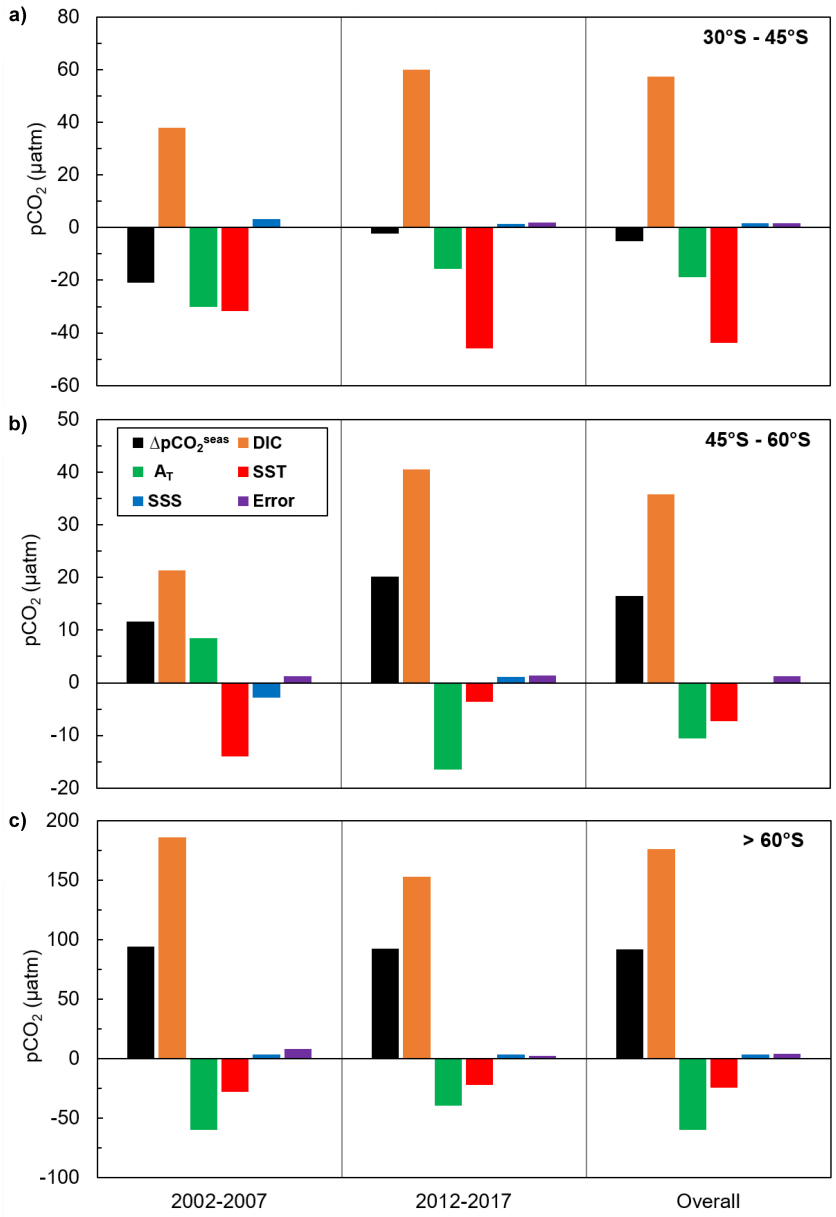


FIGURE 6 | Effects of seasonal variation in DIC, total alkalinity (A_T), temperature (SST) and salinity (SSS) on the seasonal variation in seawater pCO_2 for each latitudinal zone of the Southern Ocean for 2002–2007 and 2012–2017: **(a)** 30–45°S, **(b)** 45–60°S, and **(c)** >60°S. The seasonal variation in each parameter is calculated as the difference between the winter (JAS) mean value and the summer (JFM) mean value. The unit of all drivers is the same as the unit of pCO_2 (µatm), and their magnitudes represent their influence on seasonal pCO_2 changes (ΔpCO_2^{seas}), from summer to winter. Positive values indicate that an increase in the parameter led to an increase in pCO_2; negative values indicate that a decrease in the parameter led to a decrease in pCO_2. The only exception to this is alkalinity because an increase in alkalinity leads to a decrease in pCO_2 and vice versa. The error bars (purple) show the difference in seasonal variation between the sum of all drivers and pCO_2, indicating the extent to which the decomposition of pCO_2 into its drivers differs from the actual seasonal variation in pCO_2 (ΔpCO_2^{seas}).

between sectors across seasons and some sectors show net CO_2 release (positive ΔpCO_2) during winter (**Table 2**). For example, net CO_2 release is identified along the WAP during the austral winters of both time periods, and for distinct regions of the Western Pacific sector in all seasons for 2012−2017 (**Figure 5**). In addition, the ΔpCO_2 distribution appears to show a zone with values close to zero at approximately 50−60°S. Although this zone has been described as circumpolar (Takahashi et al., 2012), it is not clear in the Weddell Sea sector, especially considering the increased data coverage for 2012−2017. Our analysis reveals no clear trend in ΔpCO_2 overall between 2002−2007 and 2012−2017, consistent with equivalent increases in atmospheric and surface water pCO_2, and thus an increase in CO_2 sink strength, since the early 2000s (Landschutzer et al., 2015), as well

TABLE 2 | Regional average ± standard deviation of the pCO_2 difference between the surface ocean and atmosphere (ΔpCO_2), by season for two composited time periods: 2002–2007 and 2012–2017.

Season	Time Period	Southern Ocean sectors				
		Weddell Sea	Indian Ocean	Western Pacific Ocean	Ross Sea	Bellingshausen and Amundsen Seas
Summer	2002–2007	−56 ± 64	−32 ± 34	−24 ± 24	−55 ± 62	−64 ± 71
Autumn		−7 ± 31	No data	−40 ± 21	−35 ± 16	−10 ± 35
Winter		7 ± 28	−35 ± 16	−36 ± 20	−39 ± 20	15 ± 36
Spring		−3 ± 34	−34 ± 22	−18 ± 36	−20 ± 44	−11 ± 40
Summer	2012–2017	−54 ± 38	−47 ± 42	−35 ± 37	−52 ± 45	−71 ± 81
Autumn		−31 ± 42	−23 ± 13	−35 ± 21	−36 ± 19	−6 ± 25
Winter		−16 ± 30	7 ± 16	−37 ± 28	−25 ± 29	5 ± 31
Spring		−29 ± 29	−2 ± 32	−26 ± 27	−56 ± 23	−18 ± 45

Units are μatm; negative values indicate CO_2 uptake, positive values indicate CO_2 release.

as substantial variation in ΔpCO_2 changes between sectors and seasons (**Table 2**).

Changes in surface water pCO_2, and therefore ΔpCO_2 and sea-air CO_2 fluxes, are driven by biological and physical processes acting simultaneously. Whilst it is difficult to separate the biological and thermal effects, examining the seasonal changes in DIC, total alkalinity and sea surface temperature and salinity can inform our understanding of the biological and solubility pump contributions to Southern Ocean CO_2 uptake. **Figure 6** shows the influence of seasonal changes in DIC, alkalinity, temperature and salinity on seasonal changes in seawater pCO_2 in three latitudinal bands in 2002–2007 and 2012–2017 (after Takahashi et al., 2014; see **Supplementary Information 3** for details). Between 30 and 45°S, DIC and temperature exert a similar influence on pCO_2, indicating that seasonal changes in DIC driven by biological uptake in the summer and upwelling in winter are approximately balanced by seasonal changes in temperature and their control on the solubility pump. South of 45°S, and particularly in the Antarctic Zone south of 60°S, DIC and alkalinity exert a much stronger influence on pCO_2 than temperature. As the influence of DIC is almost three times that of alkalinity, this is most likely to reflect the role of biological activity in spring and summer. Upwelling increases DIC around the Sub-Antarctic Front especially in winter, but the effect of this on pCO_2 is partially compensated by the reduction in pCO_2 driven by wintertime cooling and the increase in alkalinity. These results suggest that the contributions of biological and solubility pump processes to seasonal changes in pCO_2 across the Southern Ocean are similar in magnitude for the time periods examined. Whilst it remains challenging to separate fully the effects of biological and solubility pump processes on DIC, alkalinity, temperature and salinity, and therefore pCO_2, our findings are in agreement with previous studies assessing the magnitude of the two sinks. Estimates of net community production (NCP) over a large area of the Southern Ocean (38–55°S, 60°W–60°E) based on observations and modelling suggest that biological carbon uptake accounts for a sink of 0.2 Pg C $year^{-1}$ (Merlivat et al., 2015). Compared to a total Southern Ocean (south of 35°S) sea-air CO_2 flux of –0.75 ± 0.22 Pg C $year^{-1}$ (Bushinsky et al., 2019), this suggests that the biological and solubility pumps account for a similar proportion of circumpolar CO_2 uptake. A modelling study comparing outputs from different marine ecosystem and general circulation models also shows that biological and physical forcings of pCO_2 are of the same order of magnitude for the Southern Ocean south of 44°S (Hauck et al., 2015).

CHANGES IN THE BIOLOGICAL CARBON PUMP

Key Controls on Biological Carbon Uptake and Export

The important contribution of biological carbon uptake, export and storage in organisms to the Southern Ocean carbon sink is strongly influenced by primary and secondary production. Although primary production is limited by iron availability over much of the Southern Ocean (Sections "Changes in Primary Production and Phytoplankton Species Composition" and "Changes in Micronutrient Biogeochemistry"), hotspots of productivity around and downstream of sub-Antarctic islands and submerged plateaus (e.g., South Georgia, Kerguelen, Crozet), and in upwelling and mixing zones, coastal/shelf areas and the sea ice zone where iron is not limiting can lead to substantial export of organic carbon to deep waters and/or sediments. Primary production and carbon export are particularly high in the Atlantic sector (**Figure 7a**) due to enhanced iron supply from upstream land masses (Patagonia, Falkland/Malvinas Islands, South Georgia and the WAP).

Phytoplankton species composition exerts an important control on the biological pump, with diatoms being exported quickly and promoting export compared to smaller non-diatom phytoplankton, due to their large size and ballasting by biogenic silica (Buesseler, 1998; Ducklow et al., 2001; Armstrong et al., 2009). As such, sinking diatoms are important vectors transporting organic carbon to the deep Southern Ocean (e.g., Cavan et al., 2015), with burial of whole diatoms in sediments emphasising their importance (Armand et al., 2008) and showing that they were exported directly rather than being consumed. Diatoms can escape predation after a spring bloom by transforming into resting spores that sink rapidly to the deep before returning to the surface as viable cells after winter, but

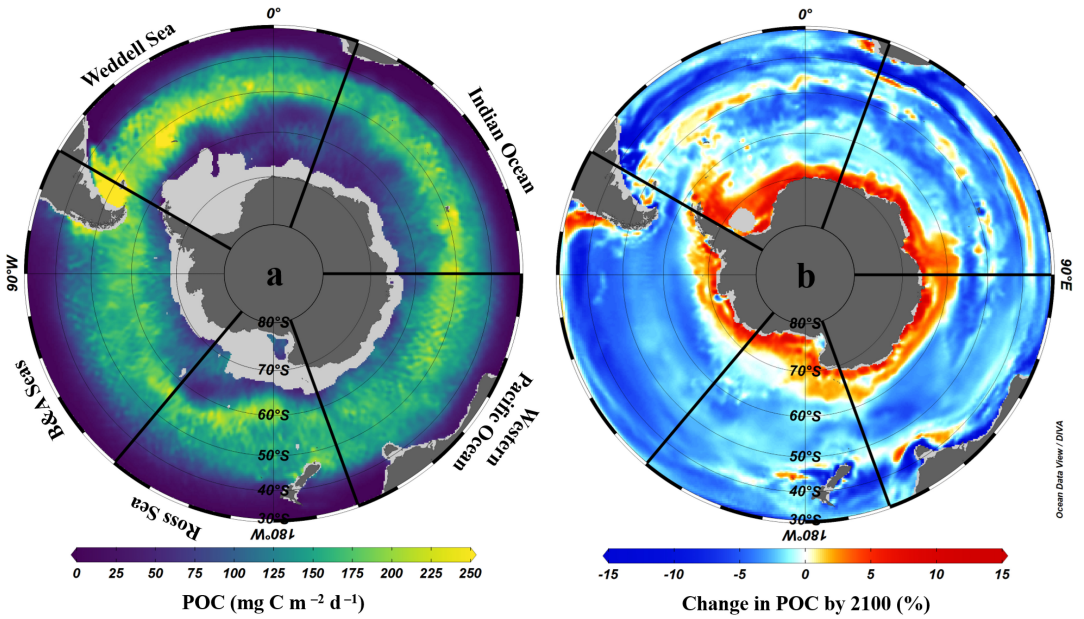


FIGURE 7 | Mean annual POC export at 100 m across the Southern Ocean; **(a)** present day (2003–2016) from LIDAR data using the Britten et al. (2017) algorithm as in Arteaga et al. (2018) and **(b)** mean change by the year 2100 according to eight CMIP5 models following methods used in Cavan et al. (2019b). Data are interpolated using the DIVA method in Ocean Data View software (Schlitzer, 2018), with scale-length for Y and X of 2 per mille. The Southern Ocean sectors are named as: Weddell Sea, Indian Ocean, Western Pacific Ocean, Ross Sea, and Bellingshausen and Amundsen Seas.

many do not return and instead remain at depth contributing to longer-term carbon storage (Rembauville et al., 2018).

Zooplankton faecal pellets also often dominate the biological carbon sink in the Southern Ocean (Cavan et al., 2015). *Euphausia superba* (Antarctic krill) are particularly prevalent in the Atlantic sector, where their swarms can release huge numbers of faecal pellets of up to 0.04 Gt C year^{-1} (Belcher et al., 2019). Whilst a large contribution of faecal pellets to sinking material can result in a large carbon flux to depth, flux efficiency varies substantially because pellets can be broken up easily before they reach the deep sea (Iversen and Poulsen, 2007). For instance, at one site near the Kerguelen Islands, in the Indian sector, only 17% of the exported material sank below 400 m even though copepod faecal pellets dominated the flux at this depth (72%) (Laurenceau-Cornec et al., 2015). Conversely at a nearby site, 58% of export reached 400 m with a more even distribution between phytoplankton and faecal pellet components (48% pellets), because primary production was dominated by large fast-sinking diatoms, which escaped grazing by copepods (Cavan et al., 2019b). This emphasises the importance of both phytoplankton and zooplankton species composition in Southern Ocean carbon export and its complex variability in time and space.

Organic matter recycling via the microbial loop reduces substantially the amount of carbon available for export and consumption by higher trophic levels (Azam et al., 1991; Azam, 1998; Sailley et al., 2013). Interactions between bacteria and viruses have been shown to contribute to these recycling processes and the resultant regeneration of nutrients including iron (Evans et al., 2009; Evans and Brussaard, 2012), as well as producing refractory dissolved organic matter, which is largely inaccessible to biological uptake by organisms (Weinbauer et al., 2011; Weitz and Wilhelm, 2012). Whilst these interactions reduce the export of particulate organic carbon, as well as carbon storage within the food web (Section "Carbon Transfer and Storage in Pelagic and Benthic Food Webs"), the large pool of refractory dissolved organic matter in the deep ocean derived from this microbial carbon pump constitutes an important carbon sink (Jiao et al., 2010; Jiao et al., 2011) that is poorly quantified and warrants further investigation.

Future Changes in Biological Carbon Uptake and Export

Changes in primary production have a direct and significant impact on biological carbon uptake. As such, changes in carbon export across the Southern Ocean are likely to follow trends in primary production, with an overall increase over the 21st century, in contrast to reductions at the global scale (Cabré et al., 2015; Moore et al., 2018). Consistent with projections of primary production (Section "Changes in Primary Production and Phytoplankton Species Composition;" Pinkerton et al., to be published in this research topic), CMIP5 model simulations project, on average, increases in carbon export in the Sub-Antarctic north of 50°S, particularly in the Atlantic sector, and south of ∼60°S in the Antarctic Zone, particularly in the Indian sector, whilst decreases are projected between 50 and ∼60°S in the open Southern Ocean (**Figure 7b**). Documented and projected increases in primary production and export for the Southern Ocean as a whole, and particularly in regions

where mode, intermediate and deep waters form and where net CO_2 uptake is already observed, suggest an increase in its capacity for biological CO_2 uptake (Del Castillo et al., 2019). This would be compounded by a projected increase in the Revelle factor over the 21st century, which increases CO_2 uptake for a given amount of export production, strongly increasing the importance of the biological carbon pump across the Southern Ocean (Hauck and Völker, 2015; Hauck et al., 2015). Increases in export are driven primarily by phytoplankton responses to increased iron inputs, shallowing mixed layers and ocean warming, both in terms of community growth rates and thus total primary production, and species composition (Cabré et al., 2015; Leung et al., 2015; Fu et al., 2016; Boyd, 2019). Some models predict that diatoms will be favoured by increased nutrient availability in Southern Ocean surface waters driven by increasing wind stress, further enhancing export, whilst others suggest equivalent increases across phytoplankton groups because warming-induced growth rate increases become the dominant effect (e.g., Laufkötter et al., 2013, 2015).

In the coastal and shelf areas, which are known to be strong local/regional CO_2 sinks (Arrigo et al., 2008b; Mu et al., 2014; Brown et al., 2019; Monteiro et al., 2020), carbon uptake may be further enhanced by increasing glacial meltwater inputs (Cook et al., 2016), because surface water cooling and freshening can augment the solubility pump, in addition to increased iron supply and primary production (Gerringa et al., 2012; Sherrell et al., 2015; Annett et al., 2017; Monteiro et al., 2020). Changes in sea ice dynamics are also likely to influence carbon uptake, because longer ice-free growing seasons and/or more stratified upper ocean conditions promote the development of phytoplankton blooms that drive the biological pump (Montes-Hugo et al., 2009; Venables et al., 2013; Moreau et al., 2015; Costa et al., 2020).

Changes in phytoplankton species composition and size distribution may reduce the efficiency of the biological pump, and thus complicate our understanding of future changes to the Southern Ocean CO_2 sink (e.g., Passow and Carlson, 2012; Laufkötter et al., 2013). At the WAP, some local increases in primary production and changes in phytoplankton development are linked to sea ice declines, increasing glacial meltwater inputs, ocean warming and freshening (Schloss et al., 2014; Hernando et al., 2015; Moreau et al., 2015; Rogers et al., 2020), and have led to a fivefold increase in summertime CO_2 uptake along the shelf in recent decades (Brown et al., 2019). However, interannual variability is pronounced, and ongoing and projected species shifts towards smaller non-diatom phytoplankton could reduce export substantially by lowering the export efficiency as well as primary production (Montes-Hugo et al., 2008, 2009; Mendes et al., 2012, 2018; Rozema et al., 2017; Schofield et al., 2017). An overall decline in biological carbon uptake has thus been hypothesised for the coming decades, in response to the continued warming and sea ice declines expected throughout the WAP region (e.g., Laufkötter et al., 2013; Brown et al., 2019). Even in regions where diatom communities thrive, reductions in diatom silica production and shifts toward smaller species with thinner shells in response to ocean acidification could reduce diatom sinking rates and diminish carbon export efficiency in the coming decades (Petrou et al., 2019). In the ACC, projected increases in iron supply could increase the amount of carbon exported with the sinking diatom flux (Assmy et al., 2013), partially offsetting the reduction in export efficiency associated with acidification, although the relative strength of these effects is unknown.

Amongst CMIP5 models, there is an order of magnitude difference in projected phytoplankton growth rates as well as spatial differences in carbon export, with some models projecting increases across the entire Southern Ocean and others suggesting increases in the marginal and seasonal ice zones but declines in the HNLC Sub-Antarctic (Bopp et al., 2013; Hauck et al., 2015; Laufkötter et al., 2016). Major uncertainties arise from future changes in the efficiency of the microbial loop, in particular the role of bacteria−virus interactions, and the impact of environmental changes on the coupling of phytoplankton and zooplankton dynamics and consequences for export. Although there is greater disparity among climate models in biological projections than in projections of nutrient distributions globally, increases in Southern Ocean primary production and carbon export are expected overall, with the potential to increase the relative importance of the biological carbon pump (Cabré et al., 2015; Hauck et al., 2015; Laufkötter et al., 2016).

CARBON TRANSFER AND STORAGE IN PELAGIC AND BENTHIC FOOD WEBS

Carbon Fixation by Primary Producers

Carbon uptake and storage by organisms in the Southern Ocean are dominated by coastal and shelf ecosystems, the marginal ice zone and downstream of Sub-Antarctic islands (e.g., Bakker et al., 2007; Blain et al., 2007; Arrigo et al., 2008a,b; Jones et al., 2012; Hoppe et al., 2017). Most carbon uptake is by phytoplankton through primary production when light and nutrients are sufficient, and carbon is stored by animal components of the food web. The major contribution of large diatoms to primary production and phytoplankton biomass, and the regional, seasonal and interannual variability in phytoplankton species composition (Section "Changes in Primary Production and Phytoplankton Species Composition"), influence the degree and duration of carbon uptake and storage within the ecosystem. Macroalgae are also important primary producers in coastal areas, and new evidence shows that macroalgal organic matter reaches the open ocean and the deep sea in several ocean basins, including the Southern Ocean (Ortega et al., 2019). Whilst carbon uptake by primary production is similar in magnitude to the direct uptake of CO_2 by solubility pump processes across the Southern Ocean (Section "Changes in the Southern Ocean Carbon Sink"), transfer of carbon fixed during primary production into heterotrophic organisms can lead to rapid sequestration, adding to the complete removal of carbon from cycling, through burial in sediments or storage as refractory carbon in the deep ocean. The immediate fate of primary production is an important food web step in determining the ultimate fate of carbon (sequestration or recycling), transfer efficiency and pathway, yet the relative proportions of these fate paths are poorly constrained.

Fate Pathways of Primary Production

Phytoplankton carbon can either be sequestered directly, broken down by microbes or eaten by pelagic animals, whose faecal pellets may eventually reach the seafloor, or by benthic consumers. Estimates of the proportion of primary production following each of these fate paths vary considerably between studies, depending on region, timescale and the number of these paths examined. **Figure 8** presents a broad overview of the approximate mean percentages across large spatial and temporal scales. Approximately 1% is sequestered directly by sinking to and burial in the seabed, avoiding complete microbial breakdown in the water column and oxygenated seafloor (Ducklow et al., 2007). This is hugely variable; for example, there is more than an order of magnitude variation between years in estimates of how much primary production reaches the WAP shelf floor (from <0.2 to 4 g C m^{-2} $year^{-1}$; Ducklow et al., 2007). Approximately half of global primary production is broken down by microbial processes in the water column or on the seabed (Azam, 1998). In the cold Southern Ocean, microbial cycling and bacterial production may be slower than elsewhere, but can account for a large proportion of primary production and contribute significantly to food web dynamics by cycling organic matter and regenerating nutrients (Azam et al., 1991; Sailley et al., 2013). Enhancement of the microbial loop by bacteria-virus interactions has also been observed in the Southern Ocean (Evans et al., 2009; Evans and Brussaard, 2012).

The second largest carbon fate is grazing by zooplankton (micro-, meso- and macrozooplankton), of which annual production can account for up to 80% of primary production (Hill et al., 2012; Garzio et al., 2013; Sailley et al., 2013; Murphy et al., 2016; Moreau et al., 2020). Consumption by benthic animals is the carbon fate characterised by the highest diversity (many animal phyla) and richness (tens of thousands of species), and has been estimated to account for up to 18% of primary production (Barnes, 2017). The nature of animal production in the water column and seabed, and therefore carbon pathways, is strongly influenced by the timing, duration and composition of the phytoplankton bloom (as well as by other factors such as sea ice). For example, *E. superba* typically prefer larger diatoms over small phytoplankton (Quetin and Ross, 1985; Haberman et al., 2003; Bernard et al., 2012), and have also been shown to graze on copepods, microzooplankton and even salps (Price et al., 1988; Atkinson and Snyder, 1997; Schmidt et al., 2006; Dubischar et al., 2012). Microzooplankton can consume almost the full range of phytoplankton size classes (Klaas, 1997; Calbet and Landry, 2004), whilst salps are non-selective filter feeders on phytoplankton as well as microzooplankton and small copepods (Bernard et al., 2012). In contrast, nanophytoplankton are preferred by benthic suspension feeders (Barnes and Clarke, 1995).

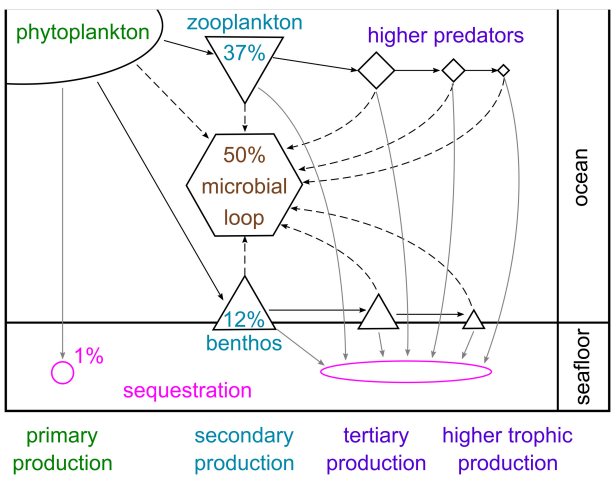


FIGURE 8 | Schematic representation of carbon flows through pelagic and benthic food webs in the Southern Ocean. The percentages given represent approximate mean proportions of total primary production sequestered in the sea floor, broken down via the microbial loop and consumed by zooplankton and benthic consumers, based on several studies from high-productivity shelf environments and the wider literature (Azam, 1998; Ducklow et al., 2007; Hill et al., 2012; Garzio et al., 2013; Sailley et al., 2013; Ballerini et al., 2014; Murphy et al., 2016; Barnes, 2017).

Strong regional and onshore-offshore differences in grazing and retention of organic carbon in euphotic surface waters show that the location of consumption also affects carbon fate (Gleiber, 2015). The type of animal consuming phytoplankton has important consequences for faecal and carcass sinking rates, and hence likelihood of reaching the seabed (carbon sequestration), support for higher trophic levels (food web carbon storage), growth rates and longevity (storage and sequestration). Larval krill are abundant at the WAP and near sea ice because sea ice provides protection from predators and an important overwintering food source of ice-derived organic material (Meyer et al., 2017). Faecal pellets of larval krill are smaller and contain less carbon than those of adults, but deeper diel vertical migrations by larvae (∼400 m) than adults (∼200 m) (Tarling et al., 2018) mean their faeces has a higher chance of reaching the sea floor (Cavan et al., 2019a). On the sea floor, the quantity and quality of the food supply from overlying waters varies considerably between the shallow coastal areas and the deep shelf, with annual accumulation of carbon by benthos at 500 m being only 10% of that at 25 m along the WAP (Barnes, 2017). Animals at slope, abyssal and deep-shelf depths are not in direct contact with the phytoplankton bloom, so are more likely to be dominated by deposit feeders and their predators.

Carbon Storage in Pelagic and Benthic Consumers

The animal pathway beyond primary consumption is typically short, but still supports considerable abundances of up to four trophic levels (Gillies et al., 2013), much of which hinges around *E. superba* as a key consumer. The number of trophic levels has a direct effect on the amount of carbon (or energy) stored in a food chain (Dickman et al., 2008), whilst the duration of carbon storage depends on the life spans of consumers. In the Atlantic sector, a highly efficient pelagic food chain consists of only three trophic levels: diatoms, krill and baleen whales (Tranter, 1982; Smetacek, 2008). Baleen whales found in the Southern Ocean are

slow-growing and can have long life spans of up to 90 years. In the Atlantic sector, blue and fin whales feed predominantly on krill, and with mean weights of ∼90 and ∼50 tonnes, respectively, store a huge amount of carbon as organic mass for almost a century (Laws, 1977). After death, most whales' carcasses sink to the sea floor, providing a rich food source for many benthic and deep-sea organisms. Microbes also decompose organic material from the whale fall, releasing large amounts of nutrients, and respired CO_2 and potentially refractory dissolved organic carbon are locked in the deep ocean for decades or even centuries (Jiao et al., 2010; Cavan et al., 2019a). Elsewhere in the Southern Ocean, such as in the central Indian sector, *E. superba* are important but do not dominate the ecosystem as they do in the Atlantic (Everson, 2000; McCormack et al., to be published in this research topic). Near Prydz Bay, cephalopods dominate the food web, with most carbon cycling through them to sperm whales and leopard seals (McCormack et al., 2019). This constitutes a longer food chain of at least five trophic levels: phytoplankton, copepods, krill, cephalopods and sperm whales or seals. Less carbon is stored in this pathway due to multiple trophic transfers and because the top predators are smaller (sperm whales weigh ∼30 tonnes and seals weigh ∼0.3 tonnes) and die younger than blue or fin whales, such that carbon may only be stored for a few decades (Laws, 1977). Smaller mammals may also sink more slowly and be less likely to reach the deep ocean, although more research into this topic is required.

Climate Change Impacts on Food Webs and Carbon Uptake and Storage

There is emerging evidence of climate forcing on Southern Ocean food webs, with complex effects on species and trophic interactions (e.g., Henley et al., 2019). Projected increases in primary production (Section "Changes in Primary Production and Phytoplankton Species Composition") are likely to be beneficial for pelagic and benthic consumers, with shifts in phytoplankton species composition favouring certain consumers and disadvantaging others. At the WAP, pronounced interannual variability in primary production, with some local increases, and changes in phytoplankton species composition (e.g., Schloss et al., 2014; Moreau et al., 2015; Kim et al., 2018) have strong implications for krill and other zooplankton (e.g., Steinberg et al., 2015). For example, summers characterised by large diatom-dominated phytoplankton blooms, associated with long-lived winter sea ice cover and stratified surface waters in spring and summer, lead to strong krill recruitment the following summer (Saba et al., 2014). Long-term sea ice declines and ongoing shifts toward smaller phytoplankton could thus drive reductions in krill populations (Saba et al., 2014). At the larger scale, there is significant debate in the scientific literature regarding decadal trends in the distribution and density of krill populations and their drivers (Johnston et al., to be published in this research topic, and references therein). There is evidence for krill populations in the southwest Atlantic sector declining and/or shifting their distribution southward, related to wintertime sea ice cover particularly in the important spawning and nursery areas around the WAP and Southern Scotia Arc, with potential linked increases in salp abundance (Atkinson et al., 2004, 2019; Hill et al., 2019). However, other studies suggest important spatial differences in observed patterns of krill variability and change, and potentially a more stable trajectory overall (Cox et al., 2018; Johnston et al., to be published in this research topic, and references therein). If krill declines are real and sustained, there could be significant disruption to higher predators as well as ecosystem functions such as ocean fertilisation and carbon cycling and storage (Dubischar et al., 2012; Alcaraz et al., 2014; Atkinson et al., 2019; Cavan et al., 2019a). Amongst benthos, both sea ice losses and ice shelf disintegration have had pronounced effects on production and carbon storage over the last two decades. New and longer phytoplankton blooms (Schloss et al., 2014; Moreau et al., 2015; Kim et al., 2018) have increased benthos growth overall despite decreased growth in the shallows due to increased iceberg scour (Barnes et al., 2018). More than a doubling of carbon storage with recent sea ice losses suggests a rare and powerful short-term negative feedback on climate by Southern Ocean biota (Peck et al., 2010; Barnes et al., 2018), although the persistence of this trend is in doubt (Brown et al., 2019).

EXCHANGE AND REDISTRIBUTION OF CARBON AND NUTRIENTS BY ANIMALS

Benthic-Pelagic Coupling and Water Column Transports

Coupling of benthic and pelagic ecosystems through a range of biological and physical processes plays a key role in modulating biogeochemistry and ecological function in the Southern Ocean. Nutrient recycling within and release from sediments, particularly of iron, and subsequent delivery to euphotic surface waters via lateral and vertical transport, is a key benthic-pelagic coupling mechanism sustaining food webs. Benthic iron fluxes are largest in continental shelf and slope regions, but can also be important in the deep Southern Ocean, and are regulated by organic carbon oxidation rates in sediments and bottom water oxygen concentrations (Tagliabue et al., 2009a; De Jong et al., 2012; Dale et al., 2015). Nutrient transport within the pelagic realm between the deeper waters, enriched with macro- and micronutrients (i.e., iron) as a result of water column remineralisation of organic matter, and the surface waters is also critical for ocean productivity and ecosystem function (Sections "Changes in Primary Production and Phytoplankton Species Composition," "Changes in Micronutrient Biogeochemistry," and "Changes in Macronutrient Biogeochemistry"). There is a growing body of evidence for krill, whales and other higher organisms enhancing the transport of these nutrients regenerated in the subsurface, deep waters and sediments into surface waters (e.g., Schmidt et al., 2011; Ratnarajah et al., 2014).

Nutrient Recycling and Redistribution by Animals

Krill have been shown to release dissolved iron, ammonium and phosphate through grazing and excretion processes

(Tovar-Sanchez et al., 2007; Ratnarajah et al., 2014; Schmidt et al., 2016), each providing a nutrient source to phytoplankton blooms (Atkinson and Whitehouse, 2000; Ariśtegui et al., 2014). Copepods also play an important role in regenerating and retaining iron in the surface ocean through grazing and rapid recycling of faecal pellets (Sarthou et al., 2008; Laglera et al., 2017). Whales produce iron-rich faeces, which constitute a highly concentrated, albeit highly localised, iron source (Nicol et al., 2010; Lavery et al., 2014). Recycling of iron is particularly important in the iron-limited regions of the Southern Ocean, and release by krill, other zooplankton, marine mammals and seabirds in the upper layers could stimulate phytoplankton productivity (Nicol et al., 2010; Ratnarajah et al., 2018; Cavan et al., 2019a). For instance, sperm whales have been shown to increase carbon export in the Southern Ocean, as primary production and carbon export stimulated by their faecal iron supply to surface waters exceeds their respiration by an estimated 200,000 t C $year^{-1}$ (Lavery et al., 2010).

Southern Ocean organisms are also important as transporters and redistributors of the nutrients that they recycle, depending on their migration and feeding behaviours (Ratnarajah et al., 2018). Krill and other zooplankton species that undergo daily (diel) vertical migrations between surface waters where they feed and deeper waters where they avoid predation (Hernández-León et al., 2001; Tarling et al., 2018) can transfer significant quantities of carbon and nutrients to the deep ocean, via defecation of organic matter as faecal pellets and release of CO_2 at their deep resting depths (Cavan et al., 2015; Belcher et al., 2017). Similarly, zooplankton species such as copepods that migrate seasonally between food-rich surface waters in spring/summer and deeper waters below the permanent thermocline in winter also transport carbon and nutrients to depth via net consumption in surface waters and net respiration at depth (Lee and Hagen, 2006; Jónasdóttir et al., 2015). Conversely, krill that live and feed at the seafloor may transfer nutrients, particularly iron, to the surface from benthic environments (Schmidt et al., 2011). Marine mammals, seabirds and squid that feed at depth can transport iron and other nutrients into the euphotic zone, where their release can stimulate phytoplankton growth (Ratnarajah et al., 2018 and references therein). Nutrient recycling through krill and other organisms in water masses that are transported north from the Southern Ocean may also impact organisms in the lower latitudes (Cavan et al., 2019a).

Land-Ocean Nutrient Transfer

Seals, penguins and other seabirds play an important role in transporting carbon, nitrogen and phosphorus from the ocean into terrestrial environments of the sub-Antarctic islands and Antarctica (Moss, 2017 and references therein). There is also evidence for nutrient supply, including iron, to coastal marine environments from seals and seabirds and their colonies in the Sub-Antarctic via faecal material and run-off from guano deposits (Wing et al., 2014; Treasure et al., 2015). Whilst these nutrient fluxes are small in the context of Southern Ocean biogeochemistry, they can be important locally for fertilising coastal phytoplankton blooms and macroalgal production, thus supporting nearshore ecosystems and benthic food webs in particular.

Turbulent Mixing by Animals

In addition to biological recycling and redistribution of nutrients by animals, large planktonic migrations consisting of many thousands of individuals have the potential to bring nutrient-rich waters from depth towards the surface by stimulating physical mixing of the water column. This has been shown in jellyfish swarms (Katija and Dabiri, 2009) but is yet to be studied in krill or other zooplankton, although mixing between density layers has been shown by brine shrimp in laboratory experiments (Houghton et al., 2018). The high abundance of *E. superba*, their relatively large size (up to 6 cm) and large migrations suggest that they could promote physical mixing and vertical nutrient transport in the Southern Ocean (Tarling and Thorpe, 2017; Cavan et al., 2019a). The contribution of these migratory behaviours to total nutrient transfer is not well constrained, and should be prioritised for future research in order to assess its role now and in the future under climate change.

OCEAN ACIDIFICATION AND ITS EFFECTS ON THE ECOSYSTEM

Ocean Carbonate Chemistry and Acidification

Uptake of CO_2 into the Southern Ocean by biological and solubility pump processes is modifying ocean chemistry and driving ocean acidification. Ocean acidification is a climate change issue impacting marine biota, marine ecosystem functioning (Fabry et al., 2008; Guinotte and Fabry, 2008), and potentially marine ecosystem services at the global scale (Cooley et al., 2009). Increasing oceanic CO_2 concentrations in response to increasing atmospheric CO_2 are altering the equilibrium between the carbonate system parameters (pCO_2, DIC, total alkalinity and pH), leading to reductions in the pH and carbonate ion concentration of seawater (Doney et al., 2009; Feely et al., 2009). Carbonate ion availability is essential for marine organisms that build their shells and skeletons out of aragonite, a metastable form of calcium carbonate, such that lowering the seawater carbonate ion concentration has adverse effects on vital processes and survival of a large number of organisms. The aragonite saturation state (Ω) is a measure of the seawater carbonate ion concentration relative to aragonite at equilibrium, with a critical threshold of $\Omega = 1$ below which seawater is undersaturated with respect to aragonite and can become corrosive to the shells and skeletons of marine organisms. The Southern Ocean is expected to experience aragonite undersaturation earlier than most other oceans (except the Arctic), particularly during winter, due to its large uptake of atmospheric CO_2 and because its carbonate ion concentration is already low due to low temperatures and upwelling of CO_2-rich deep waters (Orr et al., 2005; McNeil and Matear, 2008; Feely et al., 2009).

Observed and Expected Southern Ocean Acidification

Decadal trends of increasing DIC, decreasing pH and/or decreasing Ω have been documented in surface and deeper

waters in a number of Southern Ocean regions, including Drake Passage (Takahashi et al., 2014; Munro et al., 2015), the coastal northern WAP (Lencina-Avila et al., 2018), the Weddell Sea (Hauck et al., 2010; Van Heuven et al., 2014), and the Pacific sector (Midorikawa et al., 2012; Williams et al., 2015). Aragonite undersaturation has been observed in the Southern Ocean, and is caused by upwelling of deeper waters, advection of waters enriched with anthropogenic carbon and/or *in situ* uptake of atmospheric CO_2 (Bednarsek et al., 2012; Jones et al., 2017; Kerr et al., 2018). Model simulations project a rapid spread and increased duration of aragonite undersaturation events around 2030, affecting ∼30% of Southern Ocean surface waters by 2060 (Hauri et al., 2016). However, the combined effects of multiple natural and anthropogenic drivers (e.g., warming, freshening, meltwater inputs, oceanic water intrusions, sea-air CO_2 exchange) on the carbonate equilibrium may partially offset the trends in acidification and aragonite undersaturation and their effects in Antarctic coastal and oceanic regimes (McNeil et al., 2010; Lencina-Avila et al., 2018).

Effects of Ocean Acidification on Organisms and Ecosystem Functioning

Direct and indirect effects of ocean acidification on the Southern Ocean food web are increasingly well-documented, with benefits for some organisms and disadvantages for others. Ross Sea phytoplankton communities have been observed to shift their species composition from *P. antarctica* or pennate diatoms at low CO_2 to large centric chain-forming *Chaetoceros* diatoms at higher CO_2 (Tortell et al., 2008; Feng et al., 2010). This is consistent with increased growth rates of *C. debilis* in experiments with high pCO_2 (Trimborn et al., 2013). In contrast, high CO_2 in coastal East Antarctica has been shown to reduce primary production and favour small diatoms ($\leq$20 μm) over large diatoms and *P. antarctica*, indicating regional variation in the phytoplankton response to acidification (Hancock et al., 2018; Westwood et al., 2018). Primary production, biomass accumulation and nutrient uptake rates declined significantly above a threshold of pCO_2 three times higher than ambient levels, although photosynthetic performance showed evidence of acclimation to high CO_2 over time (Deppeler et al., 2018). Ocean acidification has also been shown to reduce diatom silica production directly at a lower threshold than diatom growth, by reducing both the cell-specific rates of silica precipitation and the relative abundance of larger species with thicker denser shells (Petrou et al., 2019). Further, iron uptake by diatoms has shown sensitivity to carbonate ion availability, such that reductions in carbonate ion concentration may also have deleterious indirect consequences for diatom growth (McQuaid et al., 2018). These studies highlight the importance of species-specific CO_2 sensitivity, species interactions and physiological processes in modifying the phytoplankton response to increasing CO_2, with a high degree of complexity over a range of spatial and temporal scales leading to changes in primary production and species composition that may act synergistically or antagonistically with the effects of changes in iron, light and temperature (Section "Changes in Primary Production and Phytoplankton Species Composition").

Changes in phytoplankton dynamics associated with ocean acidification will have indirect impacts on zooplankton communities, in addition to the direct effects of acidification on a number of zooplankton species. *Limacina helicina* pteropods from the Scotia Sea have shown shell dissolution under aragonite-undersaturated *in situ* conditions (Bednarsek et al., 2012) and reduced larval survival due to decreased shell growth and increased fragility in aragonite-undersaturated experiments (Gardner et al., 2018). In contrast, *E. superba* have shown resilience to ocean acidification in laboratory simulations by maintaining the acid-base balance of their body fluids in near-future pCO_2 (Ericson et al., 2018). However, *E. superba* in the WAP region are known to increase feeding and excretion rates under high CO_2 conditions, especially pregnant females, indicating metabolic shifts consistent with increased physiological costs of maintaining their acid-base balance (Saba et al., 2012). Combined experimental and modelling approaches suggest that important *E. superba* habitats in the Weddell Sea are likely to suffer from reduced recruitment within a century, due to the sensitivity of egg hatch rates to increased CO_2 (Kawaguchi et al., 2013).

For Antarctic benthos, there is evidence for higher tolerance to ocean acidification than expected (Catarino et al., 2012; Kapsenberg and Hofmann, 2014), with increasing temperature being a more important factor (Byrne et al., 2013). Most organisms that have been studied in shallow coastal areas can acclimate to lowered pH to at least end-century conditions given sufficient acclimation periods (Cross et al., 2015; Suckling et al., 2015; Morley et al., 2016). However, shoaling of the aragonite saturation horizon (the depth above which Ω is >1 and below which waters are aragonite-undersaturated) from its current depth of ∼700 m towards the surface over the coming decades is likely to drive threshold responses in deep-shelf benthic communities, as the waters in which they reside shift from aragonite-saturated to aragonite-undersaturated (Orr et al., 2005; McNeil and Matear, 2008; Gutt et al., 2015).

The pelagic microbial community has shown sensitivity to ocean acidification, with increases in bacterial production and/or abundance observed in high-CO_2 experiments in coastal East Antarctica (Deppeler et al., 2018; Westwood et al., 2018). In Ross Sea communities, lower seawater pH reduced bacterial diversity, but increased bacterial activity and rates of carbohydrate and lipid hydrolysis and nutrient regeneration (Maas et al., 2013). These increased rates of carbon and nutrient recycling could accelerate the microbial loop and reduce the amount of organic matter available for export or consumption. Combined with the acidification-induced reduction in diatom silica production and the likely reduction in sinking rates as a result (Petrou et al., 2019), a more efficient microbial loop has the potential to partially offset the projected increases in carbon export under climate change (Cabré et al., 2015; Laufkötter et al., 2016). There remains a significant degree of uncertainty regarding the

impacts of ocean acidification on Southern Ocean food webs and biogeochemical cycling at present. Nevertheless, aragonite undersaturation is expected, with medium confidence, to play an influential role in the Southern Ocean under multiple stressors associated with anthropogenic climate change in the near future (Gutt et al., 2015).

BOX 1 | Research gaps, progress and opportunities.

Scientific understanding of the key biogeochemical processes at work across the Southern Ocean throughout the seasonal cycle is limited by inconsistent data coverage between regions and over different timescales. Coverage is particularly poor in autumn and winter, biasing our understanding towards spring/summer processes. We lack year-round quantification of CO_2 sink dynamics in both coastal and open-ocean regions, as well as an adequate understanding of the micro- and macronutrient cycling – and particularly the supply and bioavailability of iron – that regulates biological carbon uptake. Strong spatial and temporal variability in carbon and nutrient uptake and cycling, as well as the range of atmospheric, oceanic and cryospheric forcings and ongoing changes, complicate our estimates of the strength of the Southern Ocean CO_2 sink (Lovenduski et al., 2015; Ritter et al., 2017; Woolf et al., 2019) and our projections of future changes in productivity and biogeochemical cycles. Moreover, the relative biogeochemical influence of changes in phytoplankton community rates versus species shifts remains poorly understood. Current model parameterisations cannot capture the complexity associated with the phytoplankton community response to concurrent shifts in at least five influential ocean properties, including light, iron, CO_2, nutrients and temperature (Boyd et al., 2016). As such, model outcomes may change in the coming decade as mechanistic understanding and parameterisations improve.

In order to address these challenges, innovative measurement approaches must be integrated with traditional ship-based methods and satellite-based measurements to provide efficient long-term observational programmes. For example, autonomous biogeochemical floats are driving a substantial increase in spatial and temporal coverage of pCO_2, nitrate and dissolved oxygen data (Johnson et al., 2017; Bushinsky et al., 2019). A range of autonomous platforms (e.g., gliders, powered autonomous underwater vehicles, moorings) and instrumented marine mammals equipped with a growing suite of biological and biogeochemical sensors (e.g., pH, iron, nutrients, fluorescence, bio-optics, acoustics) are increasingly supporting observational programmes across Southern Ocean regions (e.g., Henley et al., 2019). Focused experiments, process studies and increased use of novel tracers (e.g., isotopes of nitrate, silicic acid and iron), alongside and complementary to long-term observations, are augmenting our mechanistic understanding of the key processes, feedbacks and changes underway. Further investigations into species and physiological shifts in phytoplankton, zooplankton, bacterial and archaeal communities, and the importance of viruses, including molecular and other omics techniques will be critical to reducing uncertainties around projected changes in productivity, ecosystem function and biogeochemical cycling. Financial and logistical challenges associated with long-term monitoring in the Southern Ocean necessitate enhanced coordination of projects and national programmes, integration, intercalibration and, where possible, standardisation of analytical techniques, and improved access to biogeochemical data (Newman et al., 2019); for example through the Southern Ocean Observing System (SOOS) data portal SOOSmap (http://www.soosmap.aq/). Assimilation of expanding observational datasets into increasingly sophisticated models will lead to substantial improvements in our understanding of decadal changes and trends. In particular, models of iron biogeochemical cycling are enhancing our ability to project change in primary production, nutrient cycling and the Southern Ocean carbon sink (Tagliabue et al., 2016; St-Laurent et al., 2019). Only by taking an end-to-end approach to examining the ecosystem and accounting for the multiple stressors acting across a range of climate change scenarios will we achieve an integrated analysis of the entire Southern Ocean, and its central role in modulating changes in global biogeochemical cycles now and into the future (Murphy and Hofmann, 2012; Constable et al., 2014).

SUMMARY AND CONCLUSIONS

This assessment of Southern Ocean biogeochemistry has assimilated existing knowledge and presented new data that show the integral role of biogeochemical cycling – of iron, carbon and major nutrients in particular – in supporting marine ecosystem functioning and regulating sea-air CO_2 fluxes at regional and global scales. Strong variability in the key processes, controls and responses exists spatially, especially between shelf and open ocean regions, and over seasonal-to-decadal timescales.

Iron supply is extremely likely to increase in polar waters proximal to the Antarctic continent and also north of 50°S. Coupled with increasing light availability, this is very likely to increase primary production and carbon export in polar waters. Production, export and total biological carbon uptake are likely to increase for the Southern Ocean as a whole, whilst there is only medium confidence in projected increases in the Sub-Antarctic due to disparity among CMIP5 models. Changes in phytoplankton species composition are associated with higher uncertainty than changes in primary production. Three new datasets show that macronutrient uptake during summer influences nutrient availability and stoichiometry year-round in the coastal Antarctic and open Southern Ocean, despite vertical mixing and nutrient regeneration. Nutrient dynamics in the Sub-Antarctic are virtually certain to regulate the nutrient supply to the global thermocline and nutrient-limited surface waters to the north, thus modulating the global biological carbon pump. New analyses of ΔpCO_2 changes show, on average, net CO_2 sink behaviour for the entire Southern Ocean across all seasons, with similar contributions from biological and solubility pump processes and stronger CO_2 uptake during summer. Ocean acidification has already been observed in some regions, with impacts on phytoplankton, microbial communities, zooplankton and other calcifying organisms, and is likely to become an important driver of Southern Ocean ecosystems in the coming decades.

Climate-driven changes in the productivity, biomass and distribution of phytoplankton, zooplankton, higher trophic level organisms and microbial communities are virtually certain to impact Southern Ocean biogeochemistry by modifying food web carbon transfer and storage, carbon export, nutrient recycling and redistribution, and benthic-pelagic coupling. In turn, changes in Southern Ocean biogeochemistry – in particular iron supply and ocean acidification – are very likely to alter productivity and function across marine ecosystem components, with important feedbacks on carbon and nutrient cycling at regional and global scales.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The new winter nutrient data from the WOCE IO6 (2017) and A12 (2019) lines presented in Section "Changes in Macronutrient Biogeochemistry" are available at https://doi.org/10.5281/zenodo.3883618.

The biogeochemical data from the Rothera Time Series programme in northern Marguerite Bay (2013−2016) presented in Section "Changes in Macronutrient Biogeochemistry" are available through the British Oceanographic Data Centre (BODC) at https://www.bodc.ac.uk/data/published_data_library/catalogue/10.5285/98cc0722-e337-029c-e053-6c86abc02029/ (Henley and Venables, 2019).

AUTHOR CONTRIBUTIONS

SH led the study and writing of the manuscript. EC, SF, RK, and TMo provided data and contributed substantially to writing the manuscript and producing the figures. RS, AB, PB, DB, and IS contributed substantially to writing the manuscript. TMa provided data and contributed to figure production and writing the manuscript. RF and SS provided data and contributed to writing the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00581/full#supplementary-material

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frontiers in Marine Science

REVIEW
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Subsurface Chlorophyll-*a* Maxima in the Southern Ocean

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Our review of the literature has revealed Southern Ocean subsurface chlorophyll-*a* maxima (SCMs) to be an annually recurrent feature throughout the basin. Most of these SCMs are different to the "typical" SCMs observed in the tropics, which are maintained by the nutrient-light co-limitation of phytoplankton growth. Rather, we have found that SCMs are formed by other processes including diatom aggregation, sea-ice retreat, eddies, subduction events and photo-acclimation. At a local scale, these SCMs can facilitate increased downward carbon export, primary production and food availability for higher trophic levels. A large proportion of Southern Ocean SCMs appear to be sustained by aggregates of large diatoms that form under severe iron limitation in the seasonal mixed layer. The ability of large diatoms to regulate their buoyancy must play a role in the development of these SCMs as they appear to increase buoyancy at the SCM and thus avoid further sinking with the decline of the spring bloom or naturally iron fertilized blooms. These SCMs remain largely unobserved by satellites and it seems that ship-based sampling may not be able to fully capture their biomass. In the context of the Marine Ecosystem Assessment of the Southern Ocean it is important to consider that this phenomenon is missing in our current understanding of Southern Ocean ecology and future climate scenarios. The broader implications of SCMs for Southern Ocean ecology will only be revealed through basin-wide observations. This can only be achieved through an integrated observation system that is able to harness the detailed information encapsulated in ship-based sampling, with the increased observational capacity of fluorometers on autonomous platforms such as those in the biogeochemical Argo (BGC-Argo) and the Marine Mammals Exploring the Ocean Pole to pole (MEOP) programs. The main challenge toward achieving this is the uncertainties associated with translating fluorescence to chlorophyll-*a* concentrations. Until this translation is resolved, the reporting of subsurface fluorescence maxima (SFMs) in place of SCMs could still yield valuable insights with careful interpretation.

Keywords: Southern Ocean, phytoplankton, chlorophyll-*a*, chlorophyll fluorescence, subsurface chlorophyll maxima

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INTRODUCTION

Southern Ocean phytoplankton are essential for Antarctic food-webs and the regulation of global climate through the marine carbon cycle (Deppeler and Davidson, 2017). Here, phytoplankton blooms are dominated by large silica-forming diatoms which have unique physiology that is adapted to the low iron, light and temperature conditions they live in

(Cermeño and Falkowski, 2009; Soppa et al., 2014; Arteaga et al., 2018, 2019; Tréguer et al., 2018; Schallenberg et al., 2019; Strzepek et al., 2019). Residing in the mixed layer of the surface ocean, phytoplankton stocks can be observed from space using satellites due to the visibility of chlorophyll-*a* (McClain, 2009; Johnson et al., 2013). Satellite chlorophyll-a composites are routinely used in Southern Ocean ecosystem assessments of primary production, downward carbon export and food availability (Boyd et al., 2012; Siegel et al., 2014; Lee et al., 2015; Constable et al., 2016).

In the Southern Ocean, ship-based studies have presented evidence of subsurface chlorophyll-*a* maxima (SCMs), observing a build-up of chlorophyll-a below the penetration depth of satellites (10–40 m; Parslow et al., 2001; Holm-Hansen et al., 2005; Carranza et al., 2018). This phenomenon can be sustained by several ecological processes, although most of what is currently known comes from observing the tropical oceans (Cullen, 1982, 2015). In the tropics high irradiances, warm temperatures and low supply of macro-nutrients lead to the dominance of smaller picoplankton communities (Acevedo-Trejos et al., 2013, 2015). Most commonly tropical SCMs are associated with a typical stable water structure which persists through both summer and winter (Cullen, 1982, 2015). This SCM forms just above the pycnocline and is directly related to an increase in phytoplankton abundance (and biomass) that is stimulated by changes in light and macro-nutrients with depth (**Figure 1**). This mechanism of SCM formation – as a niche specialization in a stratum that receives just enough light from above and nutrient supply from below – is well understood and widely studied in the tropics and the Mediterranean Sea (Cullen, 1982; Furuya, 1990; Estrada et al., 2016; Barbieux et al., 2019).

Southern Ocean SCMs are often located at or deeper than the pycnocline, rather than above it, making them distinguishable from those of the tropics (Quilty et al., 1985; Bathmann et al., 1997; Fiala et al., 1998; Kopczynska et al., 2001; Parslow et al., 2001; Garibotti et al., 2003; Armand et al., 2008a; Gomi et al., 2010; Westwood et al., 2011; Demidov et al., 2013; Tripathy et al., 2015). The deeper SCM coupled with the macro-nutrient replete surface ocean, suggest that Southern Ocean SCMs are different to that of the tropics (**Figure 1**; Louanchi and Najjar, 2000; Moore et al., 2001; Arteaga et al., 2019). These deeper SCMs are characterized by a marked community shift toward large diatoms across the pycnocline and are referred to as "diatom SCMs" herein (Bathmann et al., 1997; Cailliau et al., 1997; Kopczynska et al., 2001; Parslow et al., 2001; Quéguiner, 2001; Armand et al., 2008a; Gomi et al., 2010; Westwood et al., 2011; Tripathy et al., 2015). Similar diatom SCMs have also been observed in other stratified regions including northern-temperate and coastal areas (Estrada et al., 1993; Kemp and Villareal, 2013, 2018). The study of how SCMs form in the Southern Ocean will help to reveal the distribution of deep phytoplankton communities which are currently hidden from satellites.

We provide a comprehensive Review of what is currently known about Southern Ocean SCMs (those that form south of the circumpolar Sub-tropical front). This includes (1) methods for their observation (2) their reported occurrences (3) the ecological processes responsible for their formation and (4) the role of SCMs in Southern Ocean ecology. In doing so, we highlight how ship-based data have been able to capture annually recurrent and widespread Southern Ocean SCMs and the ocean properties that together distinguish them from the SCMs observed in the tropics. The ecological implications of this deep phytoplankton biomass, which are not captured in satellite chlorophyll-*a* composites, are further discussed to inform the Marine Ecosystem Assessment of the Southern Ocean (MEASO).

This Review is timely in the wake of the increased sampling of chlorophyll-*a* by autonomous platforms such as those in the biogeochemical Argo (BGC-Argo) and the Marine Mammals Exploring the Ocean Pole to pole (MEOP) programs in the Southern Ocean. These programs have the capacity to fill the limited spatiotemporal resolutions of ship-based sampling (**Figure 2**; Guinet et al., 2013; Claustre et al., 2020). From this new wealth of data, the large-scale processes that control the formation of Southern Ocean SCMs can be delineated, complementing the detailed understanding of the phenomenon presented in this Review.

DEFINING SOUTHERN OCEAN SCMs

We define an SCM by the existence of a local maximum in chlorophyll-a concentrations (i.e., chlorophyll-*a* concentration in subsurface > chlorophyll-*a* concentration at surface). An SCM should form over spatial scales greater than one meter and be maintained on the timescales of a day or longer. This definition is adapted from Cullen (2015), who defines SCMs as subsurface chlorophyll-*a* maximum layers which are maintained by ecological processes. We do not follow this exact definition, since we have found some SCMs in the Southern Ocean that may be maintained by purely physical processes (see *Along-shelf subduction*). See Cullen (2015) for further discussion on terminology and its variants.

METHODS FOR OBSERVATION

Seawater Samples From Ships

Most Southern Ocean ship-based studies measure *ex situ* chlorophyll-*a* by the direct determination of extracted chlorophyll-a pigments from vertical seawater samples. SCMs are then identified subjectively, by plotting depth profiles of chlorophyll-a (Wright and van den Enden, 2000; Parslow et al., 2001; Gomi et al., 2007; Whitehouse et al., 2008; Tripathy et al., 2015). Usually this is feasible based on the experience of the investigator as the presence (or absence) of an SCM is often visually clear.

In these studies, seawater samples are filtered through glass fiber filters to remove phytoplankton cells. Pigments are subsequently extracted from these cells using an organic solvent for measurement in the laboratory (Valente et al., 2016; Davies et al., 2018) and analyzed by either high-performance liquid chromatography (HPLC) (Shoaf, 1978; Valente et al., 2016), fluorometry or spectrophotometry (Yentsch and Menzel, 1963; Holm-Hansen et al., 1965; Strickland and Parsons, 1972;

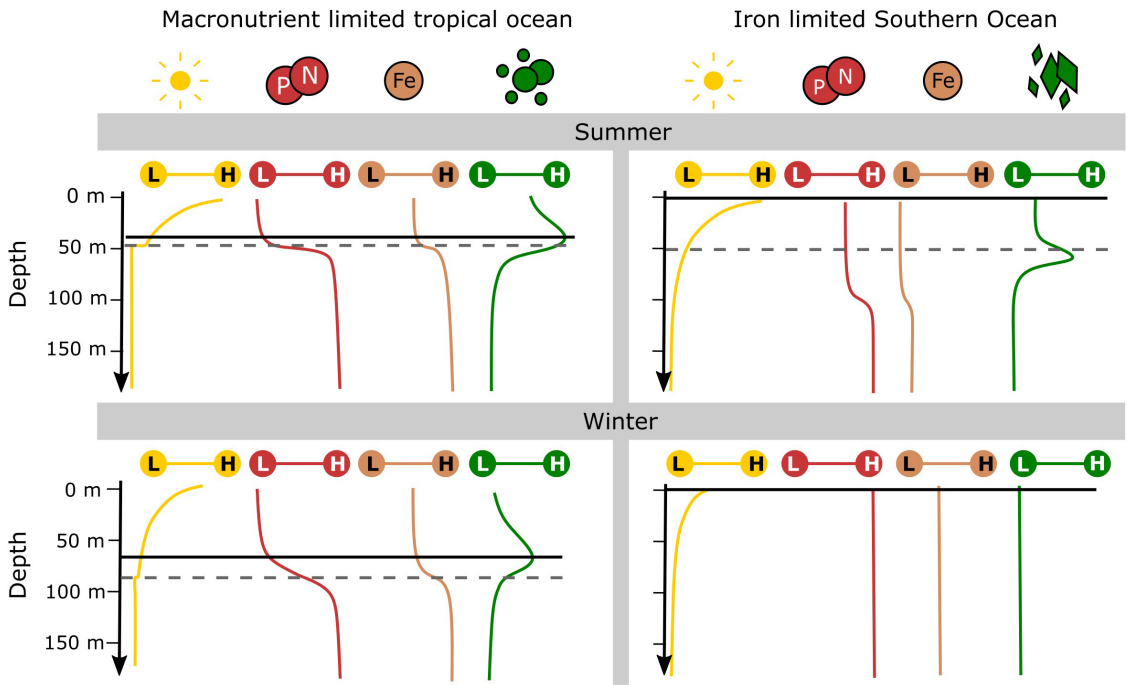

FIGURE 1 | A comparison of typical upper water column structure between the macronutrient limited tropical ocean and the iron limited Southern Ocean over summer and winter. Distributions of downward irradiance (yellow), macronutrients (red) and iron (brown) are shown on a low (L) to high (H) scale. Also shown are indications of mixed layer depths (dashed gray line) – note that mixed layer depths are highly variable and are dependent on the thresholds used to define them. Phytoplankton distributions (green) are shown for the picophytoplankton (circular) community of the tropical ocean and the high silicate community (diamond) of the polar Southern Ocean. The optimum depth of phytoplankton growth (solid black line) is determined by the distribution of light and the limiting nutrient according to the theory of nutrient light co-limitation. **Supplementary Table S1** lists supporting information used in the construction of this graphical summary.

Zeng and Li, 2015). These methods relate the absorption spectra of extracted pigments to that of chlorophyll-*a*. The HPLC method is the most accurate method, as pigments are first separated through a chromatographic column (**Figure 3**). Pigments are not separated before analysis in fluorometry or spectrophotometry and thus chlorophyll-*a* measurements are subjected to the additive effects of pigments that absorb (or emit) at similar wavelengths (Davies et al., 2018). Fluorometry is the method that has been most widely used in the Southern Ocean. This method often significantly underestimates chlorophyll-*a* concentrations which is reportedly due to the presence of chlorophyll-*b* pigments (Daemen, 1986; Murray et al., 1986; Pinckney et al., 1994; Davies et al., 2018). This underestimation has no consequence for detecting SCMs and can be corrected for by regressing measurements against coincidental HPLC derived chlorophyll-*a*.

In situ Fluorometers

Recent Southern Ocean studies have used *in situ* deployments of fluorometers on elephant seals and BGC-Argo floats to observe SCMs over larger spatial scales. These studies have had to adapt to automatically detecting SCMs using preselected criteria to accommodate a new wealth of data (Grenier et al., 2015; Carranza et al., 2018). Supervised classification methods applied to chlorophyll fluorescence have offered a solution for studying thousands of chlorophyll fluorescence profiles and can provide an added advantage of distinguishing between different types of SCMs. They can do this by automatically identifying characteristic features of a vertical structure using prescribed algorithms. These methods have only been applied in two Southern Ocean studies (Grenier et al., 2015; Carranza et al., 2018), the Mediterranean Sea (Lavigne et al., 2015; Barbieux et al., 2019) and the Arctic (Ardyna et al., 2013).

In situ fluorometers measure chlorophyll fluorescence from live phytoplankton cells. As measurements are not performed *ex situ* on extracted pigments, yields of chlorophyll fluorescence (i.e., the ratio of emitted light to absorbed light) become important by controlling fluorescence to chlorophyll-a concentration ratios (Falkowski and Kolber, 1995; Chekalyuk and Hafez, 2011; Ostrowska et al., 2012). Shifts in phytoplankton communities, photophysiological state or nutrient regimes lead to variations in chlorophyll fluorescence yields of up to 7-fold over the global ocean (Behrenfeld et al., 2009; Cheah et al., 2013; Roesler et al., 2017). In addition, a physiological process whereby phytoplankton under light stress divert energy from their photosynthetic systems, called non-photochemical quenching (NPQ), introduces a further challenge for determining chlorophyll-a concentration by decreasing chlorophyll fluorescence yield by up to 100% in surface measurements (Behrenfeld et al., 2009; Doblin et al., 2011; Thomalla et al., 2018; Xing et al., 2018; Schallenberg et al., 2019).

Correcting fluorescence-derived chlorophyll-a in the Southern Ocean for observed variations in chlorophyll

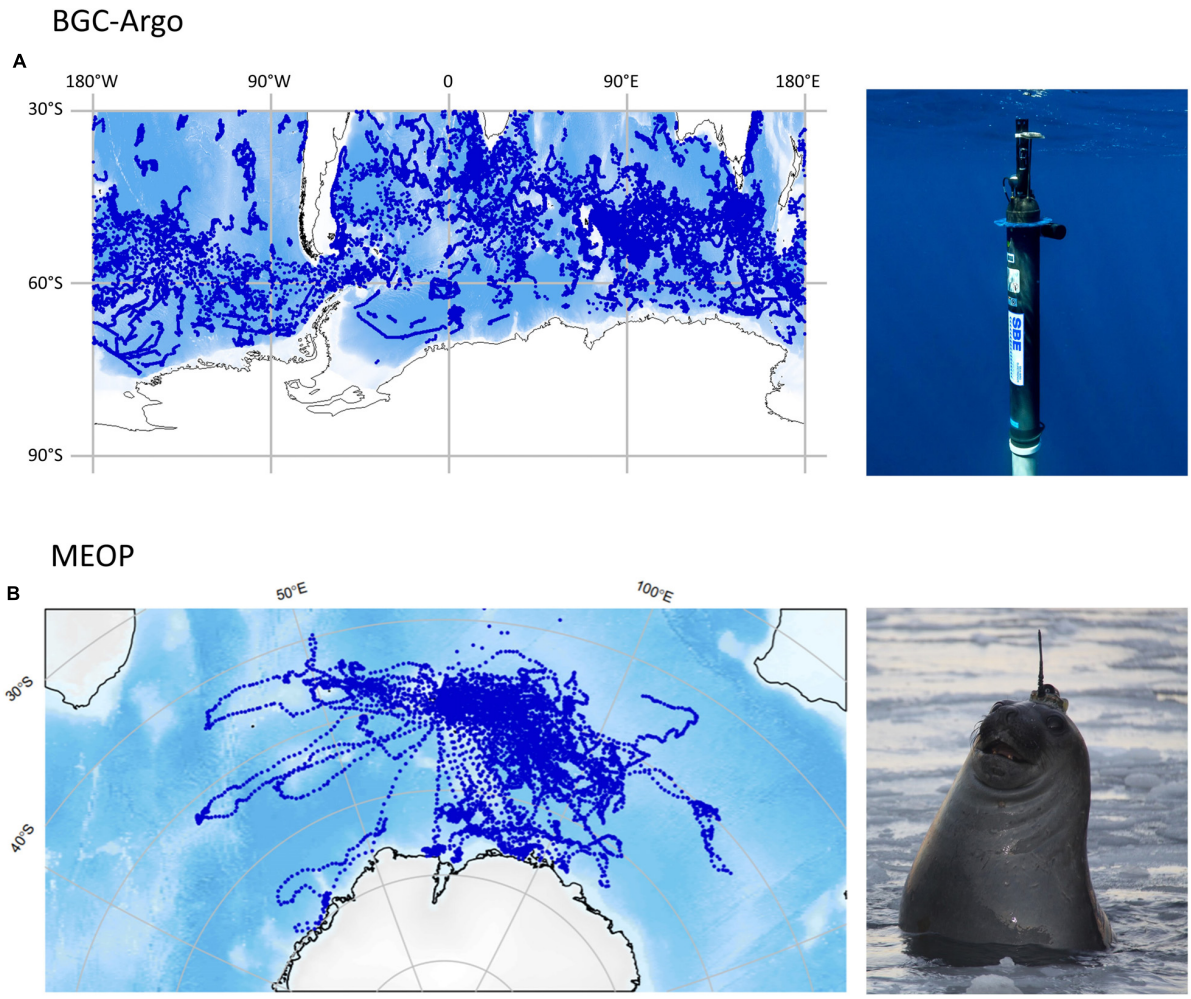

FIGURE 2 | The distribution of available fluorescence-derived chlorophyll-*a* data collected (blue dots) south of 30°S overlaid on bathymetry, alongside images of autonomous platforms used in two programs that facilitate large deployments of fluorometers in the Southern Ocean; **(A)** the biogeochemical Argo (BGC-Argo) and **(B)** the Marine mammals Exploring the Oceans Pole to pole (MEOP) programs. The distribution plots correspond to BGC-Argo data (produced by Kimberlee Baldry) that is freely available and MEOP data (produced by Professor Mark Hindell) available from the Integrated Marine Observing System through program leaders (Professor Mark Hindell and Dr. Christophe Guinet). Data shown was that available on the 28/03/2020. Credits for instrumentation images go to Christoph Gerigk at© Sea-Bird Electronics for BGC-Argo and Clive McMahon for MEOP.

fluorescence yields is done by applying a regional scaling known as the Roesler factor (Haëntjens et al., 2017; Roesler et al., 2017). The application of a single scaling factor to the entire Southern Ocean does not seem viable considering the recent observations from Schallenberg et al. (2019) which show large changes in chlorophyll fluorescence yields across the Sub-Antarctic front. The use of satellite-derived chlorophyll-*a* as a surface reference to correct fluorescence-derived chlorophyll-*a* may be a more promising approach, although consideration that the two measurements are made on vastly different spatiotemporal scales is needed (Guinet et al., 2013). This approach comes possibly at the expense of accuracy, as the accuracy of Southern Ocean satellite-derived chlorophyll-*a* algorithms has repeatedly been questioned (**Figure 3**; Mitchell and Holm-Hansen, 1991; Sullivan et al., 1993; Dierssen, 2010; Johnson et al., 2013).

NPQ decreases chlorophyll fluorescence yield toward the surface, causing a subsurface fluorescence maximum (SFM) measured by a fluorometer to appear where an SCM may not exist (Falkowski and Kolber, 1995; Biermann et al., 2015; Carranza et al., 2018; Thomalla et al., 2018; Xing et al., 2018). In the Southern Ocean, NPQ is widespread likely due to iron limitation and high summertime light levels which have led to communities lacking the nutrients to photosynthesize when light is readily available (Roesler et al., 2017; Strzepek et al., 2019; Schallenberg et al., 2020). Many methods have been suggested to correct surface fluorescence in the presence of NPQ, but an evaluation of these corrections across the Southern Ocean has not been performed. NPQ corrections have been shown to perform differently and most fail to accurately correct fluorescence when an SCM is present in the Southern Ocean (Carranza et al., 2018;

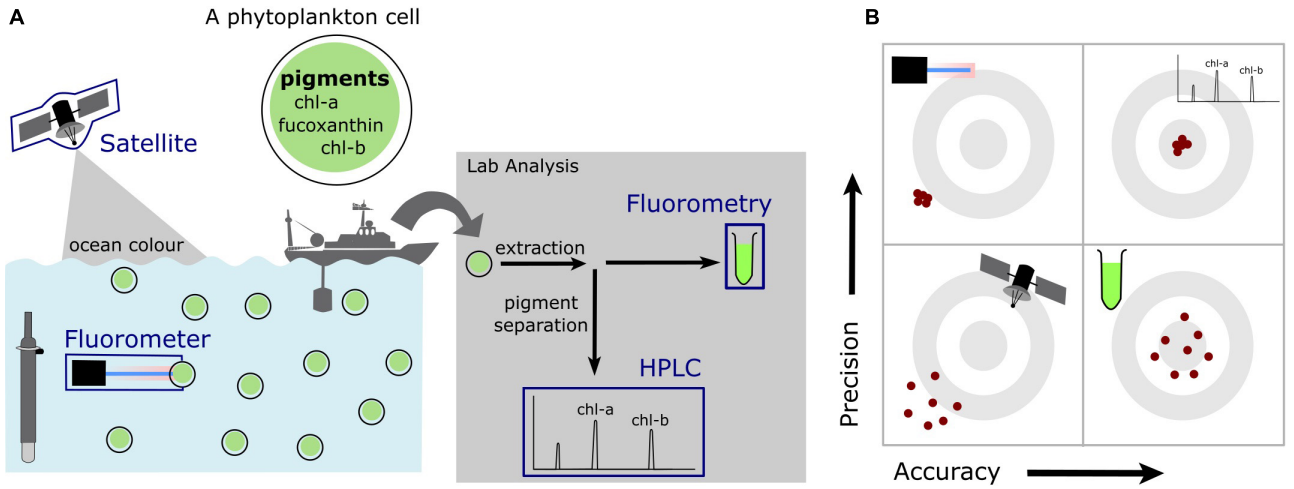

FIGURE 3 | A schematic of **(A)** the different methods of measuring chlorophyll-*a* in the ocean discussed within this review and **(B)** a representation of differences in precision and accuracy for these methods. The gray concentric circles illustrate targets, where the center is indicative of an accurate and precise measurement, with the red dots illustrating the differences between accuracy and precision. Four targets are presented to illustrate varying degrees of precision and accuracy.

Thomalla et al., 2018; Xing et al., 2018). The comparison of day-time corrected fluorescence with night has been used in studies as a good test of the performance of an NPQ correction (Carranza et al., 2018; Thomalla et al., 2018; Xing et al., 2018). However, this test could be subject to the effects of diurnal controls on 'real' SCM formation which are largely unknown, as well as differences *in situ* sampling locations between day and night (Cullen, 2015; Carranza et al., 2018).

As a consequence of variable chlorophyll fluorescence yields, Southern Ocean *in-situ* fluorescence measurements are not inter-comparable with measurements derived from extracted chlorophyll-*a* (i.e., HPLC, fluorometry, spectrophotometry) and are best interpreted in terms of subsurface fluorescence until disparities are quantified and better understood (Carranza et al., 2018). From an alternative perspective, chlorophyll fluorescence has the potential to provide further insight on the photophysiological state of phytoplankton and could be used to distinguish the amount of light energy being used in primary production. This would allow a more accurate representation of basin primary production in ecosystem assessments, rather than assuming a constant photosynthetic efficiency per unit chlorophyll-*a* for in estimates (Behrenfeld et al., 2009; Boss et al., 2018; Schallenberg et al., 2019, 2020).

The type of supervised classification method chosen, the post-processing method for fluorescence measurements (e.g., despiking, smoothing), sampling resolution and measurement error are all expected to affect the detection of SCMs (Grenier et al., 2015; Carranza et al., 2018). To remain comparable, future studies should clearly consider the effect of these variables on their results. Furthermore, targeted study on the accuracy of fluorometers in the Southern Ocean is needed to assess the impacts of chlorophyll fluorescence yields and NPQ on ecosystem assessments of primary production, downward carbon flux and food-webs made through large scale deployments of fluorometers.

REPORTED OCCURRENCES

Southern Ocean SCMs were suggested to be both prevalent and annually recurrent by two early studies. Parslow et al. (2001) reported the first evidence of annually recurrent SCMs south of Australia around the Polar front, along the WOCE SR3 line (140°E). Here, SCMs form in late spring around 50 m and deepen to 100 m by early autumn (Parslow et al., 2001). Following this Holm-Hansen et al. (2005) reported geographically wide occurrences of SCMs in the Southern Ocean by synthesizing ship-based studies. The authors associated SCMs with low surface chlorophyll, iron limitation and with the temperature minimum layer of Antarctic waters.

A more recent study by Carranza et al. (2018) confirmed both the earlier reported annually recurrent and widespread SCMs. Their study identified SCMs using SFMs collected by an array of *in situ* fluorometers on BGC-Argo floats and elephant seals. SFMs begin to form in late-spring and decline from late-summer to early-autumn. At the peak of summer SFMs are detected in 60% of the dataset which is constrained mostly to the open Southern Ocean around the Polar front. These SFMs appear to show synergies with episodic wind events, forming only during calm conditions, and may coincide with increased phytoplankton biomass. This study demonstrated the capabilities of fluorometers to provide a basin-wide view of SCMs from the interpretation of SFMs, despite the widespread day-time NPQ of fluorescence, by considering only measurements made at night.

In addition to SCMs in the vicinity of the Polar front (Kopczynska et al., 2001; Parslow et al., 2001; Armand et al., 2008a; Westwood et al., 2011; Tripathy et al., 2015; Rembauville et al., 2016a), *ex situ* measurements have found summer SCMs around the continental slopes of Antarctica and Southern Ocean islands (Garibotti et al., 2003; Holm-Hansen and Hewes, 2004; Demidov et al., 2007; Armand et al., 2008a; Whitehouse et al., 2008; Erickson et al., 2016), around eddies (Clementson et al.,

1998; Daly et al., 2001) and in the Seasonal Ice Zone (Mikaelyan and Belyaeva, 1995; Bathmann et al., 1997; Cailliau et al., 1997; Wright and van den Enden, 2000; Gomi et al., 2007; de Villiers et al., 2015). During summer, a recurrent and notable absence of SCMs has only been reported in the permanently open ocean zone of Antarctic waters (Cailliau et al., 1997; Gomi et al., 2007; Rigual-Hernández et al., 2015a,b) and the Sub-Antarctic zone south of Australia (**Figure 4**; Clementson et al., 1998; Parslow et al., 2001; Westwood et al., 2011).

This is the limited viewpoint that the literature to date offers on the prevalence and persistence of Southern Ocean SCMs. The field is at a tipping point of observational power through the BGC-Argo and the MEOP programs (**Figure 2**; Guinet et al., 2013; Claustre et al., 2020). This power will see an unprecedented increase in reported observations of SFMs and SCMs (Carranza et al., 2018).

PROCESSES THAT MAINTAIN SOUTHERN OCEAN SCMs

Identifying the ecological and physical processes (*sensu* Cullen, 2015) that maintain SCMs is difficult. Ancillary environmental data are required to disentangle these processes and to test hypotheses. Eighteen Southern Ocean studies have been identified to contain ancillary data that could be used to evaluate processes that form SCMs (**Figure 4** and **Supplementary Table S2**).

The studies were identified through a literature search that revealed 145 scholarly articles published between 1991 and 2019. The search was performed using the *Web of Science Core Collection* and *Scopus* databases together with the key search terms "Subsurface chlorophyll-*a* maxima" and "Southern Ocean." Derivatives of "subsurface chlorophyll-a maxima" were also implemented (**Supplementary Text S1**). Results from these studies are discussed below in the context of Southern Ocean biogeochemistry. We have summarized this information in new conceptual models for Southern Ocean regions to guide future research (**Figure 5**).

Nutrient-Light Colimitation in an Iron Limited Ocean

The stability of the tropical SCM relies on vertically mixed inputs of a limiting nutrient across a pycnocline into the base of the mixed layer combined with a light field that decreases exponentially with depth. This creates a depth of optimum growth for phytoplankton, at the SCM, usually just above the pycnocline (**Figure 1**). Below the SCM, growth is limited by light, and by nutrients above the SCM. At the SCM community shifts can occur due to low rates of mixing as different phytoplankton groups respond differently to changing light, nutrient availability and disproportionate grazing pressures (Strom, 2001; Cullen, 2015; McKie-Krisberg et al., 2015; Latasa et al., 2016, 2017). Despite these shifts, the community is dominated by picoplankton through the water column (Furuya, 1990; Estrada et al., 2016; Latasa et al., 2017). In the darker environment of the SCM phytoplankton may also undergo photo-acclimation, increasing intracellular chlorophyll-*a* concentration (Cullen, 2015; Estrada et al., 2016; Latasa et al., 2017). If there are high rates of surface mixing, the SCM is destroyed (see Cullen, 2015 for further discussion).

Sufficient subsurface inputs of the limiting micro-nutrient iron are not widely present across the Southern Ocean to sustain the light-nutrient co-limitation characteristic of tropical SCMs. Iron-depleted mixed layers have been shown to coincide with SCMs in the open Southern Ocean (Boyd et al., 2001; Holm-Hansen et al., 2005), but iron concentrations are still remarkably low below the mixed layer from late-spring to summer leading to small diffusive fluxes (Sohrin et al., 2000; Tagliabue et al., 2012, 2014; Klunder et al., 2014; Bowie et al., 2015). This can be attributed to the rapid use of winter iron repositories as the mixed layer shoals during the initial spring bloom (Tagliabue et al., 2014). The presence of SCMs at or deeper than the pycnocline and a consistent, marked community shift toward large diatoms at the SCM are further features which do not fit with the conceptual model of the tropical SCM (Kopczynska et al., 2001; Parslow et al., 2001; Holm-Hansen et al., 2005; Westwood et al., 2011; Moore et al., 2013; Carranza et al., 2018). Instead we find that an assortment of Southern Ocean processes may be important for maintaining diatom SCMs including stratification, buoyancy regulation by large diatoms, persistent iron limitation and grazing.

Theoretically, iron fertilization could relieve iron limitation in the mixed layer to induce an SCM sustained by light-nutrient co-limitation, by allowing silicate or nitrate, which have vertically mixed inputs, to become the limiting nutrient. The primary sources of iron to the Southern Ocean are coastal margins, shallow bathymetry, dust, hydrothermal venting and sea-ice melt (Blain et al., 2008; Raiswell et al., 2008; Boyd and Ellwood, 2010; Boyd et al., 2012; Graham et al., 2015; Ardyna et al., 2019). Coastal inputs of iron and sea-ice melt have been associated with the development of SCMs which we explore further (see *Iron fertilization by land masses* and S*ea-ice retreat*), however the role of other iron sources in SCM formation is purely speculative due to a lack of coincident observations.

Diatom SCMs

Large diatoms find an environmental niche in the pycnocline under severe iron limitation and high stratification, remaining in the upper ocean when other phytoplankton taxa cannot. This leads to their accumulation forming the diatom SCM which have been observed around the Polar front (Bathmann et al., 1997; Kopczynska et al., 2001; Parslow et al., 2001; Armand et al., 2008a; Gomi et al., 2010; Westwood et al., 2011; Tripathy et al., 2015), on the Kerguelen Plateau (Armand et al., 2008a), off the continental slope of Antarctica (Quilty et al., 1985; Fiala et al., 1998; Garibotti et al., 2003) and in the Seasonal Ice zone (Cailliau et al., 1997; Wright and van den Enden, 2000; Gomi et al., 2007). The most striking observation of this phenomenon was made in the Seasonal Ice Zone by Quilty et al. (1985) who encountered a diatom SCM of remarkably high biomass, dominated by *Thalassiothrix antarctica*.

The tendency of large diatoms to dominate the diatom SCM has been revealed by microscopy and CHEMTAX analysis

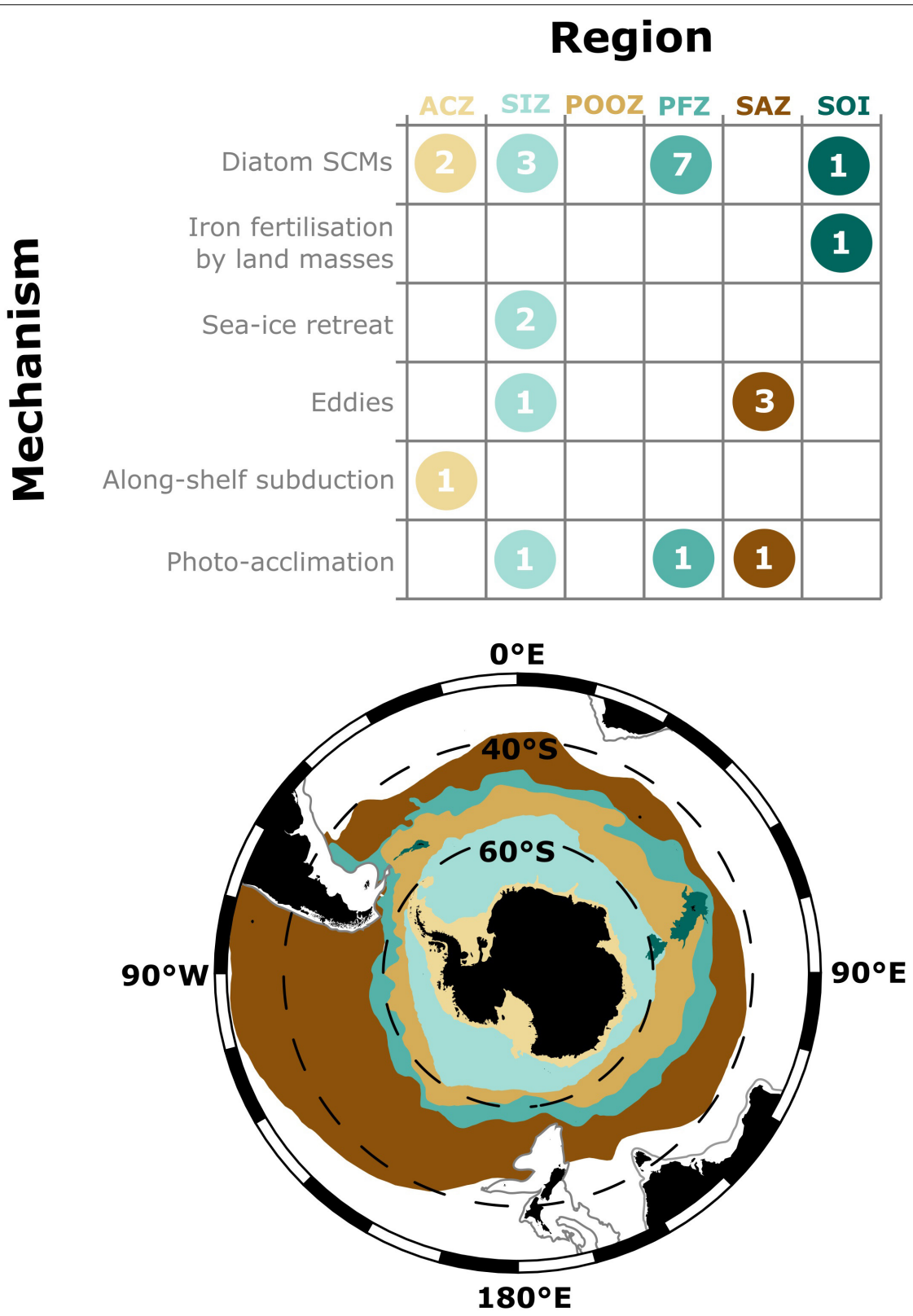

FIGURE 4 | The number of studies that identify a mechanism of formation discussed in this review presented by region of the Southern Ocean. The evidence each study has given for these mechanisms is given in **Supplementary Table S2**. Regions are as defined in Deppeler and Davidson (2017), however, note that the location of fronts and sea-ice extent are highly variable. ACZ, Antarctic Coastal Zone (including continental slope to 2000 m); SIZ, Seasonal Ice Zone; POOZ, Permanently Open Ocean Zone; PFZ, Polar Frontal Zone; SAZ, Sub-Antarctic Zone; SOI, Southern Ocean Islands. The 2000 m isobar is shown as a gray line.

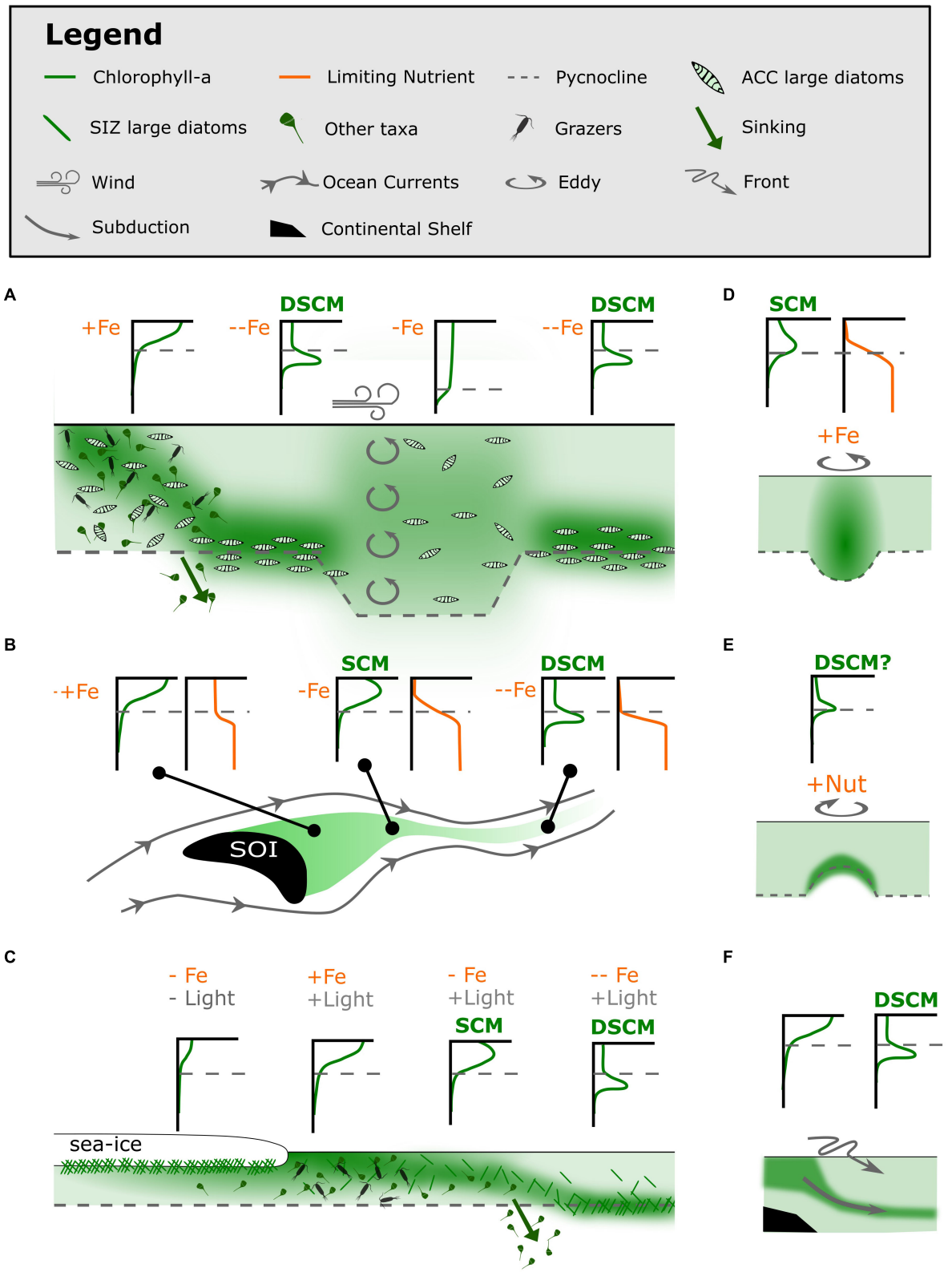

FIGURE 5 | Proposed conceptual models for the formation of Southern Ocean SCMs and diatom SCMs (dSCMs) **(A)** in the oceanic HNLC regions, **(B)** downstream of Southern Ocean Islands (SOI), **(C)** following sea-ice retreat, **(D)** in warm-core eddies in the Sub-Antarctic Zone, **(E)** in cold-core eddies in the Sub-Antarctic Zone and **(F)** by subduction along the continental shelf (as in Erickson et al., 2016). Conceptual models are presented as schematics, with examples of what vertical measurements of chlorophyll-*a* and limiting nutrients might look like.

of accessory pigments (Quilty et al., 1985; Bathmann et al., 1997; Fiala et al., 1998; Wright and van den Enden, 2000; Kopczynska et al., 2001; Gomi et al., 2007, 2010; Armand et al., 2008a; Westwood et al., 2011). Further measurements of the accessory pigment fucoxanthin and biogenic silica have indicated increased diatom dominance at the SCM compared to coincident surface communities (Parslow et al., 2001; Quéguiner, 2001; Armand et al., 2008a).

Diatom SCMs only appear to form in the absence of a surface bloom and have been linked to severe iron depletion of surface waters (Parslow et al., 2001; Holm-Hansen and Hewes, 2004; Holm-Hansen et al., 2005). Further, the taxa that dominate diatom SCMs are found in upstream surface blooms, where upstream refers to island or coastal blooms (Armand et al., 2008a; Gomi et al., 2010; Westwood et al., 2011; Tripathy et al., 2015). We speculate that the diatom SCM is formed following the decline of the surface bloom as conditions fade under persistent iron or silicate limitation (**Figure 5A**). This could explain the regime shifts from a well-mixed surface bloom to a diatom SCM across continental shelves (Fiala et al., 1998; Garibotti et al., 2003; Holm-Hansen and Hewes, 2004), downstream from Southern Ocean Islands (Armand et al., 2008a) and with sea-ice retreat (Cailliau et al., 1999; Wright and van den Enden, 2000; Gomi et al., 2007).

The connectivity of phytoplankton communities between coastal and oceanic regions is most evident from studies conducted in the Indian sector of the Southern Ocean. Around the Polar front diatom SCMs were found to consistently contain significant communities of the large diatoms *Fragilariopsis kerguelensis* and *Dactyliosolen antarcticus,* which are both observed to bloom in the surface waters around the Kerguelen Plateau (Kopczynska et al., 2001; Armand et al., 2008a; Gomi et al., 2010; Westwood et al., 2011). In the Seasonal Ice Zone community composition is significantly different to that around the Polar front. While *Fragilariopsis kerguelensis* is often present in the mixed layer (downstream from the Kerguelen plateau), large diatoms *Pseudo-nitzschia prolongatoides*, *Pseudo-nitzschia* spp., *Corenthon pennatum* and *Chaetoceros* spp. dominate in the Seasonal Ice Zone (Fiala et al., 1998; Gomi et al., 2007, 2010). The decline over time and dominance in the diatom SCM of *Pseudo-nitzschia* spp. and *Chaetoceros* spp. (sea-ice diatoms), over *Fragilariopsis kerguelensis* suggests that SCMs formed in the Seasonal Ice Zone are most likely short lived and independent of SCMs formed around the Polar front (Gomi et al., 2007).

Ecological and physiological adaptions of large diatoms must be responsible for the ability of these taxa to survive for long periods at the pycnocline when conditions are not suitable for a surface bloom. The ability of large diatoms to regulate buoyancy over nutrient gradients, using vacuolar control of solute balance, should play a large role in sustaining their dominance at the SCM and prevent their export into the mesopelagic ocean (Waite et al., 1992; Fisher and Harrison, 1996; Kemp and Villareal, 2013). Interestingly, Southern Ocean large diatoms have been observed to increase their buoyancy under bloom conditions, iron addition and decreased light, leading to reduced downward carbon export (Waite et al., 1992; Fisher and Harrison, 1996; Waite and Nodder, 2001; Acuña et al., 2010). Diatoms efficiently use nutrients, due to their ability to take up nutrients rapidly and maintain large nutrient reserves (Lomas and Glibert, 2000; Litchman et al., 2006; Kemp and Villareal, 2013, 2018; Hansen and Visser, 2019). This coupled with adaptions to low-light environments – including optimized photosystems and photonic crystals that enhance light harvesting - allows large diatoms to be active producers in the pycnocline which receives pulses of nutrients via internal waves (Holligan et al., 1985; Kemp and Villareal, 2013; Strzepek et al., 2019; Goessling et al., 2020).

Heavy silicification and large spines to resists heavy grazing pressure also confer some protection against the depletion of these aggregations (Smetacek et al., 2004; Assmy et al., 2013). A disproportionate grazing pressure across species may also aid bloom-decline and contribute to the maintenance of the diatom SCM in the open ocean (Assmy et al., 2013). However the diatom SCM is not immune to grazing pressure as targeted grazing by microzooplankton, copepods and heterotrophic dinoflagellates is indicated by the presence of empty frustules and a maximum of zooplankton abundance (Froneman and Perissinotto, 1996; Kopczynska et al., 2001; Parslow et al., 2001; Armand et al., 2008; Gomi et al., 2010; Rembauville et al., 2016).

It is unknown if silicate, iron or light is most important in buoyancy regulation of Southern Ocean large diatoms. It may depend on the limiting nutrient of these communities which is not completely resolved (Waite et al., 1992; Fisher and Harrison, 1996; Boyd et al., 2005). Shallow bathymetry could support large subsurface reservoirs of lithogenic silica, potentially aiding in the persistence of diatoms at depth as they are carried around with the Antarctic circumpolar current (Parslow et al., 2001; Quéguiner, 2001; Robinson et al., 2016). Hopkinson et al. (2007) is the only study that has conducted an iron-addition experiment to observe iron limitation in an oceanic Southern Ocean SCM. This study found that the SCM community in the West-Antarctic Peninsula was iron limited and *in situ* iron was still remarkably low below the pycnocline. Unfortunately, few studies that observe an SCM have reported vertical profiles of iron and silicate concentrations.

The stratification of the water column to form a shallow pycnocline over spring and summer is important for the maintenance of diatom SCMs (**Figure 5A**). In late-autumn the deepening of the pycnocline leads to the destruction of the diatom SCM and a "fall dump" event leads to the export of the community as light levels become too low for survival (Smetacek, 1985; Kemp et al., 2000). Observations of SFMs further suggest that disturbing the pycnocline via episodic storms likely leads to the re-suspension of communities and the subsequent re-formation of the diatom SCM when calm conditions prevail (Carranza et al., 2018). If these SFMs correspond to diatom SCMs around the Polar front, this may point toward the survival of the diatom SCM community during episodic storm events.

Iron Fertilization by Land Masses

In the high-energy environments of Southern Ocean islands in the path of the Antarctic circumpolar current, lateral flow is strongly zonal. A persistent supply of iron in the vicinity of and downstream of these islands is observed to be in excess of the demand of phytoplankton growth (Blain et al., 2001, 2008;

Planquette et al., 2007; Chever et al., 2010; Bowie et al., 2015; Robinson et al., 2016; Schlosser et al., 2018). This iron supply facilitates large oceanic surface blooms that decline with distance from a land mass, as a limiting nutrient becomes depleted in the surface layer (Graham et al., 2015; Robinson et al., 2016). SCMs have been observed to form above the pycnocline in the wake of high chlorophyll plumes around the Kerguelen Plateau and South Georgia Island (Blain et al., 2001; Armand et al., 2008a; Whitehouse et al., 2008; Grenier et al., 2015). These SCMs are likely a result of a transient light-nutrient co-limited state as the surface bloom declines (**Figure 5B**; Whitehouse et al., 2008; Grenier et al., 2015). The limiting nutrient is silicate downstream from South Georgia Island, but may be silicate or iron downstream from the Kerguelen Plateau (Blain et al., 2007; Mongin et al., 2007; Whitehouse et al., 2008; Closset et al., 2014; Robinson et al., 2016).

Over the Antarctic continental shelf, high levels of iron persist through the water column due to high inputs of iron from sediments and the movement of circumpolar deep water to the surface (Blain et al., 2008; Tagliabue et al., 2012; Klunder et al., 2014; Dinniman et al., 2020). Even in this iron rich region surface waters can exhibit persistent iron limitation due to the demands of rapid phytoplankton growth in spring and summer (Martin et al., 1990; Coale et al., 2003; Bertrand et al., 2007). There is an absence of SCMs above the pycnocline in these surface waters which suggests that phytoplankton deplete subsurface sources of iron over shallow bathymetry more quickly than it is supplied (Martin et al., 1990; Coale et al., 2003; Bertrand et al., 2007; Alderkamp et al., 2015). This is further evident from records of iron limitation near the pycnocline in the Amundsen Sea (Alderkamp et al., 2015). This key difference from Southern Ocean Islands near the ACC is likely due to relatively weak surface currents in the low-energy, sheltered region and the transient nature of sea-ice as an iron source (Fahrbach et al., 1992; Dinniman et al., 2011, 2020; Stewart and Thompson, 2013; Park et al., 2014; Robinson et al., 2016).

Southern Ocean studies have often suggested iron-light co-limitation as a driver of SCM formation over the continental shelf due to decreasing iron supply by land masses (Garibotti et al., 2003; Holm-Hansen et al., 2005; Kahl et al., 2010). These oceanic SCMs develop below the pycnocline, suggesting that light-nutrient co-limitation plays no part in facilitating their formation. We reframe these observations by acknowledging that while iron limitation may play a role in maintaining these SCMs, the distribution of nutrients through the water column does not control their formation, leading us to suggest that these are diatom SCMs.

Sea-Ice Retreat

Sea-ice retreat facilitates intense phytoplankton blooms in surface waters (Raiswell et al., 2008; Death et al., 2014; Duprat et al., 2016). These blooms are thought to be initiated by seed phytoplankton released from sea-ice (Grossi et al., 1987; Suzuki et al., 2001; Gomi et al., 2007; Mangoni et al., 2009; Lizotte, 2015), the release of light limitation from sea-ice cover (Lancelot et al., 1993; Taylor et al., 2013) or the release of bio-available iron as the ice melts (Lannuzel et al., 2016), or a combination of all these mechanisms. Following surface blooms, diatom SCMs have been observed to trail sea-ice retreat (**Figure 5C**; Cailliau et al., 1999; Wright and van den Enden, 2000; Gomi et al., 2007). These diatom SCMs could be related to the diatom SCMs that are frequently observed over the continental slope of Antarctica.

Surface blooms at the sea-ice edge rapidly sink when nutrients quickly become depleted from meltwater (Smetacek et al., 1992; Wright and van den Enden, 2000; Ambrose et al., 2005; Wright et al., 2010; Boetius et al., 2013) or and are heavily grazed (Stretch et al., 1988; Smetacek et al., 1990; Scharek et al., 1994; Michel et al., 1996; Gomi et al., 2007). After sea-ice retreat, phytoplankton community composition is initially uniform with depth and dominated by diatoms and *Phaeocystis* spp., as seen by microscopy and pigment analysis (Cailliau et al., 1999; Wright and van den Enden, 2000; Gomi et al., 2007). It is at this stage, Gomi et al. (2007) detected sea-ice algae (*Phaeocystis* spp. and *Pseudo-nitzschia prolongatoides*). Cailliau et al. (1999) used a combination of pigment and lipid analysis to suggest that the subsequent diatom SCM in a sea-ice zone was formed by a selective export of nanoflagellates (inc. *Phaeocystis* spp.) due to grazing, while diatoms are left behind in the SCM. The ability of diatoms to regulate their buoyancy across nutrient and light gradients, thus preventing their sinking could prevent their immediate export and survival at the diatom SCM as bloom conditions decline (Waite et al., 1992; Fisher and Harrison, 1996; Moore and Villareal, 1996; Waite and Nodder, 2001; Kemp et al., 2006; Acuña et al., 2010).

The fate and spatial extent of these diatom SCMs associated with sea-ice retreat has not been explored. Further, the ability of sea-ice to fertilize blooms is inconsistent, as demonstrated in Bathmann et al. (1997). They followed the retreat of sea-ice for 6 weeks and observed little phytoplankton growth at the ice-edge, even though ice-algae and meltwater were detected. This may have been due to high wind conditions inhibiting the ice-edge blooms (Lancelot et al., 1993; Fitch and Moore, 2007; Pellichero et al., 2020) or intense zooplankton grazing at the ice-edge like that exerted by large krill swarms (Stretch et al., 1988; Smetacek et al., 1990; Scharek et al., 1994). Consequently, these diatom SCMs may not be observed around the entire marginal ice zone.

Eddies

Eddies are abundant and ubiquitous in the Southern Ocean, resulting from the instabilities at high energy fronts. Particularly intense eddy activity occurs where fronts interact with shallow bathymetry (Bryden and Heath, 1985). A small number of SCMs have been attributed to eddies spinning off the Subtropical front, the Sub-Antarctic front and the Antarctic Divergence (Clementson et al., 1998; Wright and van den Enden, 2000; Daly et al., 2001; Westwood et al., 2011; de Villiers et al., 2015). To date, eddies are speculated to facilitate Southern Ocean SCMs by two mechanisms; (1) nutrient-light co-limitation within warm-core eddies from the Subtropical front and (2) increased growth at the pycnocline cold-core eddies from the Sub-Antarctic Front, likely due to the injection of nutrients (**Figures 5D,E**).

An SCM observed by Clementson et al. (1998) exhibited a nitrate limited tropical SCM at the center of a warm-core eddy that had come from the nitrate-poor Subtropical zone into the

nitrate-rich Sub-Antarctic zone, where SCMs are consistently not observed (Clementson et al., 1998; Wright and van den Enden, 2000; Daly et al., 2001; Westwood et al., 2011). Westwood et al. (2011) also detected an eddy associated SCM above the pycnocline, revealing the warm-core eddy's capacity to transport iron-rich waters into the Sub-Antarctic zone. This study observed higher concentrations of iron at the surface in the eddy, compared to below which would allow a nitrate limited tropical SCM to exist (**Figure 5D**). The fate of this type of eddy-associated SCMs and their biogeochemical implications is unknown.

Another SCM that was uncharacteristically observed in the sub-Antarctic zone at 120–160 m depth by Daly et al. (2001) was in a cold-core eddy spun off the Sub-Antarctic front in summer. The SCM community likely originated from near the Polar front, where diatom SCMs can be observed at similar depths. The SCM within the cold-core eddy was observed to be of higher biomass than those around the Polar front, which was speculated to be sustained by an injection of nutrients from shoaled isopycnals (**Figure 5E**). This is supported by evidence from diatom SCMs in the Arctic which thrive under nutrient pulses via internal waves and eddies (Kemp and Villareal, 2013). The fate of the SCM was likely to sink with the weakening of the eddy, and contributing to downward carbon export, as communities were not well sustained in the Sub-Antarctic zone.

Detecting eddy-associated SCMs with autonomous platforms could further reveal the fate of these SCMs and their significance in the Southern Ocean, providing insight into this narrow view displayed by the literature.

Along-Shelf Subduction

SCMs could be formed by the subduction of productive surface waters off the coastal shelf (**Figure 5F**). Wright and van den Enden (2000) observed a band of SCMs along a subduction zone associated with the Antarctic Divergence. This mechanism has merit but is difficult to prove with one dimensional ship-based data.

Erickson et al. (2016) provided the strongest evidence that productive waters move along isopycnals that are subducted along the continental shelf to below the pycnocline as seen by glider transects. This community was also speculated to remain productive below the upper mixed layer. This leads to the question of whether the large diatom aggregation (comprised mostly of *Thalassiothrix antarctica*) observed by Quilty et al. (1985) was also formed as a result of this subduction combined with the ability of large diatoms to regulate buoyancy (Waite and Nodder, 2001; Kemp and Villareal, 2013).

Photo-Acclimation

Photo-acclimation enables phytoplankton to harvest light more efficiently in low light environments by increasing cellular chlorophyll-a. This has been observed in the pycnocline in the Seasonal Ice Zone and around the Polar front in the Southern Ocean (Mikaelyan and Belyaeva, 1995; Rembauville et al., 2016a). This process can also occur in the mixed layer if mixing rates are slower than the rate of photo-acclimation (Cailliau et al., 1997; Dusenberry et al., 2000).

Observations conducted at the cellular level under a microscope by Mikaelyan and Belyaeva (1995) were made in the absence of a deep diatom-dominated SCM, confirming photo-acclimation by Southern Ocean phytoplankton communities. Increased cellular concentrations of chlorophyll-*a* could be an indication of a community shift (diatoms often have high cellular chlorophyll-*a*), when chlorophyll-*a* concentrations are compared to particulate organic carbon concentrations (as in Rembauville et al., 2016a). Consequently, it is difficult to distinguish photo-acclimation from community shift in chlorophyll-*a* concentration profiles unless additional pigment or microscopic analysis is performed.

Grazing

Evidence of SCM formation by top-down grazing pressure was not evident in the key literature but has been explored through models. Mixotrophs exert uneven grazing pressure through the water column with higher grazing rates observed at the surface due to light-aided digestion and photooxidative stress (Strom, 2001; McKie-Krisberg et al., 2015). Thus, it has been shown through a model that this uneven grazing pressure could lead to the formation of a SCM in the tropics (Moeller et al., 2019). Mixotrophs may play a significant role in Southern Ocean ecosystems, suggesting the validity of these hypothesis in this region (Froneman and Perissinotto, 1996; Christaki et al., 2008; Moorthi et al., 2009; Norbury et al., 2019). However, their relative abundance is significantly less compared to the tropics and so the importance of this process in controlling SCM formation as revealed by the tropical model may be subdued (Edwards, 2019).

THE ECOLOGICAL ROLE OF SCMs IN THE SOUTHERN OCEAN

Without extensive observations of SCMs, assessments of their impact in Southern Ocean ecology is limited. Regional process studies observed that SCMs contribute to water column primary production (Parslow et al., 2001; Westwood et al., 2011; Tripathy et al., 2014, 2015), facilitate large downward carbon export events (Kemp et al., 2000; Llort et al., 2018), are sites of macrofauna foraging (Dragon et al., 2010; Kahl et al., 2010; Williams et al., 2011; Saijo et al., 2017; Rivière et al., 2019; Siegelman et al., 2019) and are sites of intense zooplankton grazing (Atkinson et al., 1992; Froneman and Perissinotto, 1996; Kopczynska et al., 2001; Parslow et al., 2001; Gomi et al., 2010; Rembauville et al., 2016a). The ecological significance of an SCM is enhanced when they also represent a subsurface biomass maximum, or high primary production, or both. SCMs can exist independently of subsurface biomass maxima and increased primary production, due to changes in cellular chlorophyll-*a* concentrations either by photo-acclimation or a community shift (Cullen, 2015).

To date, diatom SCMs are the most widely observed type of SCM in the pelagic Southern Ocean. They have been recurrently observed south of Tasmania, Australia over several years (Parslow et al., 2001) as well as in the Atlantic and Indian sectors (Bathmann et al., 1997; Tripathy et al., 2015). From fluorometers mounted on BGC-Argo profiling floats and elephant seals, mostly around the Polar front, summertime SFMs occurring at the

pycnocline have been found in 60% of observations (Carranza et al., 2018). This begs the question; Are diatom SCMs responsible for all SCMs/SFMs around the Polar front, and if so, what is the significance of this seasonal and wide-spread persistence?

Southern Ocean SCMs often occur in very low light environments so their contribution to water column integrated primary production may be small. If formed above the pycnocline, SCMs are expected to be active contributors to water column production because they will likely be exposed to sufficient light (Herbland and Voituriez, 1979; Estrada et al., 1993; Cullen, 2015). It is difficult to discern if an SCM that forms below the pycnocline is a productive or senescent feature without measurements of primary production, because communities shift, and communities below the pycnocline function differently to those above (Parslow et al., 2001; Westwood et al., 2011; Tripathy et al., 2014, 2015). Basin-wide observations of SCMs, alongside a better understanding of the photosynthetic efficiencies and biomass of deep communities, are required to assess the potential impacts of SCMs on total water column primary production and the regulation of the global carbon cycle.

Regardless of their contribution to primary production and biomass, diatom SCMs at the pycnocline in the Southern Ocean support unique food webs and contribute to downward carbon export. The ability of a diatom SCM to act as a subsurface biomass maxima is variable and the subsequent relationship of biomass to primary production is complex (Kopczynska et al., 2001; Parslow et al., 2001; Armand et al., 2008; Gomi et al., 2010). Diatom SCMs are active contributors to total summer water column productivity around the Polar front (Parslow et al., 2001; Westwood et al., 2011; Tripathy et al., 2014, 2015). This productivity supports selective grazing by microzooplankton, copepods and heterotrophic dinoflagellates at the SCM, creating a unique trophic structure (Froneman and Perissinotto, 1996; Kopczynska et al., 2001; Parslow et al., 2001; Gomi et al., 2010; Rembauville et al., 2016a). While their growth may be light limited for long periods, diatoms are a form of new production with a high downward carbon export efficiency. Their unique photosynthetic apparatuses have large light harvesting complexes, enhancing their ability to photosynthesize at <1% surface light (Parslow et al., 2001; Tripathy et al., 2015; Goessling et al., 2020). These light levels are extremely low and would halt primary production for most species of phytoplankton. Adding to their remarkable photosynthetic capacities, some species can survive long periods of darkness by forming a resting spore (Ferrario et al., 1998; Armand et al., 2008a,b; Salter et al., 2012). The mass formation of these resting spores off the Kerguelen plateau is a source of large downward carbon export events to the seafloor (Armand et al., 2008b; Salter et al., 2012; Rembauville et al., 2016b). In addition to this, large "fall dump" events occur as the deepening of the pycnocline in autumn forces these deep diatom aggregates to sink (Kemp et al., 2000; Rigual-Hernández et al., 2015b).

The diatom SCM is likely an ecological stage between the coastal bloom and mass export event, apparently employing unique physiological and ecological adaptions to survive in turbulent, low-iron oceanic conditions, where other taxa cannot. It is well established that this subsurface biomass only persists in iron depleted waters where low surface chlorophyll-a is observed (Parslow et al., 2001; Garibotti et al., 2003; Holm-Hansen et al., 2005), but these communities may display successional connectivity with coastal areas driven by ocean physics (Kopczynska et al., 2001; Graham et al., 2015) and diatom life stage (Ferrario et al., 1998; Armand et al., 2008b; Salter et al., 2012). This is suggested by the common coastal occurrence of phytoplankton associated with oceanic SCMs, their eventual deposition on the seafloor (Kemp et al., 2000, 2006; Kemp and Villareal, 2013) and regional differences in community structure (Gomi et al., 2007, 2010).

Other observations of SCMs, not necessarily attributed to diatom SCMs, have shown that Adelie penguins and elephant seals target krill and mesopelagic fish that congregate around SCMs (Dragon et al., 2010; Kahl et al., 2010; Williams et al., 2011; Saijo et al., 2017; Rivière et al., 2019; Siegelman et al., 2019). For elephant seals, this is true both in oceanic regions around the Kerguelen plateau and around the ice-edge. Elephant seals particularly target areas of high kinetic energy, and their prey may be supported by high downward carbon export to the mesopelagic zone via eddies (Saijo et al., 2017; Rivière et al., 2019; Siegelman et al., 2019).

DISCUSSION

This Review presents evidence of Southern Ocean SCMs as a widespread and recurrent summer feature. The formation of these SCMs differs from the processes that form the better-known tropical SCM (**Figure 1**). The most common Southern Ocean SCMs are widespread diatom SCMs which potentially contribute to downward carbon export and primary production. Satellite composites of chlorophyll-a miss these features, introducing biases toward surface communities in ecosystem assessments of downward carbon export, primary production and food-webs that will likely be used in MEASO. Going forward, an integrated platform approach is needed that draws on detailed understandings available from ship-based observations – as presented in this Review – alongside the new wealth of observations from widespread deployments of fluorometers through the BGC-Argo and MEOP programs.

Diatom SCMs are not only missing from ecosystem assessments of the present Southern Ocean but are also missing in future biogeochemical trajectories. Paleo-sediment records have identified increased deposits of opal (a proxy for diatom concentration) around the Polar front, coincident with periods of increasing atmospheric carbon dioxide as seen in Antarctic ice cores (Gottschalk et al., 2016). This negative feedback mechanism, which may be stimulated by increased stratification promoted by warmer and fresher surface waters, is not captured in current biogeochemical models used to make ecosystem assessments of future ocean trajectories (Kemp and Villareal, 2013, 2018).

Incorporating these diatom SCMs, and the processes that lead to their formation, into models has been limited by past observational capacities. These relatively thin features (1–10 m

thick) are not fully captured by coarse ship-based observations (Kemp et al., 2006; Kemp and Villareal, 2013, 2018). Further, knowledge on the active buoyancy regulation of large diatoms is fragmented with the ability to buoyancy regulate and active sinking only recorded for experiments on a few species of large diatoms (Villareal, 1988; Waite et al., 1992; Moore and Villareal, 1996; Fisher and Harrison, 1996; Waite and Nodder, 2001; Boyd et al., 2005; Acuña et al., 2010; Gemmell et al., 2016). Parameterizations for the control of light and nutrients on buoyancy regulation in large diatoms are needed in order to model the behavior of these communities and their interaction with ocean mixing.

Translating widespread observations of SFMs made by the BGC-Argo and MEOP programs to diatom SCMs is essential to understanding the environmental controls of these biogeochemical niches. Key studies discussed here suggest that the composition and prevalence of diatom SCMs communities may be delineated by bathymetry, fronts and sea-ice (**Figure 4**). BGC-Argo can observe these deep diatom-dominated communities as floats routinely samples at <2 m resolution, whilst the ability of MEOP to capture these features under the broken stick sampling method – which represents profiles using a subsample of data based on points of high variability - has not yet been assessed (Guinet et al., 2013).

With increased observation density in time and space, coupled with ocean models, the role of environmental drivers including ocean physics, bathymetry and sea-ice can be explored as it has been for surface chlorophyll-*a* concentrations from satellites (Grant et al., 2006; Graham et al., 2015; Ardyna et al., 2017; Dawson et al., 2018). Connecting coastal processes to diatom SCMs may also be possible by testing the possible links to fertilization of iron by land-masses, sea-ice retreat and along-shelf subduction that have been revealed in this Review. Further the role of frontal structures, eddies, subduction and stratification in controlling other types of SCMs can also be explored.

The greatest limitation in studying subsurface phytoplankton distributions in the Southern Ocean is the translation of chlorophyll fluorescence to chlorophyll-*a* and biomass concentrations. Specifically, the presence of day-time NPQ is the greatest source of inaccuracy to the study of SCMs, causing a SFM to exist where an SCM may not. The variability of fluorescence and chlorophyll to carbon also presents a challenge for conversions to biomass estimates. Further uncertainties introduced along with variations in surface community Chl:C ratios (Behrenfeld et al., 2005; Thomalla et al., 2017), are community shifts with depth to diatoms which contain higher intracellular chlorophyll and more gradual increases of intracellular chlorophyll due to photoacclimation (Mikaelyan and Belyaeva, 1995; Kopczynska et al., 2001; Armand et al., 2008; Gomi et al., 2010; Rembauville et al., 2016a). Understanding these ratios is important for representing Southern Ocean SCMs in biogeochemical models (Galbraith et al., 2010; Aumont et al., 2015; Verdy and Mazloff, 2017).

Until the accuracy of fluorescence-derived chlorophyll-*a* has been resolved, an integrated framework for carefully studying SCMs, through SFMs measured at night is needed. Their translatability to SCMs could be assessed using sparse ship-based data possibly equipped with fluorometers for paired assessments. The potential benefits of this is highlighted by our discussion of Carranza et al. (2018), who may have observed widespread deep diatom-dominated communities around the Polar front through SFMs. When considering ship-based observations in the literature it seems likely that these are oceanic diatom SCMs. Combining the evidence from process studies and autonomous platforms, the role of episodic storms in destroying the stability of diatom SCMs and their subsequent re-formation under calm conditions becomes apparent.

Consequently, ship-based observations will still play a large part in the future discussion on subsurface distribution and production of phytoplankton. Particularly, the role of iron and silicate in mediating SCMs and subsurface production at the pycnocline cannot be studied autonomously and we have found this to be still largely enigmatic. Iron and silicate addition experiments that include deep-diatom communities, as well as cooccurring measurements of iron, silicate and chlorophyll through the water column are needed in the future. These measurements will be particularly important for resolving the role of nutrients in sustaining stable diatom SCMs and SCMs above the pycnocline found near retreating sea-ice and Southern Ocean islands.

Southern Ocean SCMs can no longer be ignored in ecosystem assessments. Our review presents evidence of widespread diatom SCMs that may play an important role in Southern Ocean ecology and climate. Further progress on this topic will only be made through extensive data sharing and collaboration between international researchers to achieve an integrated observation framework (Brett et al., 2020). This framework must use both ship-based studies and autonomous technologies.

AUTHOR CONTRIBUTIONS

KB reviewed the literature and led the production of the manuscript. PS, NH, and PB assisted in conceptual developments and production of the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00671/full#supplementary-material

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PERSPECTIVE
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Overcoming the Obstacles Faced by Early Career Researchers in Marine Science: Lessons From the Marine Ecosystem Assessment for the Southern Ocean

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Pressure in academia and science is rapidly increasing and early career researchers (ECRs) have a lot to gain from being involved in research initiatives such as large international projects. But just how inclusive are they? Here we discuss experiences of ECRs directly involved in the Marine Ecosystem Assessment for the Southern Ocean (MEASO), an Australian led international research project to assess the status and trends of Southern Ocean ecosystems. We review the benefits of ECR involvement in large-scale initiatives to the project deliverables, the leadership team and ECRs themselves. Using insights from MEASO, we outline the obstacles that may become barriers to ECRs in scientific research in general but with a focus on large-scale research projects and suggest potential actions to overcome these at the individual, institutional and scientific community level. We consider the potential for ECRs to lead future Antarctic science programmes with a focus on science communication and applied research for policy makers within a global setting.

Keywords: ECR, mentorship, diversity and inclusion, polar science, interdisciplinarity

INTRODUCTION

The successful delivery of high quality and long-term research in most disciplines, including Antarctic and Southern Ocean research, requires both international and inter-generational collaboration. It is therefore imperative that Antarctic research initiatives involve the next generation of polar scientists and prepare them to become effective future leaders of such

initiatives. Historically as with other disciplines, polar research has predominantly focused on the achievements of more established scientists, particularly senior career-staged males (Nash et al., 2019). Although inequities have been reduced in recent history, for example 46% of the projects from the Chilean Antarctic program were led by women in 2019 (INACH, 2019) and the establishment of Pride in Polar Research in 2018[1], Antarctic and Southern Ocean research still lacks diversity across gender, sexuality, cultural background, and experience. The involvement of early career researchers (ECRs), defined as researchers within 5 years of a terminal degree, in large-scale initiatives fosters many benefits. These benefits may include promoting diversity, capacity building and greater transference of Southern Ocean knowledge to the next generation by allowing ECRs to draw upon their scientific expertise, experience, and innovation. However, there are numerous obstacles to ECR involvement in such initiatives (Patterson et al., 2013; Sobey et al., 2013; Jaeger-Erben et al., 2018; Pannell et al., 2019). Examples include a lack of relevant research or support networks (Bridle et al., 2013; Macoun and Miller, 2014; Freeman, 2018), scarcity of long-term contracts (Sobey et al., 2013), failure to include contributing ECRs in papers (Maestre, 2019), a lack of travel support (Bradley et al., 2020) and a competitive academic hierarchy (Pannell et al., 2019). In this manuscript, we explore these obstacles and suggest actions to overcome these barriers using our experiences from the Marine Ecosystem Assessment for the Southern Ocean (MEASO) initiative. We also identify the role ECRs can have in Antarctic and Southern Ocean research moving forward although it is also applicable to research in general.

Marine Ecosystem Assessment for the Southern Ocean is an ongoing international collaborative Antarctic and Southern Ocean research project begun by the Antarctic Climate & Ecosystems Cooperative Research Centre (ACE CRC) in Hobart, Australia, in 2018. The overarching aim of MEASO was to assess the status and trends of Southern Ocean habitats, species, and ecosystems. The outcomes of these assessments are presented in this Research Topic and, in future, in a summary for policymakers.

The participation of ECRs in large-scale initiatives like MEASO not only enriches scientific and political debates with diverse and "fresh" perspectives, but also provides an opportunity for ECRs to develop collaborative skills such as networking, communication, interdisciplinary knowledge, leadership and team-building. In addition to the above, these opportunities boost ECR self-esteem, foster wider collaborations that can lead to job opportunities and encourage ECRs to stay in science. They can also cultivate competencies frequently required by funding agencies, which can be difficult to develop within traditional academic training processes (Hindshaw et al., 2018). Large organizational bodies, such as the Scientific Committee on Antarctic Research (SCAR), recognize that providing opportunities for ECRs to voice their opinions on the development of international research priorities, themes and collaborations is valuable. SCAR and associations organizational bodies, such as the Association of Polar Early Career Scientists (APECS) provide many opportunities for ECR involvement including specific ECR workshops and reviewing opportunities such as the review of the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report[2].

ECRs as a Part of MEASO

From the outset, MEASO has involved community consultation, whereby both stakeholders and academics of all stages, including ECRs, have been encouraged to participate in the assessment process at any level of engagement. The first milestone in the MEASO process was the MEASO2018 international conference held in Hobart, Australia[3]. The conference was an important opportunity for the scientific community to engage with policymakers, the private sector, and civil society toward a common goal of assessing the Southern Ocean. In total, 175 participants from 23 countries attended the conference. ECRs represented approximately one-third of all attendees (see **Figures 1A,B** for additional statistics on ECR contributions to MEASO).

Early career researchers were pivotal in the pre-conference organization, including contacting and inviting potential contributors. Direct contact with the MEASO steering committee allowed for a welcoming environment in which ECRs were encouraged to share ideas, network with other attendees, and participate in breakout groups. In addition, a pre-conference ECR workshop was co-hosted with APECS which focused on ECR involvement in large international initiatives[4]. ECRs were also offered to partake in a mentorship programme whereby they were paired with a more senior attendee, who could be a point of contact and provide guidance during the conference. Mentoring programmes like the one offered at MEASO2018 are not universal but have been a major contributing factor to the success of other research programmes such as the 2007–2009 International Polar Year (Baeseman et al., 2011). A unique component of the MEASO2018 conference was a day-long research-policy forum, which provided an opportunity for ECRs to experience discussions among scientists, policymakers, and industry to identify ways to achieve a sustainable future for the Southern Ocean. These discussions were used to structure the core papers of the MEASO Research Topic in Frontiers in Marine Science.

Following the conference, ECRs participated in a range of essential roles related to the MEASO assessment process. One of the more significant roles included co-authoring, and in some cases, leading articles for this Research Topic as well as previous MEASO publications [e.g., Brasier et al. (2019)]. Another unique role involving ECRs included writing, editing and the reviewing of Wikipedia-style MEASO biota pages for

[1]https://www.scar.org/general-scar-news/celebrating-polar2018/

[2]https://www.apecs.is/news/apecs-news/3571-call-for-reviewers-of-the-second-draft-of-working-group-i-contribution-to-ipcc-sixth-assessment-report-ar6.html

[3]http://www.MEASO2018.aq

[4]http://www.measo2018.aq/apecs

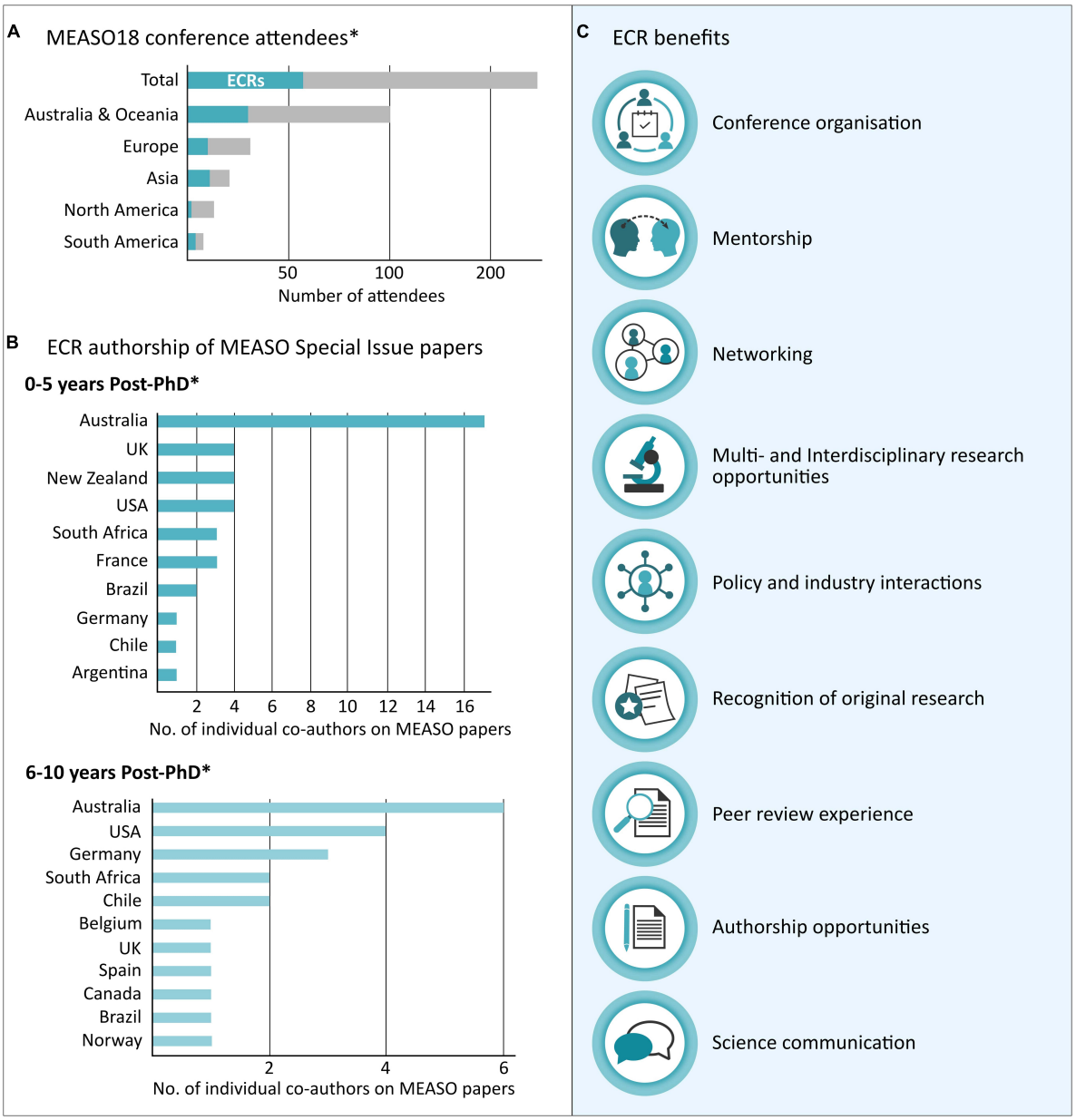

FIGURE 1 | Early career researcher (ECR) participation and resulting benefits from their involvement in the Marine Ecosystem Assessment for the Southern Ocean (MEASO). **(A)** attendance at the MEASO2018 conference by continent **(B)** ECR and mid-career researcher (MCR) authorship of MEASO Research Topic papers by country **(C)** a list of benefits and opportunities created for ECRs during the MEASO project. * Continents/countries represent institutional affiliation not nationality of individuals. ECRs are defined as researchers being within 5 years of finishing a Ph.D. or other terminal degree, which is the definition used by the Scientific Committee on Antarctic Research and MCRs as those within 5–10 years of their Ph.D. Data used in this figure is supplied in the **Supplementary Material**.

the Southern Ocean Knowledge and Information wiki (SOKI)[5]. ECRs also developed and managed the MEASO Twitter page (@MEASO20), producing new infographics targeted at general audiences and sharing research outcomes and projects weekly. **Figure 1C** highlights the aspects of the MEASO process in which ECRs were engaged, and their potential to greatly benefit ECR experience in polar research.

This article presents perspectives of 16 ECRs from 8 different countries directly involved in the MEASO project (e.g., conference attendees, SOKI contributors and/or authors within the MEASO Research Topic). Specifically, the aims of this manuscript are to:

(1) Discuss the benefits of ECR involvement in large research projects such as MEASO, to both ECRs and the project itself.

[5]http://soki.aq/

(2) Identify obstacles to ECRs in science and their involvement in large international research projects, how MEASO faced these obstacles, and how the research community could further overcome these obstacles to support ECRs.
(3) Provide a MEASO ECR perspective on the role of ECRs in the future of Antarctic and Southern Ocean research.

OBSTACLES AND ACTIONS

Overall, MEASO created an inclusive working space for many ECRs engaged in the project. However, long-term obstacles to ECR involvement in similar initiatives do exist in Antarctic and Southern Ocean research and across other scientific disciplines (Chapman et al., 2015; Mallaband et al., 2017; Ayala et al., 2019). We summarize eight key obstacles (**Table 1**) and suggest potential actions from the perspective of the MEASO ECR community that can be implemented at the individual, institutional and research community level to enhance scientific engagement. See the expanded version of **Supplementary Table S1**.

Pressure to Network

The highly competitive nature of modern academia, where there are more applicants than available jobs, places significant pressure on ECRs to network with senior researchers at conferences and meetings. However, as stated in Sobey et al. (2013) "most networking opportunities are found at higher levels." We (the MEASO ECR community) encourage ECRs to engage in mentoring programmes, research groups within their community and seek sponsors who can enhance their confidence, visibility, credibility, and professional networks (Ansmann et al., 2014; Fenton et al., 2016; Gottlieb and Travis, 2018; Bohleber et al., 2020). The academic environment has changed rapidly over the last decades (Pitt and Mewburn, 2016), and the issues ECRs face now are most likely different from those their mentors faced earlier in their careers. For this reason, we encourage institutions and the wider research community to invest in and promote mentoring training programmes.

Early career researcher Mentors (i.e., those officially assigned through a mentoring scheme or an ECR supervisor), across all disciplines could engage in faculty training targeted at providing a space in the academic pipeline for ECR career progression (Sood et al., 2016). Funding for such initiatives could coincide with organizations, universities and institutes investing in training opportunities for ECRs. Training may include workshops on career advice, writing manuscripts, science communication, mental health, ethics and schemes aimed at tackling inappropriate behavior toward ECRs, which may go unreported and lead to career attrition in science (Nash et al., 2019). Institutions should provide advice for mentors not only focused on mentorship, but also on the idea of "sponsorship" to provide collaborative and supportive outcomes that advance an ECR's career. This would help generate positive wellbeing in the workplace (increasingly important in modern academia; Maestre, 2019), improve grant success (Libby et al., 2016) as well as competence and retention of a diverse workforce (Sood et al., 2016). Thus, there are many social and economic reasons for institutes to invest in mentor training, beyond just the benefit to ECRs.

Competition

The imbalance between the number of ECRs and research positions and grants has resulted in immense competition between researchers for funding opportunities. With many grant applications being specific to ECRs they are constantly competing against their peers. Such competition can prevent collaborations and negatively impact working relationships (Anderson et al., 2007). This could inhibit their involvement in large-scale research initiatives. Furthermore, with limited research positions available, ECRs may be competing with mid-career and senior researchers for institutional positions. We encourage ECRs and their institutes to invest in technical and research training opportunities and promote a more humane, collaborative, and healthy work environment that discourages competition (Maestre, 2019). It is important to develop the soft skills and confidence of ECRs to improve their working relationships (Boeren et al., 2015; Hindshaw et al., 2018).

Pressure to Publish

Researchers are evaluated based on publications, especially in high impact journals, and citation numbers (Chapman et al., 2019), resulting in an increasing pressure to publish across research disciplines. Whilst many ECRs publish within their Ph.D., they may not be established enough to be invited to co-author manuscripts (Elmassry, 2020). This may deter them from getting involved in large-scale research initiatives or using other methods of science communication due to being viewed as less valuable or a lower priority. Publishing in high-impact journals frequently depends more on the research team than the ECRs themselves. We suggest increasing the value of alternative research outcomes and activities, such as leadership of small projects, public science articles or policy contributions, and the facilitation of co-authorship of papers within research groups and large research initiatives.

Academic Job Market and Career Uncertainty

The lack of jobs in academia and the highly competitive nature of funding schemes can make relocation an essential part of a research career in most scientific disciplines (Skakni et al., 2019). However, the short-term contracts offered to many ECRs can limit their outputs, create career uncertainty and impact their mental well-being (Nash et al., 2019; Woolston, 2020). We encourage ECRs to join interdisciplinary networks, perhaps by using associations such as APECS and SCAR working groups as a starting point. ECRs can actively follow the APECS job board[6] and SCAR working groups, which circulate job postings on request. ECRs can also seek support from institutions to provide longer term contracts, career development and workshops on how to attract funding with salary support (Sobey et al., 2013).

[6]https://www.apecs.is/career-resources/job-board.html

TABLE 1 | Major obstacles often experienced by early career researchers (ECRs) in science and the possible key actions that can be taken to improve them at the individual (I), institutional (In), and Antarctic and Southern Ocean research community level (RC) that may also apply to other marine and science disciplines.

Obstacles	Key actions	MEASO examples
(1) Pressure to network	• Provide mentoring and sponsorship programmes at conferences and within institutes and universities (In, RC) • ECR involvement and inclusion in organizations and research networks (I) • Utilize social media platforms to connect with other researchers (I) • International and diverse supervisory teams (In) • Offer remote attendance for those ECRs unable to travel to conferences or workshops (In, RC)	• 2018 Conference had a mentoring program • ECRs were involved in the conference planning, organization and running • Conference registration fee waived for ECR organizers and prize winners • Co-hosted an ECR workshop with APECS • An ECR led Pew funded project resulting in a Nature publication (Cavan et al., 2019) • Remote attendance was offered for the 2019 United Kingdom workshop
(2) Competition	• Promote a more humane, collaborative, and healthy work environments that discourage competition (In) • Promote skill development including technical and research training (In) • Where possible offer in-house training or ECR discounted attendance fees (In, RC)	• ECRs specifically asked to provide content for the SOKI pages on Antarctic and Southern Ocean biota and ecosystems
(3) Pressure to publish	• Value and fund alternative research outcomes and activities e.g., science communication, articles, policy reports (RC) • Facilitate the successful publication of ECR research (e.g., funding the publication costs for open access articles) (In) • Create and support co-authorship opportunities (In, RC)	• ECR presentations and posters were awarded at the end of the conference. • ECRs were interviewed by local radio stations during the conference • ECRs participated as lead and co-authors in this special issue as well as in earlier MEASO publications (e.g., Brasier et al., 2019)
(4) Academic job market and career uncertainty	• Join interdisciplinary networks (I) • Minimum term contracts >1 year in funding for ECR salary in large research projects (In) • Provide workshops on obtaining funding (In, RC)	• Employed several temporary ECR workers from 6 to 18 months
(5) Work-life balance	• Project councils and committees should lead by example (In, RC) • Prioritize well-being and long-term sustainability of working collaborations (In, RC) • Accessible and freely available counseling support (In) • Dedicated time and funding for student support roles (In)	• Conference provided free on-site childcare facilities and personnel for all attendees • Meeting notes were circulated for those unable to attending online lead author and committee meetings
(6) Language barriers	• Offer free language training (In) • Free Language support e.g., copy editing and translation (In) • Provide translated or plain language summaries of key research outcomes (In, RC) • Encourage English speakers to learn another language (In) • Non-English events at conferences (RC)	• MEASO will publish a plain English summary highlighting key messages for policymakers and stakeholders with the potential for translation into languages used by the Antarctic Treaty System
(7) Voicing an opposing opinion	• Respect all scientific opinions (In, RC) • Encourage scientific discussion (In, RC) • Code of conduct to prevent harassment (In, RC)	• The MEASO process aimed to provide an unbiased assessment of the literature which represented diverse scientific perspectives
(8) Discrimination	• Zero tolerance policy of discrimination of any kind (In, RC) • Promote diversity groups such as Women in Polar Science and Pride in Polar Research (In, RC) • Clear and accessible reporting mechanisms for harassment, abuse and bullying in the workplace and science events (In, RC)	• Conference hosted a Women in Antarctic Science breakout session • MEASO ensured that on-site participation for the United Kingdom workshop in 2019 was diverse across gender, nations, expertise, and experience

We highlight examples of such actions used during the MEASO project. An extended table with more detailed actions is available in the ***Supplementary Material****.*

Lack of Work-Life Balance

Maintaining a work-life balance benefits academic productivity and publication outputs (Bielczyk et al., 2019). Without consideration for personal well-being, researchers, disproportionately PhDs and ECRs (Mitra and McAlpine, 2017; O'Neill and Schroijen, 2018), run the risk of experiencing burnout and mental health issues (e.g., Petersen, 2011). Recognizing this at higher-levels and leading by example to implement flexible working arrangements and well-being support systems across institutions sets a standard of work-life balance. This standard must include those with (or planning) a family, or in caring roles (Calisi and A Working Group of Mothers in Science, 2018). Consequently, institutions and research laboratories incorporating these work ethics show improved productivity and creativity (Hunter, 2019). We also encourage mid-career and senior members of the research community to lead by example to promote working more effectively and efficiently over working more hours (Powell, 2017).

Language Barriers

Research communities are made up of multiple nationalities and languages, however, English remains the primary scientific language. This disadvantages ECRs that come from non-English speaking countries by limiting their potential output, hindering expression of their ideas and restricting their networking abilities and the reach of their research, along with associated racial biases. Additionally, terminology between disciplines can be a barrier for collaboration across science, policy, and the social sciences (Pannell et al., 2019). We encourage free language training, translation, and copy-editing services to non-native English speakers but also the translation and plain language summaries of key publications. Institutes could also provide language training for English speakers to learn another scientific language and conferences could host non-English speaking events.

Voicing an Opposing Opinion

Early career researchers can be hesitant to publish controversial research or object to proposed projects for fear of damaging their future career. By utilizing research networks and institute workshops, ECRs should be able to discuss these perspectives in a safe and supportive environment. Supervisors should also be trained to encourage everyone to contribute, even if they have opposing views.

Discrimination

Early career researchers bring new perspectives and a diverse set of skills to large-scale research initiatives (Fritz et al., 2015; Hindshaw et al., 2018). Valuing the opinions and perspectives of emerging researchers in science facilitates the identification of previously unexplored gaps and diverse ways of thinking. However, despite these benefits, in some cases, the opinions and perspectives of ECRs tend to be dismissed by more established researchers. Discrimination as a result of age, career stage, class, race, sexuality and gender should not be tolerated. To promote diversity in research we encourage researchers to join diversity groups such as Women in Polar Science (@WomeninPolarSci on Twitter), Minorities in Polar Research (@PolarImpact on Twitter) and Pride in Polar Research (@PolarPride on Twitter). Institutes and the wider research community can lead by example, such as ensuring diverse representation on selection panels and committees (Nash et al., 2019).

PERSPECTIVES OF ECRS ON THE FUTURE OF ANTARCTIC AND SOUTHERN OCEAN RESEARCH AND THEIR ROLE IN IT

Across many disciplines there is a shifting research culture from individualistic, competitive practices to models of interdisciplinary collaboration and transparency which may help address many of the challenges faced by ECRs today (**Table 1**). Whilst such a shift requires changes to be made at multiple organizational levels (from individual projects up to large institutional and multinational goals), appreciating diverse views and adopting a broad vision for the application of research findings across fields can help build a more inclusive environment. Doing so may advance our ability to address the ever more complex and *trans*-disciplinary challenges (e.g., Global Change) being faced today (Hossain et al., 2017).

Antarctic and Southern Ocean research needs to be high-quality and evidence-based to contribute to decision making and policy development for ultimate protection of vulnerable Antarctic ecosystems (Kennicutt et al., 2015; Hughes et al., 2018). Protecting and understanding these ecosystems is of global importance as environmental change within Antarctica has implications for global climate, sea level, biodiversity, and society (Kennicutt et al., 2014). ECRs are well-placed to conduct this research with the modern research landscape requiring ECRs to be generalists, working across disciplines with a wide range of collaborators. ECRs able to travel between institutes to establish such collaborations need travel support from their project budget or schemes such as the SCAR/Council of Managers of National Antarctic Programs (COMNAP) fellowships[7]. In addition, ECRs are actively trained in science communication using the most updated technologies and platforms as well as traditional methods. This training will benefit discussions and correspondence between researchers, policymakers and the general public, as well as fostering integrated, cross-disciplinary research teams. These cross-disciplinary and communicative skill sets of ECRs may also assist in the integration of Antarctic and Southern Ocean research into global policies and initiatives such as IPCC reports (for example, IPCC, 2019) and the United Nations Decade of Ocean Science for Sustainable Development (Pendleton et al., 2020), which will facilitate recognition of the impacts and importance of Antarctic and Southern Ocean research.

Evaluating research projects and the scale upon which they are likely to be relevant to policymakers and the broader

[7]https://www.scar.org/awards/fellowships/overview/; https://www.comnap.aq/expert-groups/education-outreach-training-expert-group/comnap-antarctic-fellowship/).

scientific community continues to be an important priority in today's dynamic management and political culture. This may be challenging for ECRs striving to generate impactful and timely research, with many working on projects with short timescales and limited access to long-term observations. In such circumstances, large collaborative initiatives provide the necessary opportunities for ECRs to participate in larger-scale initiatives relevant to policy (Chapman et al., 2015; Evans and Cvitanovic, 2018). For long-term initiatives, such as national research programs, engaging with ECRs in the early stages of planning, may offer significant benefits to their long-term success. For example, a range of new infrastructures and research initiatives are coming to fruition within many national polar research programmes, which, once established, will require engagement from today's ECRs. The predicted lifespan of new research vessels is around 30 years (e.g., the RSV *Nuyina*)[8], during which time today's ECRs are set to be highly involved over their research careers in planning scientific activities on-board the ship, including the management and execution of cruises. We encourage ECRs to engage in longer-term initiatives and action plans within national programmes as this could promote opportunities in the future.

FINAL REMARKS

The opportunity for ECRs to engage directly at a high level in comprehensive projects such as MEASO, while historically rare, is increasingly becoming the standard in marine research. Whilst ECRs need to take a proactive approach, they also need support from supervisors, mentors and research institutes to facilitate these opportunities. Overall, MEASO created positive opportunities and outcomes for a small number of ECRs. We have suggested specific future actions for ECRs and the marine research community to support ECRs in improving their potential longevity in this space and capacity to lead future research programmes. ECR engagement in initiatives such as MEASO provides ECRs with the experience and skills to help acquire funding for their own research projects, which contributes to the development of their own independent research teams (Majaneva et al., 2016; Hindshaw et al., 2018). However, many barriers remain to ECR involvement in such initiatives that must be addressed at the organizational, institutional, and community level, before today's ECRs will be able to lead a second MEASO in the future.

We have provided a general ECR perspective on the future of marine research with a focus on how science is delivered. We feel that the future success of marine research will require the following: (1) effective communication of research outcomes to diverse audiences, and (2) its incorporation into globally relevant and impactful reporting aligned with global research initiatives beyond an Antarctic and Southern Ocean focus. We encourage further discussions and qualitative surveys from an ECR perspective to investigate the priorities, gaps, trajectories and pathways to overcome barriers to ECR engagement in marine research.

[8]http://www.antarctica.gov.au/icebreaker/about-the-ship

DATA AVAILABILITY STATEMENT

All datasets presented in this study are included in the article/ **Supplementary Material**.

AUTHOR CONTRIBUTIONS

MB and SM conceptualized this manuscript and sought co-authors and created an outline of the manuscript. All authors were involved in discussion regarding the aims and content of the manuscript. MB and CW led manuscript production including the designation of sections to co-authors, editing, and streamlining text contributions. MB, CW, and CO wrote the introduction and section "Obstacles and Actions" with JC and JE contributing significantly to the benefits of ECRs in large research projects. Section "Perspectives of ECRs on the Future of Antarctic and Southern Ocean Research and Their Role in It" was designed by MB and EC with text contributions from EC, BF, PP, SH, and RS. SM created **Figure 1** based on ideas from co-authors. Additional text in section "Perspectives of ECRs on the Future of Antarctic and Southern Ocean Research and Their Role in It" was written by JE, SM, EC, NB, and SM. AH, SM, BF, and CW wrote section "Final Remarks" and MB wrote the final remarks incorporating opinions of all co-authors. All co-authors commented on and edited draft versions of the manuscript. MB finalized the manuscript for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00692/full#supplementary-material

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Conflict of Interest: JE was currently employed by the Cawthron Institute, a private research institution that also offers a range of commercial services.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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frontiers in Ecology and Evolution

REVIEW
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Marine Ecosystem Assessment for the Southern Ocean: Birds and Marine Mammals in a Changing Climate

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The massive number of seabirds (penguins and procellariiformes) and marine mammals (cetaceans and pinnipeds) – referred to here as top predators – is one of the most iconic components of the Antarctic and Southern Ocean. They play an important role as highly mobile consumers, structuring and connecting pelagic marine food webs and are widely studied relative to other taxa. Many birds and mammals establish dense breeding colonies or use haul-out sites, making them relatively easy to study. Cetaceans, however, spend their lives at sea and thus aspects of their life cycle are more complicated to monitor and study. Nevertheless, they all feed at sea and their reproductive success depends on the food availability in the marine environment, hence they are considered useful indicators of the state of the marine resources. In general, top predators have large body sizes that allow for instrumentation with miniature data-recording or transmitting devices to monitor their activities at sea. Development of scientific techniques to study reproduction and foraging of top predators has led to substantial scientific literature on their population trends, key biological parameters, migratory patterns, foraging and feeding ecology, and linkages with atmospheric or oceanographic dynamics, for a number of species and regions. We briefly summarize

the vast literature on Southern Ocean top predators, focusing on the most recent syntheses. We also provide an overview on the key current and emerging pressures faced by these animals as a result of both natural and human causes. We recognize the overarching impact that environmental changes driven by climate change have on the ecology of these species. We also evaluate direct and indirect interactions between marine predators and other factors such as disease, pollution, land disturbance and the increasing pressure from global fisheries in the Southern Ocean. Where possible we consider the data availability for assessing the status and trends for each of these components, their capacity for resilience or recovery, effectiveness of management responses, risk likelihood of key impacts and future outlook.

Keywords: marine ecosystem assessment, marine predators, climate change, fisheries interactions, conservation management, Antarctic

INTRODUCTION

The massive number of seabirds and marine mammals – hereafter referred to as top predators[1] – is one of the most conspicuous and iconic components of the Antarctic and Southern Ocean (**Figure 1**; Ropert-Coudert et al., 2014). Some species solely inhabit the polar region, adapted to survive and thrive year-round in this highly seasonal environment, such as the emperor penguin (*Aptenodytes forsteri*) famous for breeding on the ice during the austral[2] winter (Stonehouse, 1952). Others are based on the scattered subantarctic islands, and commute between prey patches at sea and their breeding sites, sometimes covering extraordinary distances to do so, like the wandering albatross (*Diomedea exulans*). Still other populations, notably baleen whale species such as the humpback whale (*Megaptera novaeangliae*), undertake mass migrations poleward to capitalize on the high marine productivity during the spring and summer periods. These migratory movements connect the apparently isolated Southern Ocean environment with the temperate and tropical regions (see Murphy et al., to be published in this research topic), and in some cases even pole-to-pole, as in the case of the Arctic tern (*Sterna paradisaea*) (Egevang et al., 2010).

Rapid climate-related change is already manifesting in the physical environment and biological dynamics of the Southern Ocean (high confidence) (Meredith et al., 2019; Rogers et al., 2020). Within this apparently remote region, seabirds and marine mammals are also increasingly influenced by other human-related impacts (e.g., Erbe et al., 2019; Rodríguez et al., 2019; Ropert-Coudert et al., 2019). While relatively well-studied compared to other ecosystem components, knowledge of marine predators is still biased by accessibility (e.g., land-based versus oceanic or pack-ice breeders, also cryptic deep divers), seasonality (primarily summer studies) and also in relation to age or life-history stages (e.g., paucity of knowledge on juvenile, non-breeding individuals). Key trophic processes supporting oceanic and ice-related food webs are still being unraveled.

The first Marine Ecosystem Assessment for the Southern Ocean (MEASO) is an activity of the IMBer-SCAR program Integrating Climate and Ecosystem Dynamics in the Southern Ocean. The primary aim of MEASO is to assess the risks to Southern Ocean marine ecosystems from climate change and related change processes. As a core MEASO contribution, this paper summarizes the vast literature on Southern Ocean seabirds (flying and diving) and marine mammals (fur and true seals, and baleen and toothed cetaceans) to present the current state of knowledge. We provide an overview of the key pressures, arising from natural and human causes, that these animals face at sea and on land, recognizing the overarching effect that environmental changes – driven by global climate change – have on the ecology of these species. We also evaluate direct and indirect interactions between marine predators and other key stressors including the impacts of historical harvesting, the increasing pressure from fisheries in the Southern Ocean, global pollution, disease and stress, and terrestrial disturbances.

Different Southern Ocean marine systems are affected by and respond to change in different ways. Effects on species' ecology, and their status and trends, are species-specific and variable depending on location. Yet all seabirds and marine mammals feed at sea, their fitness, survival and reproductive success depending on the food availability in the marine environment. Their dependency on lower trophic level prey, such as Antarctic krill (*Euphausia superba*) linked directly to primary productivity, makes them particularly sensitive to bottom-up environmental changes driven by climate change. Therefore, top predators are widely considered useful indicators integrating the state of marine resources (Hazen et al., 2019).

DATA, METHODS AND TOOLS

Quantitative knowledge of the ecology of Southern Ocean top predators has rapidly increased in recent decades, facilitated by: (1) more researchers visiting more Southern Ocean sites, often for longer periods; (2) new and cheaper methods, technologies and techniques for collecting and analyzing data (**Figures 2, 3**) recognition of the importance of long-term, longitudinal data sets by researchers and funding organizations. Concurrently, the

[1]Not all species covered here are top predators, some refer to these diverse taxa as "meso- and top-predators" but, for simplicity, we will use the term top predators throughout.

[2]Seasons referred to are austral seasons throughout.

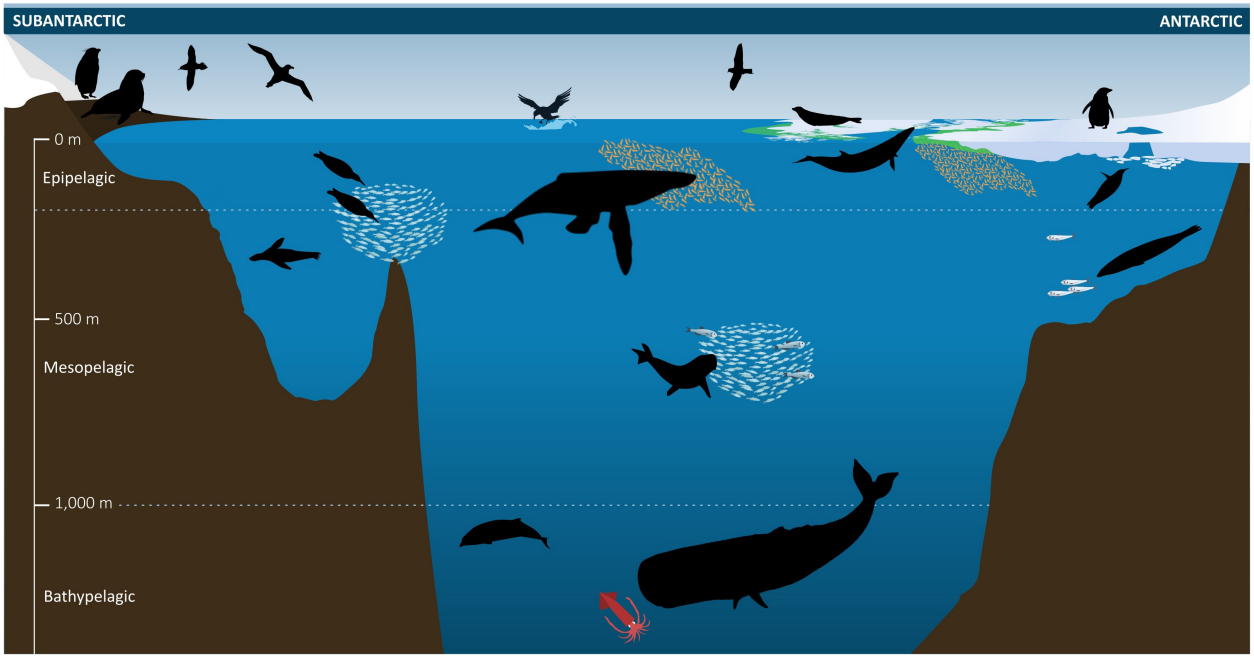


FIGURE 1 | Top predators (black) distribute throughout the Southern Ocean, horizontally, from the continent to the subantarctic islands, as well as vertically, with deep-diving species following their prey down to >2000 m.

role of freely accessible datasets has become widely recognized because of their contributions to diverse initiatives and because no single research group can obtain sufficient data over the spatial and temporal scales relevant to marine predators.

Methods for Studying Marine Predators

Population Monitoring

At sea, shipboard observations are a traditional way of estimating the presence of given taxa. These observations may be from "platforms of opportunity" (e.g., regular transits to supply Antarctic stations, tourism vessels, commercial fishing vessels) or dedicated surveys. The observations are only available along ship tracks, but once collected in atlases (e.g., De Broyer et al., 2014) they can provide a holistic circumpolar view of the spatial distribution of top predators, albeit that the providence of observed individuals remains unknown. Further, survey data (ships, helicopters, fixed-wing aircrafts) can be used to estimate the abundance of species for a given area (e.g., Southwell et al., 2004; Williams et al., 2014) using density surface modeling methods relating observations to environmental covariates and estimating relative spatial distributions (e.g., Friedlaender et al., 2006).

On land, population counts via direct observation (e.g., Wege et al., 2016a), or aerial photography by aircraft (e.g., Weimerskirch et al., 2018), gliders (e.g., Kahl et al., 2010), drones (e.g., Goebel et al., 2015; Gray et al., 2019; Johnston, 2019) or kites (Delord et al., 2015) have been conducted at key sites for many decades. This yields detailed information on interannual patterns in abundance (e.g., Wege et al., 2016a) or intra-annual behavior, for example, phenology (e.g., Barbraud and Weimerskirch, 2006), but sites where counts are routinely conducted in longitudinal studies are spatially very limited. Remote observation might improve this (e.g., Southwell and Emmerson, 2015; Labrousse et al., 2019) and satellite surveillance can enable remote area assessment, at large scale and much reduced cost (LaRue and Knight, 2014). Counting animals from satellite images manually can be time-consuming and researchers are harnessing Deep Learning (e.g., Gonçalves et al., 2020) and citizen science through crowdsourcing, where online volunteers identify animals in the images (LaRue et al., 2019).

Long-term programs where individuals are marked or tagged enable trends in demographic parameters to be related to natural and anthropogenic environmental variation (e.g., Crawford and Cooper, 2003; Pardo et al., 2017). Increasingly, this information is linked to other aspects of a population or individual's ecology, such as genetic information (e.g., Forcada and Hoffman, 2014) or habitat use (e.g., Hindell et al., 2017).

Animal-Borne Technologies

Biotelemetry, where positional data are sent to a radio base (radio-telemetry) or relayed by satellite to a land-based platform (satellite telemetry), became widespread in the early 1990s, when it revealed the impressive distances that some species can cover (e.g., Jouventin and Weimerskirch, 1990). Satellite telemetry is now commonly used, especially to track species or life-history stages for which recapture is difficult or impossible, such as fledglings and juveniles (e.g., Orgeret et al., 2016). A key limitation is the quantity of data that can be transmitted to available satellites during the short surface times of diving animals. Nonetheless, thousands of individuals have been tracked

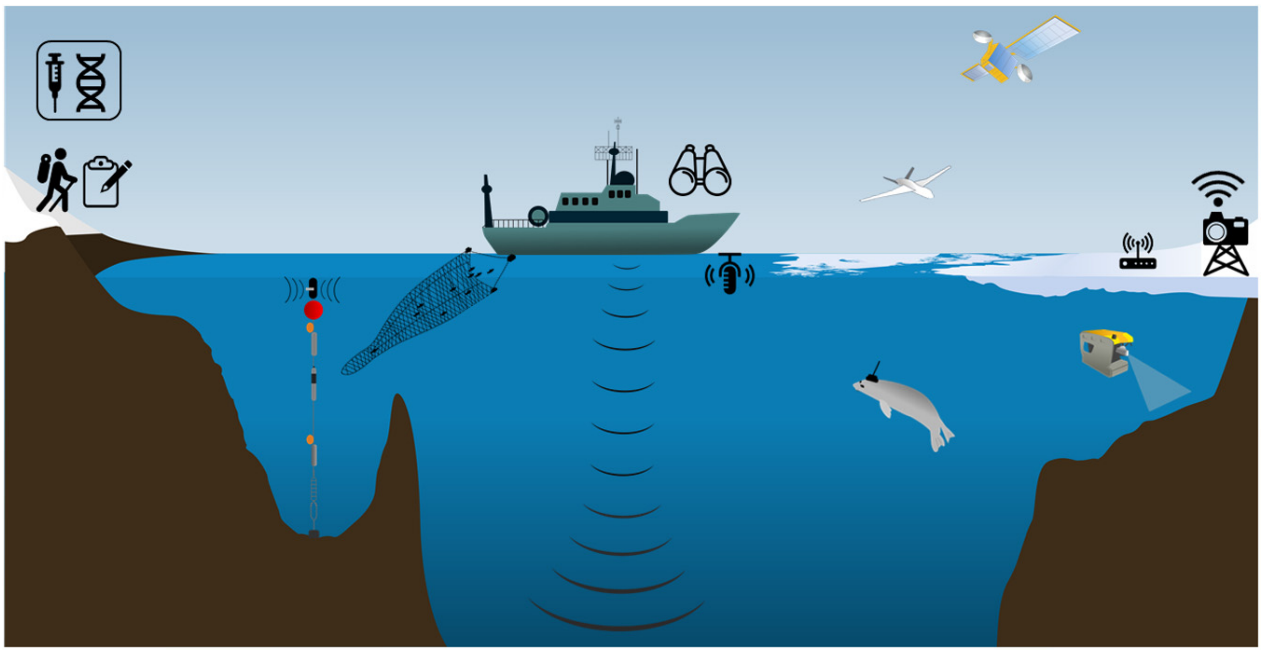


FIGURE 2 | Observational capacity, from traditional direct observations (visual population census, biological sampling) through to (semi-)automated processes (e.g., census counts via aerial photography from drones, satellite-based images and networks of remotely operating cameras). Vertical distribution is an important element constraining observational capacity. Underwater observations can be ship-based from active (e.g., echosounder) and passive (e.g., sonobuoy) acoustics, but are increasingly from technological advances in biotelemetry, automated underwater vehicles and underwater moorings (e.g., the Southern Ocean hydrophone network monitoring trends in whale abundance, distribution, and seasonal presence through use of passive acoustic techniques).

in the Southern Ocean using biotelemetry and bio-logging techniques (Ropert-Coudert et al., 2020), contributing to our understanding of the at-sea distribution and behavior of top predators (e.g., Reisinger et al., 2018; Hindell et al., 2020; **Figure 3**).

In comparison, archival bio-logging devices (Ropert-Coudert and Wilson, 2005; Ropert-Coudert et al., 2012) allow high quantities of continuous high-resolution streams of environmental and biological data to be recorded inside/outside animals and stored in onboard memory with ever-growing capacities. The disadvantage is the necessity to recapture individuals to retrieve devices. A new generation of devices combining the advantages of both biotelemetry and bio-logging (e.g., Heerah et al., 2019) has enabled cross-disciplinary studies, recording not only the georeferenced physiological and behavioral activity of animals, but also enabling measures of *in situ* physical parameters of the environment directly surrounding the animal. International programs like the Marine Mammals Exploring the Oceans Pole to Pole (MEOP) (Treasure et al., 2017) illustrate this well, as about 70% of oceanographic profiles measured south of 60°S come from bio-loggers (Fedak, 2013).

Regarding foraging ecology, bio-loggers were developed to measure the temperature inside the stomach (Wilson and Culik, 1991) or the esophagus (Ancel et al., 1997) of seabirds to detect prey ingestion and to some extent, size (but see Grémillet and Plös, 1994). Other approaches used beak movements (Wilson et al., 2002a), speed changes (Wilson et al., 2002b), accelerometry (Yoda et al., 2001), changes in diving profiles (Bost et al., 2007), a combination of these (Ropert-Coudert et al., 2001), or video-cameras mounted on animals (e.g., Krause et al., 2015; Thiebot et al., 2017) to infer prey encounter and/or ingestion.

Biomolecular Methods

Foraging

Information on predators' feeding ecology is required to understand how changes in their prey might affect their status, as well as understand the status of their prey. Methods for learning about feeding ecology have evolved from early dietary studies collecting stomachs from dead animals, through using stomach evacuation procedures on live animals (Wilson, 1984), to modern genetic and other techniques for assessing prey composition from feces or tissue samples (McInnes et al., 2017a).

Stable isotope analysis has become popular for investigating predator diet and foraging habitat (e.g., Newsome et al., 2010). Most often, nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotope ratios are used to estimate trophic level and foraging habitat, respectively. The latter relies on the strong baseline $\delta^{13}C$ latitudinal gradient, or "isoscape" in the Southern Ocean (e.g., Jaeger et al., 2010; Brault et al., 2018). Oxygen stable isotope ratios ($\delta^{18}O$) provide additional dietary information in some cases (e.g., Connan et al., 2019). Multiple tracers can be used together in mixing models to estimate predator diet (e.g., Lübcker et al., 2017), provided potential prey values are also measured, or to investigate the isotopic niche of different individuals, populations or species (e.g., Connan et al., 2019). The analysis of "archival"

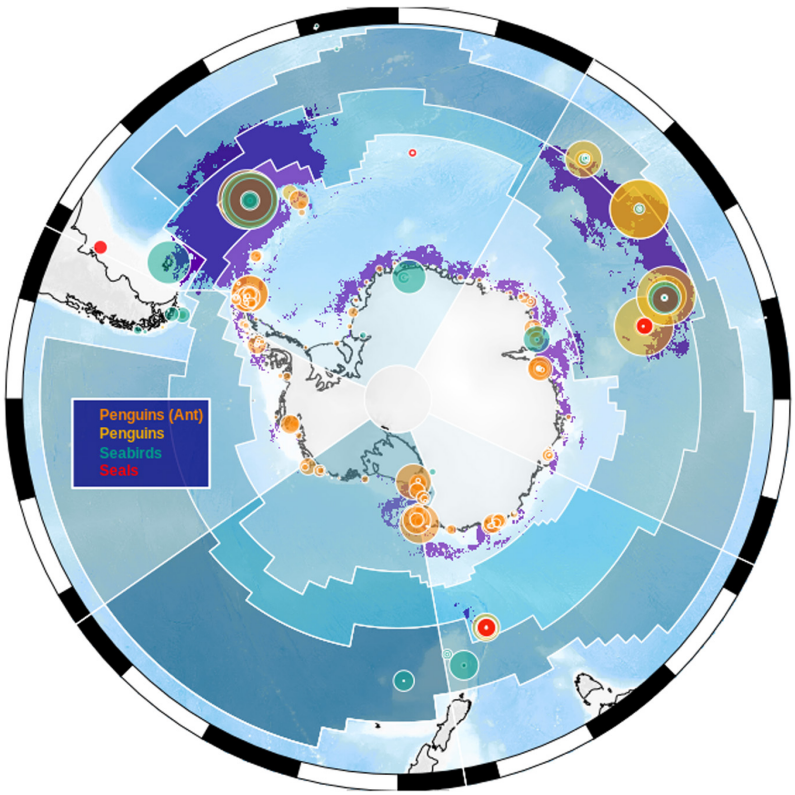


FIGURE 3 | Circumpolar distribution of top predator breeding and foraging sites in relation to the MEASO spatial areas. Purple shading indicates areas of ecological significance for multiple top predators (Hindell et al., 2020). Colored circles are scaled relative to colony size for 14 species (following Hindell et al., 2020; largest count is for macaroni penguins (*Eudyptes chrysolophus*) at Crozet with >2 million birds, Crossin et al., 2013). Blue shading demarcates the MEASO spatial areas.

tissues such as whiskers (e.g., Lübcker et al., 2017) or teeth (e.g., Authier et al., 2012) can provide time series of stable isotope ratio values. Commonly, these use bulk analysis but more recently, compound-specific stable isotope analysis has proved to be a powerful tool for enabling more nuanced ecological inference (e.g., Brault et al., 2019).

A less-used biomolecular method for studying marine predator diets is fatty acid analysis of adipose tissues (e.g., Bradshaw et al., 2003) or stomach oils (e.g., Connan et al., 2014). When prey fatty acid signatures are also available, quantitative signature analysis of blubber in marine mammals, or subcutaneous adipose tissue in seabirds allows dietary reconstruction (Iverson et al., 2004).

Genetics

Molecular genetic markers can estimate the abundance, diversity, connectivity or distribution of populations, species and ecosystems, and track changes in these parameters over time (Schwartz et al., 2007). Genetic analyses have been conducted on a wide variety of Antarctic predators, for example to understand the geographical features that separate populations, monitor population abundance and effective size in colonies, identify species that are not readily recognizable and measure genetic diversity. The commonly used genetic markers have evolved from allozyme analyses to study protein-based differences between individuals (e.g., Smith and McVeagh, 2000), to mitochondrial DNA, useful for understanding maternally inherited patterns (e.g., Christiansen et al., 2018). Rapidly evolving nuclear microsatellite markers enable individuals to be identified, measurement of effective population size (e.g., Hoffman et al., 2011), detecting levels of population differentiation (e.g., Amaral et al., 2016) and monitoring of population changes over management-relevant timescales (e.g., Forcada and Hoffman, 2014). Finally, single nucleotide polymorphism markers (SNPs) can be obtained in their thousands via restriction site-associated (RAD) or whole genome sequencing approaches (e.g., Clucas et al., 2018; Cole et al., 2019).

For cetaceans and seabirds, most genetic studies have focused on population connectivity and diversity across breeding sites or oceanic areas. Levels of diversity and connectivity are important to gauge the level of isolation and vulnerability, particularly of exploited or threatened populations. Baleen whales from geographically distinct wintering grounds often mix within their Southern Ocean feeding grounds, so patterns of spatial genetic structure are usually weak (e.g., Amaral et al., 2016; Attard et al., 2016). Genetic diversity is particularly low for southern right whales (*Eubalaena australis*); following three centuries of exploitation, populations such as that in the New Zealand Auckland Islands exhibit low mitochondrial DNA diversity (Patenaude et al., 2007), with genetic differentiation between

calving grounds suggesting demographic independence between populations (Carroll et al., 2015). Multiple markers are required to reliably detect weak structuring. RAD-Seq analyses of four penguin species uncovered weak population structuring across their Southern Ocean range, indicating regular long-distance migratory movements between colonies (Younger et al., 2016; Clucas et al., 2018). In contrast, gentoo penguins (*Pygoscelis papua*), with their restricted, coastal distribution, are much more genetically isolated (Levy et al., 2016; Clucas et al., 2018). Hoffman et al. (2011) used SNPs to assess the pre-exploitation abundance and subsequent population bottleneck of Antarctic fur seals (*Arctocephalus gazella*) at South Georgia due to sealing, finding robust evidence for a recent population decline consistent with over-exploitation. Genetic monitoring of colonies over time can also be extremely valuable to understand population abundance, survival rates and response to local environmental conditions. Regular genetic monitoring of Weddell seals (*Leptonychotes weddellii*) on White Island has enabled pedigree reconstruction since 1990, facilitating annual estimation of effective population sizes. Across three reconstructed generations, heterozygosity declined from past to present and is likely to decline further if the current generation of pups continue to interbreed (Gelatt et al., 2010).

Physiological Status

The physiological status of top predators is now being monitored by measuring various parameters in a range of tissues. In humpback whales steroid hormones are measured in blubber samples to determine pregnancy and obtain demographic rates (Pallin et al., 2018), providing some baseline against which to assess impacts of change. Steroid hormones have recently been measured sequentially in the whiskers of three seal species and this approach can be used to study reproductive cycles in mammals with cryptic life stages, or study links between animal stress and environmental variation (Lübcker et al., 2020). In response to stressors, secretion of glucocorticoid dramatically increases to mediate breeding and foraging decisions (review in Wingfield et al., 1998). The importance of oxidative stress in influencing fitness components and the resolution of life history trade-offs is attracting increasing attention (Monaghan et al., 2009). Adélie penguins (*Pygoscelis adeliae*) modulate their oxidative status by adopting different foraging behavior (Beaulieu et al., 2010). In humpback whales an adiposity index measured in blubber biopsy samples cycled over 8 years in synchrony with environmental variables (e.g., sea-ice concentration, negative relationship) and climate indices (e.g., ENSO, positive relationship) (Bengtson Nash et al., 2018).

Developing an Integrated Perspective

The suite of tools developed over the past decades, briefly summarized above, are increasingly used in combination on the same individuals and populations. Advances in micro technologies, lab analyses and field techniques have made this possible practically and ethically. In less than 10 min, an animal can be instrumented, and blood and/or feces sampled with minimally invasive approaches. Data on individual performance/condition can be collected at regular intervals, at least for land-based breeding species, and when paired with demographic parameters at the population level, they turn top predators into "living observatories" (**Figure 4**), the biological counterpart to the physical sciences observatories.

Biases and Regional Coverage

Data collected on top predators are commonly biased toward certain groups. Overwhelmingly, the individuals studied are adults but there is a concerted effort to learn more about juveniles (e.g., Orgeret et al., 2016). In seals, studies are biased toward adult females since adult males are relatively large and difficult to restrain physically. Most work has focused on seals and seabirds – since they are easier to observe, catch and/or handle when they return to their terrestrial sites – than cetaceans which remain at sea, although technological advances are making it possible to study new aspects of their lives (Nowacek et al., 2016). While commercial whaling provided substantial historical data, this again contains very little information on juveniles due to the target catch of the industry. Three dedicated abundance surveys (**Table 1**) provided standardized circumpolar data on whale abundance, distribution and trends, however, many cetacean species are rare and remain infrequently observed.

Relative to the MEASO areas, many of the longitudinal datasets come from locations where researchers have access to breeding, resting or molting sites on land and ice, frequently near research infrastructure on Subantarctic islands in the Atlantic, Central Indian and East Indian sectors, at the Antarctic Peninsula, as well as in east Antarctica and the Ross Sea in the Antarctic zone.

Open Data and Computing

Antarctic scientists are acutely aware of the necessity of making their data publicly available and shareable, following from the requirement of Article III of the Antarctic Treaty. Accordingly, the Scientific Committee on Antarctic Research houses groups that are dedicated to the proper curation and sharing of data and metadata such as the Standing Committee on Antarctic Data Management or the Expert Group on Antarctic Biodiversity Informatics (Van de Putte et al., to be published in this research topic). While there is disparity in practices and data standards among research groups, there are several international efforts promoting free data and/or metadata access of top predator studies (**Table 1**). Furthermore, a push toward better reproducibility of results accompanied by the growth of open-source computing has meant that many projects and researchers now make their computer code freely available (e.g., the Antarctic/Southern Ocean rOpenSci community; Raymond and Sumner, 2018).

BIOLOGY, DRIVERS AND FUNCTIONAL RELATIONSHIPS

Marine Predators in a Changing Climate

A core component of the MEASO work program has been to provide a source of standardized and validated information on

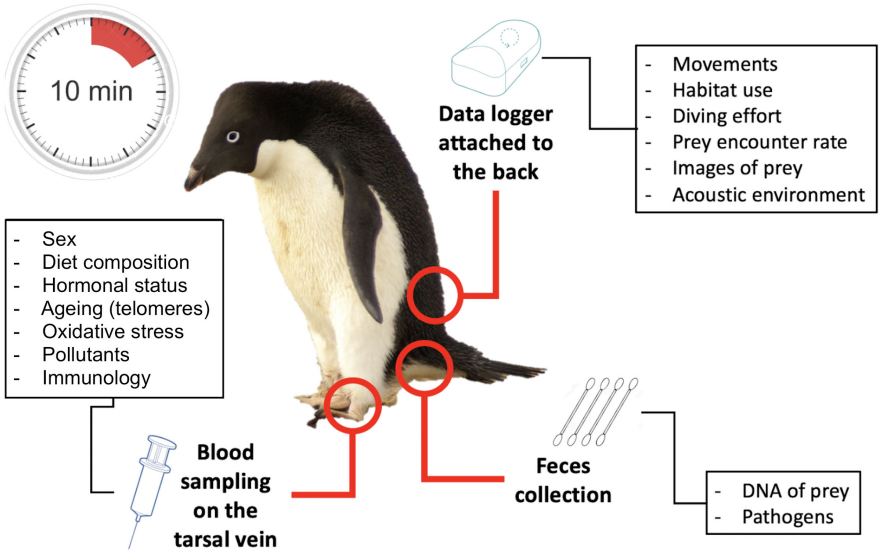


FIGURE 4 | Example of a living observatory, an Adélie penguin, demonstrating the diversity of information that can be obtained from individual-based studies.

TABLE 1 | A non-exhaustive list of existing large-scale initiatives to collate and make openly available data on Southern Ocean marine top predators.

Antarctic and Southern Ocean initiatives			
Population trends	Mapping Application for Penguin Populations and Projected Dynamics (MAPPPD)	http://www.penguinmap.com/	Humphries et al. (2017)
Distribution at sea	Biogeographic Atlas of the Southern Ocean (SCAR product)	http://atlas.biodiversity.aq/	De Broyer et al. (2014)
	Retrospective Analysis of Antarctic Tracking Data (RAATD)	https://github.com/SCAR/RAATD	Hindell et al. (2020); Ropert-Coudert et al. (2020)
Abundance and distribution	International Whaling Commission (IWC) Southern Ocean Whale and Ecosystem Research Programme (SOWER)*	https://iwc.int/sower	E.g., Branch (2011)
	Antarctic Pack Ice Seals (APIS) Programme*	https://www.seals.scar.org/pdf/IntAPISSummUpdateRevis.pdf	Southwell et al. (2012)
Oceanographic data from animal-borne devices	Marine Mammals Exploring the Oceans Pole to Pole (MEOP)	http://www.meop.net/	Treasure et al. (2017)
	The Penguiness Book of dive records	http://www.penguiness.net/	Ropert-Coudert et al. (2018a)
Trophic information	Southern Ocean Dietary Database (an EGABI product)	https://data.aad.gov.au/trophic/	Raymond et al. (2011)
Related initiatives			
Distribution	Movebank for Animal Tracking Data	https://www.movebank.org/cms/movebank-main	Kranstauber et al. (2011)
Animal distribution and bio-physical data from animal-borne devices	Integrated Marine Observing System	http://imos.org.au/ https://portal.aodn.org.au/	Harcourt et al. (2019)
Distribution	BirdLife International Seabird Tracking Database	http://www.seabirdtracking.org//	E.g., Lascelles et al. (2016)

**Indicates inactive initiatives.*

the Southern Ocean Knowledge and Information wiki (SOKI). The SOKI biota pages[3] summarize basic information for a species or taxonomic group for flying birds, penguins, seals, baleen whales, dolphins and toothed whales, and how the status and ecology of the group may be changing over time. We refer the reader to this resource for detailed species-level information including life history parameters (where available), population estimates and dynamics, movement and distribution, diet and energetics, and species interactions and dependencies. In this section we provide a high-level overview of drivers and functional relationships, from an ice-dependent and oceanic perspective, and highlight the overarching importance of climate change impacts upon Southern Ocean top predators.

Ice-Dependent Predators

Depending on their affinity for sea ice, marine predators are either directly influenced by sea ice as a platform on which to forage or rest (and other stages of life cycle), or indirectly

[3]http://soki.aq/display/MEASO/MEASO+Biota

through associated processes such as biological production and prey aggregation (Murphy et al., 2007; Massom and Stammerjohn, 2010; Flores et al., 2012). Antarctic sea ice extent shows interannual variability with marked regional variation (Zwally et al., 2002; Cavalieri and Parkinson, 2012; Hobbs et al., 2016; Parkinson, 2019). Changes in extent and seasonality have important implications for the structure and functioning of Southern Ocean ecosystems (Massom and Stammerjohn, 2010; Morley et al., to be published in this research topic). Predators exhibit differential usage of sea-ice areas with distinct characteristics, from north to south the: (i) marginal ice zone; (ii) pack ice; (iii) coastal zone comprising landfast (fast) ice with recurrent polynyas and flaw leads.

Sea-ice obligate pack-ice seals – crabeater (*Lobodon carcinophaga*), leopard (*Hydrurga leptonyx*), Ross (*Ommatophoca rossii*) and Weddell seals – and the emperor penguin use sea ice as a platform for breeding and molt. Volant seabirds such as snow (*Pagodroma nivea*) and Antarctic petrels (*Thalassoica antarctica*) spend long periods sitting on icebergs or large ice floes (Delord et al., 2020). Crabeater, leopard, and Ross seals avoid areas of consolidated pack ice where freeze-ups are frequent and restrictive (Ribic et al., 1991). Crabeater and leopard seals are predominantly southern pack-ice species year-round. In contrast, Ross seals spend ∼70% of their time 500–1000 km from the ice edge. They haul out in the pack ice mainly during the December–January molt, and in October–November when they breed (Arcalís-Planas et al., 2015).

Although southern elephant seals (*Mirounga leonina*) mate, breed and molt on subantarctic islands, a significant proportion forage within the Antarctic sea ice region in winter (Hindell et al., 2017). Compared with other marine mammals, whales have limited capacity to make breathing holes through ice (Nicol et al., 2008). Antarctic minke whales (*Balaenoptera bonaerensis*) are known to overwinter in the Antarctic; although sighted within the winter pack ice the proportion of the population that remains year-round is unknown (Perrin et al., 2018). At least two different ecotypes (B and C) of killer whales (*Orcinus orca*) are present near or within the Antarctic sea-ice region (Pitman, 2011). "Pack ice killer whales" (B-types) forage mainly among the pack ice around the entire continent. "Ross Sea killer whales" (C-types) live deep in East Antarctic pack ice and use leads (cracks) in the fast ice, often far from open water. Sei whales (*Balaenoptera borealis*), southern right whales, A-type and D-type killer whales are not, or rarely, seen close to the sea-ice edge.

In the Southern Ocean baleen whale diets are predominantly euphausiid based, reflecting the available biomass of different krill species, but with the super-abundant Antarctic krill being the primary prey for many whales and other species (**Box 1**) (see also Rogers et al., 2020; Johnston et al., to be published within this research topic; and references therein). The small size of minke whales allows them to enter the pack ice zone and affords access to Antarctic krill there. In addition, their ability to filter large quantities of krill provides an advantage over smaller krill predators that feed on individual prey (Friedlaender et al., 2014). Humpback and fin whales (*Balaenoptera physalus*) are also krill specialists but are more oceanic-dwelling and less associated with sea-ice habitats or continental shelf areas (see Nicol et al., 2008). Humpback whales generally arrive in Antarctic waters in December and their numbers increase throughout summer months (e.g., Andrews-Goff et al., 2018; Bestley et al., 2019). Antarctic blue (*Balaenoptera musculus intermedia*) and fin whales appear to show up comparatively later in the summer (Širović et al., 2009).

Sea-ice predator populations do not respond uniformly to sea-ice changes around Antarctica (**Table 2**). Different functional relationships and contrasting population trends reflect regionally specific differences in sea ice change and variability, and in species ecology and life history (Jenouvrier et al., 2005; Massom and Stammerjohn, 2010; Constable et al., 2014; Southwell et al., 2015). Sea ice characteristics affect foraging behavior (e.g., Le Guen et al., 2018) and breeding habitat (Jenouvrier et al., 2017), with consequences on vital rates (reproduction: Jenouvrier et al., 2003; Massom et al., 2009; Stroeve et al., 2016; Ropert-Coudert et al., 2018a; survival: Barbraud and Weimerskirch, 2001b; Jenouvrier et al., 2005; Kooyman et al., 2007; Fretwell and Trathan, 2019), ultimately affecting population dynamics (Jenouvrier et al., 2003, 2012; Ainley et al., 2010) and species persistence (Jenouvrier et al., 2014).

Predators employ a diversity of foraging strategies within the sea-ice zone (**Supplementary Material 1**). Knowledge of the present and predicted effects of sea-ice changes on predators around Antarctica is limited for whales compared with other vertebrate predators for which long-term demographic data exist (**Table 2**). However, extended feeding seasons for humpback and minke whales' habitat use were tightly correlated with presence of sea ice (Friedlaender et al., 2006; Williams et al., 2014).

Predictions about the effect of Antarctic sea ice changes and variability on predators is a complex question, arising from three factors. First, there remain important uncertainties in understanding of sea-ice variability, change, climate model configurations and forecasts. Sea-ice dynamics (timing and duration), sea icescapes (ephemeral and persistent latent heat polynyas, icebergs, and leads) and sea-ice extent are highly variable in time and space. In most ecological studies the scales used are too coarse to accurately or realistically understand the reliance of Antarctic predators upon sea ice (Jenouvrier et al., 2012). New approaches, using drones (Torres et al., 2018), high resolution satellite imagery (LaRue et al., 2019) or animal-borne sonar (Lawson et al., 2015) can investigate fine-scale features relevant to the foraging scale of predators.

Second, diversity in behavior and individual phenotypic plasticity makes predator responses to sea-ice changes highly variable between sites, individuals and across species. The response of predators is governed by their physiological plasticity to tolerate change, adapt to new environmental conditions or migrate to alternative foraging grounds that enable survival.

Third, the complexity of trophic interactions within the sea ice region is poorly understood, limiting the understanding of how sea ice changes would affect predators through changes in the availability of resources. The role of winter sea ice as a main feeding ground for Antarctic krill larvae was recently challenged, as the pack ice zone may be a food-poor habitat for larval development compared with the marginal ice zone (Meyer et al., 2017). Diet indicators suggest that larvae feed on sea-ice

BOX 1 | Food web interactions of Southern Ocean top predators.
Climate-driven changes are influencing the timing, duration and intensity of primary production in the Southern Ocean, with marked regional variability (high confidence) (IPCC, 2019), and through a cascading effect modifications in the lower trophic level planktonic communities transfer up the food web (Constable et al., 2014; Rogers et al., 2020). Many climate-driven changes impacting predators can therefore manifest through changes in the timing and availability of key prey resources (medium confidence), with consequences for aspects of predator's life history, phenologies, migratory schedules, foraging distributions and spatial ranges as detailed in see section "Biology, Drivers and Functional Relationships." One often-cited example of such bottom-up control is through Antarctic krill: this crustacean play a central role in high latitude Southern Ocean food webs, as grazers and prey for baleen whales, seals, penguins and seabirds (Trathan and Hill, 2016), although its abundance and importance does vary between regions (McCormack et al., 2017). The Antarctic krill life cycle is tightly synchronized to take advantage of the seasonal availability of sea-ice habitat and the phenology of Southern Ocean phytoplankton productivity. Bottom-up ecosystem changes have been reviewed extensively, including for primary (Pinkerton et al., to be published in this research topic) and secondary production (zooplankton and krill: Johnston et al.; fish and squid: Caccavo et al., to be published in this research topic). Top-down control can additionally be important in Southern Ocean ecosystems, as an overabundance of predators can lead to local prey depletion thereby releasing the pressure that these prey species exerted on primary producer levels (Ainley et al., 2007). The state of knowledge regarding key regional Southern Ocean food web structures, function and dynamics are reviewed by McCormack et al. (to be published in this research topic), together with prognoses for how the relative importance of trophic pathways will change under climate change.

resources when available but can still persist in the water column when they are not (Walsh et al., 2020).

Extensive research is yet to be done regarding foraging activity by predators below the ice and quantification of key dependencies, particularly during the autumn and winter. Three main questions are: (1) How do oceanographic conditions shape predator distribution at-depth under sea ice? Key associations of interest relate to *in situ* temperature and salinity gradients, specific water mass properties, topographic structures (creating local upwelling or sub-mesoscale structures) within the different ice zones and latent-heat polynya dynamics. (2) Where and when does primary and secondary production occur within sea ice and latent-heat polynyas during autumn? The sea-ice region is still considered a biological desert in winter although predators forage there successfully throughout the year. Sparse data are due to limited ship access, and non-detection of ice-associated phytoplankton in conventional satellite ocean-color images. (3) How do predators track the zooplankton, ichthyoplankton and macrofauna distribution at the ice-ocean interface down to mesopelagic depths? The suite of complementary data-collection and monitoring tools (see section "Data, Methods, and Tools") can help address these questions.

Oceanic Processes and Marine Predators

In the Special Report on the Ocean and Cryosphere in a Changing Climate (SROCC; IPCC, 2019), medium confidence was attributed to the identification and location of environmental features that facilitate the aggregation of prey, and in turn influence the spatiotemporal distribution of Antarctic marine mammals and birds (Meredith et al., 2019). However, changes in predators' biology and activity patterns are interpreted with high confidence to be the result of increasing environmental variability and climate change (Meredith et al., 2019).

Circulation (advection) and fronts

Changes to the ocean circulation and structure are considered by Morley et al. (to be published in this research topic). Circulation can impact biological productivity, prey abundance and distribution, thereby determining foraging hot spots (Hunt et al., 2016; Atkinson et al., 2019). In the subantarctic region of the Antarctic Circumpolar Current (ACC), the advection of biologically enriched waters downstream from major bathymetric features (Cotté et al., 2015), and the transport of zooplankton and micronekton in the lee vicinity of islands, is postulated to supply much of the food necessary for the survival of the land-based predators feeding offshore (Perissinotto and McQuaid, 1992). Subantarctic (*Arctocephalus tropicalis*) and Antarctic fur seals from the Prince Edward Islands displayed less searching behavior associated with foraging when current speed increased (Wege et al., 2019). The decline of several seal and bird populations at the Prince Edward Islands has been linked to long-term decline in inshore primary productivity driving changes in prey availability, associated with regional scale shifts in ACC circulation (Allan et al., 2013). Recent research has found no long-term trend in the zonally averaged latitude of ACC transport and no evidence of an increase in the ACC transport (Chidichimo et al., 2014).

The ACC fronts are associated with boundaries between the major water masses. These circumpolar features exhibit high biological production due to upwelling or changes in the vertical distribution of resources (Moore and Abbott, 2000). They offer important foraging habitat for top predators (Tynan, 1998; Bost et al., 2009; Arthur et al., 2016). Despite representing relatively predictable foraging grounds, frontal areas are also characterized by a complex pattern of multiple locations corresponding to different jets (Sokolov and Rintoul, 2009). Large-scale climatic anomalies generating interannual variability in the latitudinal location of fronts impacts the foraging trip distances and feeding depths of king penguins (*Aptenodytes patagonicus*), with consequences for population size (Bost et al., 2015). Potential change in the transport and location of the ACC and its fronts, in response to the increasingly positive Southern Annular Mode, is expected to affect subantarctic foraging top predators (Allan et al., 2013). However, satellite altimetry and temperature time-series show consensus on the lack of poleward frontal displacement over recent decades (Gille and Meredith, 2017; Chapman et al., 2020). Consequently, frontal proxies such as sea surface temperature (SST) are unreliable for projection studies because a decoupling with the location of the fronts (spatial gradients or isopycnal slopes) may occur due to strong surface warming (Cristofari et al., 2018; Meijers et al., 2019). However, temperature is an important parameter for the investigation of predators foraging habitat within frontal areas since it controls prey distribution and availability (Reisinger et al., 2018).

TABLE 2 | Reviews the existing state of knowledge on effects of sea-ice drivers upon Southern Ocean top predators.

Driver	Effect	Species name	Brief summary of impact	Geographic zone	References
Decreased sea-ice extent	Negative	Antarctic fur seal/gentoo and macaroni penguins/black browed albatrosses (*Thalassarche melanophris*)	Population number/frequency of years of low reproductive output	South Georgia	Reid and Croxall, 2001
	Negative	Emperor penguins	Decline by 50% of emperor penguin population	Terre Adélie, East Antarctica	Barbraud and Weimerskirch, 2001b
	Negative	Adélie penguins	Krill availability, foraging activity	Western Antarctic Peninsula	Fraser and Hofmann, 2003
	Negative	9 seabird species	Later arrival and laying than in early 1950s	East Antarctica	Barbraud and Weimerskirch, 2006
	Negative	Snow petrels/emperor penguins	The emperor penguin population has declined by 50% whereas snow petrels showed their lowest numbers in 1976, but were able to skip reproduction	Terre Adélie, East Antarctica	Jenouvrier et al., 2005
	Negative	3 whale species	Increased spatial overlap due to shift of fin whales foraging range to higher latitudes where blue and minke whales used to feed	Circumpolar	Nicol et al., 2008*
	Negative	Crabeater/Weddell/elephant seals	Limitation in the available breeding and foraging habitat	Western Antarctic Peninsula	Costa et al., 2010*
	Negative	Adélie/Chinstrap (*Pygoscelis antarcticus*) penguins	Decreased in both populations, change in their main prey	Western Antarctic Peninsula	Trivelpiece et al., 2011
	Negative	Crabeater/Weddell/leopard seals	Reduced food resources for pack-ice seals, predicted loss of seal habitat (1979/2011)	Western Antarctic Peninsula/Western Weddell Sea	Forcada et al., 2012
	Negative	Adélie penguins	Prediction of population going extinct; potential mitigation by local recruitment	Edmonson Point, Ross Sea	Ballerini et al., 2015
	Negative	Adélie penguins	Negative influence on population growth rate for conditions 4 years prior (1982–2015; may be site dependent)	Circumpolar	Che-Castaldo et al., 2017
	Negative	Antarctic minke whales	Decreased preferred foraging habitat and shelter from predation leading to displacement and competition with other krill predators (e.g., humpback whales)	Circumpolar	Risch et al., 2019*
	Negative	Arctic terns	Impact on foraging behavior	East Antarctica	Redfern and Bevan, 2020
Decreased sea-ice extent and duration	Negative	Adélie/chinstrap penguins	Replacement of Adélie by chinstrap penguins due to change in resources	West Antarctic Peninsula	Ducklow et al., 2007
	Negative	Crabeater seals	Prediction of direct (pupping platform and protection from predators) and indirect (food supply) influences	Circumpolar	Siniff et al., 2008*

(Continued)

TABLE 2 | Continued

Driver	Effect	Species name	Brief summary of impact	Geographic zone	References
Decreased sea-ice concentration	Negative	South polar skuas (*Stercorarius maccormicki*)	Population size and number of breeders	Terre Adélie, East Antarctica	Pacoureau et al., 2019
Increased/decreased sea-ice concentration	Negative	Emperor penguins	Predicted colony declines (bell shape curve)	Circumpolar	Jenouvrier et al., 2012, 2014, 2019
Increased sea-ice extent	Negative	Emperor penguins	Fecundity (1952–2000)	Terre Adélie, East Antarctica	Barbraud and Weimerskirch, 2001b
	Positive	Emperor penguins	Adult survival (1952–2000)	Terre Adélie, East Antarctica	Barbraud and Weimerskirch, 2001b
	Positive	Snow petrels	Overall breeding success and fledging body condition the following year (1973–1999)	Terre Adélie, East Antarctica	Barbraud and Weimerskirch, 2001a
	Negative	Weddell seal	Weaning masses decreased	Erebus Bay, Ross Sea	Proffitt et al., 2007
	Positive	Emperor penguins	Chick abundances correlated with sea ice extent during July-September	Western Ross sea	Barber-Meyer et al., 2008
	Negative	Adélie penguins	Foraging trip duration, distance walked, starving time of chicks	Terre Adélie, East Antarctica	Ropert-Coudert et al., 2018b
Increased sea-ice duration	Negative	Elephant seals	Negative influence on female abundance in breeding colonies with a 3y lag, likely due to preventing access to profitable prey areas	Western Ross sea	van den Hoff et al., 2014
Increased sea-ice extent and duration	Positive	Adélie penguins	Food resources	Palmer, Western Antarctic Peninsula	Saba et al., 2014
Reduced/thinner fast ice	Negative	Emperor penguins	Population numbers	Western Pacific/Ross Sea	Ainley et al., 2005
	Negative	Weddell seals	Prediction of changes for pupping and breeding platforms	McMurdo Sound, Ross Sea/Antarctic Peninsula	Siniff et al., 2008*
	Positive	Emperor penguins	Lower-than-average fast ice extent and persistently short distances to nearest open water (foraging grounds)	Terre Adélie, East Antarctica	Massom et al., 2009
	Negative	Emperor penguins	Prediction of decrease of ∼50% of the colonies for 2025–2052	Circumpolar	Ainley et al., 2010
Altered ice floe size and structure	Negative	Crabeater seals	Prediction of direct (pupping platform and protection from predators) and indirect (food supply) influences	Circumpolar	Siniff et al., 2008*
	Negative	Ross seals	Prediction of changes for pupping and molting platforms	Circumpolar	Siniff et al., 2008*
Changed polynya activity	Positive	Adélie penguins	Larger Ross sea polynya/access to food sources	Western Pacific/Ross Sea	Ainley et al., 2005
Increased precipitation/snowfall	Negative	Adélie penguins	The change in the icescape following the calving of the Mertz glacier in 2010, with increase in precipitation and changes in sea-ice firmness led to 2 years of massive breeding failure	Terre Adélie, East Antarctica	Ropert-Coudert et al., 2018b
	Negative	Adélie penguins	Prediction of decrease of ∼75% of the colonies for 2025–2052	Circumpolar	Ainley et al., 2010
Early fast-ice breakup	Negative	Emperor penguins	Substantial loss of chicks	Cape Crozier, Ross Sea	Schmidt and Ballard, 2020
Increased iceberg mobility	Negative	Emperor penguins	Low chick numbers	Western Ross sea	Barber-Meyer et al., 2008

**Indicates Review paper.*

Mesoscale eddies and mixed layer dynamics

The ACC is a turbulent flow with high levels of meandering and eddy energy. These mesoscale features bring nutrient-rich deep water to the surface, consequently locally fueling primary production and sustaining trophic webs (Kahru et al., 2007). The importance of mesoscale eddies has been reported for flying (Nel et al., 2001) and diving birds (Cotté et al., 2007; Scheffer et al., 2016), and seals (Campagna et al., 2006; Bailleul et al., 2010; Massie et al., 2016). Tracking studies have highlighted behavioral adjustments of birds and mammals focusing on distinct mesoscale eddies characterized by their type, level of retention (weeks to months, d'Ovidio et al., 2013), and the history and trajectory of the water parcel (Cotté et al., 2015). Eddies can assist with foraging because of enhanced production, prey aggregation and increased prey accessibility (Della Penna et al., 2015), but not all species, sexes and age-classes interact with eddies in a consistent pattern (see e.g., Dragon et al., 2010; Tosh et al., 2015). Recently, submesoscale features (filaments and small-scale fronts) induced by the interaction between eddies, and characterized by elevated physical and biological activity, were also reported to be favored by southern elephant seals (Cotté et al., 2015; Della Penna et al., 2015; Rivière et al., 2019; Siegelman et al., 2019). Similarly, chinstrap penguins, macaroni penguins, and Antarctic fur seals from Bouvetøya targeted negative sea-level anomalies and sub-mesoscale fronts (Lowther et al., 2014). An increase in eddy energy (McHogg et al., 2015) as a response to the strengthening of westerly winds will affect the mixed layer depth and stratification in the ACC (Hausmann et al., 2017). This will impact the vertical flux of nutrients and limiting elements into the surface layer. Such projected physical change should influence the spatial distribution of production, the role of eddies in structuring the prey field by bottom-up or aggregation processes and the resulting trophic transfer of energy to top predators.

The mixed layer temperature gradient also acts as a barrier for some vertically migrating prey and therefore plays an important role in foraging behavior of deep-diving marine predators (Biuw et al., 2010). Conductivity-temperature-depth data have shown southern elephant seals were less successful foragers when diving in warmer water (McIntyre et al., 2011). Shallow diving-predators, targeting the bottom of the shallow mixed layer depth (e.g., in certain regions or time of the year/day) will be affected by mixed layer depth variations given their physiological inability to dive deep. For example, southern right whales feeding on surface swarming krill, favored areas with a temperature difference of 10–15°C in the upper 200 m of the water column, but also preferred shallower mixed layer depths when foraging (Torres et al., 2013). Increasing temperatures and changes to the mixed layer depth mean that marine predators will have to dive deeper more frequently, i.e., at a greater cost, to obtain the same amount of resources.

Climate Change and Marine Predator Responses

Temperature increase in some areas of the Southern Ocean has been particularly rapid leading to major oceanographic changes which, in turn, are impacting marine predators (Forcada and Trathan, 2009; Barbraud et al., 2012; Convey and Peck, 2019). Climate change can directly or indirectly impact predator demographics, phenology, distribution, diet and behavior (Sydeman et al., 2015). Separating demographic changes related to climate from other causative mechanisms (e.g., fisheries) is challenging – these are often not independent as impacts may be cumulative – but important to evaluate to develop effective mitigation strategies (Rolland et al., 2010; Trathan et al., 2015). This is especially the case in the Southern Ocean where the recovery of previously exploited species represents a changing influence on community structure and prey dynamics (Ainley et al., 2007).

A number of studies have linked population changes to climate effects. For example, changes in winter SST negatively affected the survival of juvenile black-browed albatrosses and consequently population growth (Jenouvrier et al., 2018). King penguins from Crozet are particularly vulnerable to climate change, partly due to shifting distribution of their major foraging grounds (Péron et al., 2012; Bost et al., 2015; Cristofari et al., 2018). The low adult survival of southern rockhopper penguins (*Eudyptes chrysocome*) is linked to warmer SST, presumably due to the negative influence on prey (Dehnhard et al., 2013). At Macquarie Island, the long-term population decline (−1.45% p.a. over seven decades) of southern elephant seals has been linked to complex changes in ice dynamics along the Victoria Land coast and in the Ross Sea, as increasing ice concentration and extent restricts access of the seals to these foraging areas, forcing them to leave earlier (Hindell et al., 2017). Global climate indices influence southern right whale breeding success by determining variation in food (krill) availability (Seyboth et al., 2016). Coupled climate-biological modeling projected long-term population declines of varying magnitude across five baleen whale species, related primarily to increased competition for reduced prey (copepods/krill) under ocean warming (Tulloch et al., 2019).

The increasing frequency and magnitude of extreme weather events as a result of climate change (high confidence) (IPCC, 2019) also place top predators at risk. Marine predators are philopatric to foraging and/or breeding sites; individuals develop strategies for behavioral specialization and memory effects which can have profound effects on fitness and population persistence (Bradshaw et al., 2004; Grémillet and Boulinier, 2009; Wege et al., 2016b). Philopatric species relying on long-term strategies may be more vulnerable to disruption by increased frequency and intensity of anomalous weather events. Snowstorms, for example, negatively influence breeding success in Antarctic petrels (low confidence) (Descamps et al., 2015). Exceptionally heavy precipitation in East Antarctica disrupted the breeding activity of Adélie penguins on land, while weak katabatic winds preserved the sea ice around the colony, thereby affecting chick provisioning by adults, causing mass mortality of chicks (Ropert-Coudert et al., 2015).

A recent global meta-analysis found only limited shifts in seabirds' reproductive timing over 1952–2015 (Keogan et al., 2018), but changes in breeding or migratory phenology have been reported for several Southern Ocean species. These often represent later rather than earlier onset of breeding, particularly for sea-ice associated species (Barbraud and Weimerskirch,

2006; Chambers et al., 2014). Nonetheless, Lynch et al. (2012) demonstrated an advancement in clutch initiation with increasing temperatures in three pygoscelis penguin species (Adélie, gentoo and chinstrap). Among humpback whales migrating from Central and South America the arrival time at the Antarctic peninsula has advanced by nearly 30 days in 30 years (Avila et al., 2020). Meanwhile, tracking reveals whales are remaining in ice-free Antarctic Peninsula waters well into winter (Weinstein et al., 2017), leading to longer regional residence times. More detailed investigation may reveal that climate change is differentially affecting population components.

Environmental changes can induce distributional shifts in both the breeding (Forcada and Trathan, 2009) and at-sea foraging distribution of marine predators. Antarctic (*Pachyptila desolata*; Grecian et al., 2016) and thin-billed (*Pachyptila belcheri*; Quillfeldt et al., 2010) prions shifted their non-breeding distribution southward over the past century. The strengthening of westerly winds has resulted in a poleward shift in the foraging distribution of wandering albatrosses but also increased their foraging efficiency and ultimately breeding success (Weimerskirch et al., 2012). Shifts in the latitudinal range of flying seabird species were related to wind and temperature changes during the last decades, depending on the water masses they visited in the Southern Indian Ocean (Péron et al., 2010). Arthur et al. (2018) used species distribution models and satellite-derived ocean data to recreate historical winter (non-breeding) foraging habitats of female Antarctic fur seals from three populations. At Marion and Bird islands, foraging habitat has remained relatively consistent over 20 years, but not at Cape Shirreff; here, reduced sea-ice cover has improved habitat accessibility but also increased the overlap with fisheries. Few studies have used future climate projections to see how predators such as king penguins may shift their movements poleward in response to climate change (medium confidence) (Péron et al., 2012; Cristofari et al., 2018) and how this will impact population abundance. Habitat and climate models applied to tracking data from seven seabird species projected range contractions and poleward shifts (strong likelihood) (Krüger et al., 2018). In the subantarctic region, there is an urgent need for studies that use climate models to create projections of what will happen in the future.

Long-term dietary studies at many Southern Ocean locations have improved understanding of lower trophic level community structure (Ratcliffe and Trathan, 2011), including the trophic roles of krill, myctophids (e.g., Saunders et al., 2019) and other prey resources for specialist (krill or mesopelagic) and more generalist predators (the Southern Ocean Diet and Energetics Database is a key resource, **Table 1**). Nonetheless, few Southern Ocean studies have associated dietary shifts to climate change (but see Carpenter-Kling et al., 2019, who demonstrated that diet composition of gentoo penguins at Marion Island responds to climate-mediated changes in the position of the subantarctic Front). In the Ross Sea isotopic analyses show that the long-term trophic niche of Weddell seals has not shifted, but the baseline of their food web has, i.e., the primary producer community has changed in this region (Hückstädt et al., 2017).

Interactions With Commercial Fisheries and Resource Extraction

Commercial Exploitation Throughout the Southern Ocean – Past and Present

In the early 20th century, whalers decimated whale populations sequentially from largest to smallest in the Southern Ocean (Hofman, 2017). In total, >2 million whales were taken from the Southern Ocean (Rocha et al., 2014). The International Convention for the Regulation of Whaling (carried out by the International Whaling Commission, or the IWC) came into force in 1946 as an effort to encourage the sustainable harvest for the world's whales. As whale populations continued to decline, the IWC agreed on a whaling moratorium, which came into force in 1985. In 1994, the IWC designated the entire Southern Ocean as a whale sanctuary (Friedheim, 2001). Southern right whales (which were heavily exploited at lower latitudes since the 1600s, de Morais et al., 2016) are now recovering at ∼7% per annum at key sites around the Southern Hemisphere, but are not recovering at others (including Chile-Peru and southeast Australia) (IWC, 2013b; Tulloch et al., 2018). Humpback whale populations are increasing rapidly at ∼11% per annum in many areas (Branch, 2011), and in some cases are close to recovery, such as southwest Atlantic (Zerbini et al., 2019) and east Australia (Noad et al., 2019), while other populations are recovering more slowly (e.g., Oceania; Constantine et al., 2012). In contrast, the Antarctic blue whale was estimated to be at <1% of pre-whaling abundance in 1997 (Branch et al., 2004) and is still critically endangered (Thomas et al., 2016). The status of fin and sei whales are less certain due to lack of abundance estimates (Thomas et al., 2016), although see Tulloch et al. (2018) for a model-based assessment of fin whale recovery. Despite the moratorium and sanctuary status, Antarctic minke whales remained subject to low-level whaling as Japan continued to harvest under a national scientific permit until 2019. At the Southern Ocean level, the population is thought to be declining but with low confidence in this trend because of uncertainty in recent abundance estimates and varying trends at a regional level (IWC, 2013a; there is debate whether different abundance estimates are due to minke whale sea-ice usage biasing their availability for survey over time). Currently there is no whaling in the Southern Ocean.

The commercial exploitation of seals began in the late 18th century (Scully, 1978). The sealing trade peaked in the 1820s, with Macquarie Island a key harvesting location for southern elephant seals, Antarctic and subantarctic fur seals. Crabeater and Weddell seals were also hunted but in limited numbers primarily to supply food for sled dogs (Basberg and Headland, 2008). The dramatic surge in fur sealing during the early 19th century saturated the market for seal oil and pelts leading to a gradual decline in prices and imports, and to its cessation in the early 1830s (Basberg and Headland, 2008). With the advent of new sources of lighting, this market slowly faded by the turn of the century (Ling, 1999). While difficult to quantify, given the poor record-keeping, 1.6–1.7 million fur seals and >1 million southern elephant seals

are believed to have been killed during this era (Basberg and Headland, 2008 and references therein). In 1978, the Convention for the Conservation of Antarctic Seals (CCAS) came into force, setting quotas for all Southern Ocean seal species, with only the Soviet Union conducting exploratory commercial sealing of crabeater seals (N = 4,014), leopard seals (N = 649), Weddell seals (N = 107), Ross seals (N = 30) and southern elephant seals (N = 2) near the Balleny Islands (Twiss et al., 1985). In contrast, penguins were targeted by commercial sealers and whalers, primarily as a source of food and fuel for fires for those working ashore, though commercial hunting of king penguins for oil was conducted (Trathan and Reid, 2009). Currently there are no sealing operations in the Southern Ocean and while most historically harvested populations have recovered, the status of most seals remains poorly known, especially for pack ice seals (Forcada et al., 2012; Southwell et al., 2012).

Southern Ocean Fisheries Interactions

Most of the Southern Ocean comprises internationally managed waters apart from maritime Exclusive Economic Zones around several subantarctic islands. The interplay between internationally managed waters, the Antarctic Treaty System (the suite of agreements that govern the Antarctic) and national jurisdiction creates a complex challenge for fisheries management and sustainable use.

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is the multinational body which governs marine living resources in the Southern Ocean, including responsibility for managing impacts of resource harvesting on dependent and related species. CCAMLR is not a regional fisheries management organization as its primary objective is conservation; however, in the CAMLR Convention "conservation" includes rational use. CCAMLR manages Southern Ocean fisheries (see also Waller et al., to be published in this research topic) including Antarctic krill, toothfish (*Dissostichus spp.*) and mackerel icefish (*Champsocephalus gunnari,* **Supplementary Material 2**). CCAMLR manages for direct operational interactions between fisheries and top predators, implementing a range of strict seabird mitigation measures and other entanglement measures (see section "Operational Interactions – Bycatch"). In line with a precautionary and ecosystem-based management approach[4] (Kock et al., 2007) CCAMLR also manages for indirect interactions (see section "Food web effects of fishing"), through spatially allocated quotas designed to consider competition with predators, for example through precautionary total allowable catches for Antarctic krill. We return to top predator governance mechanisms more broadly in section "Integrated Conservation Under Uncertainty and Change."

Operational interactions

Bycatch. There was a major expansion in the 1970s of demersal fishing in the Southern Ocean, and of pelagic longlining (for tuna and other billfish), demersal longlining and trawling in subtropical and continental shelf waters (Tuck et al., 2003). The associated incidental mortality (bycatch) of seabirds had catastrophic impacts, particularly on albatrosses and large petrels (Phillips et al., 2016; Pardo et al., 2017). Data are sparse on the magnitude of bird bycatch pre-mitigation, but an estimated 6,000 seabirds were killed per year in 1997 in the Patagonian toothfish (*Dissostichus eleginoides*) fishery around South Georgia (Croxall and Nicol, 2004; **Figure 5A**), and around 13–14,000 seabirds were killed per year in 2001/03 around Crozet and Kerguelen (Delord et al., 2005; **Figure 5B**). A suite of mitigation measures were gradually introduced into CCAMLR toothfish fisheries in the late 1990s and early 2000s, including a heavier line-weighting (sinking hooks more rapidly below maximum diving depths), streamer (bird-scaring or Tori) lines behind vessels (discouraging birds from attacking baited hooks), bans on both offal discharge (reducing attraction to vessels) and setting during daylight (when albatrosses are most active). At South Georgia and around Heard Island, a seasonal closure during summer (when most seabirds breed) was implemented as an additional mitigation measure. Together, these measures reduced seabird bycatch to negligible levels (Croxall and Nicol, 2004; **Figure 5A**). The impact on seabirds of the pelagic trawl fishery for icefish around several subantarctic islands during the period of high fishing effort in the late 1970s and early 1980s is undocumented. However, 50–100 albatrosses and petrels were killed each year in the early 2000s, by which time effort in this fishery was much reduced (Kock, 2007).

While seabird bycatch rates are now very low in fisheries within CCAMLR's jurisdiction, many populations of albatrosses and petrels breeding in the subantarctic still face serious threats from fisheries in subtropical waters. Wandering albatrosses and white-chinned petrels (*Procellaria aequinoctialis*) are at high risk since their foraging distributions overlap with fisheries without effective bycatch mitigation during both the breeding and non-breeding seasons (Delord et al., 2010; Jiménez et al., 2016). Other species are killed largely during the non-breeding season, when they overlap with tuna fisheries in the High Seas, or demersal longline or trawl fisheries on highly productive continental shelves (Delord et al., 2014; Clay et al., 2019). Although combined mitigation measures can reduce seabird bycatch to negligible levels, regulations beyond CCAMLR waters and some EEZs are not best-practice and monitoring of compliance and bycatch rates is often woeful (Phillips, 2013). Until this is remedied, many populations will remain threatened, despite the efforts of parties to international treaties such as the Agreement on the Conservation of Albatrosses and Petrels (ACAP), and advocacy and education campaigns by dedicated NGOs such as BirdLife International (Phillips et al., 2016).

Antarctic fur seal bycatch occurs in the commercial krill fishery of the South Atlantic sector of the Southern Ocean (CCAMLR Area 48). Although the fishery developed in the 1970s, seal bycatch went unreported to CCAMLR until 2003. In that year, 73 seals were reported by-caught in trawls of one vessel; 26 mortalities and 47 released alive (CCAMLR, 2018c; **Figure 6**). In 2004, the reported number increased to 292 when monitoring was extended to additional vessels.

[4]CCAMLR has a clear set of ecological objectives, describing the ecosystem approach as management that: "takes into account all the delicate and complex relationships between organisms (of all sizes) and physical processes (such as currents and sea temperature) that constitute the Antarctic marine ecosystem" (CCAMLR, 2001).

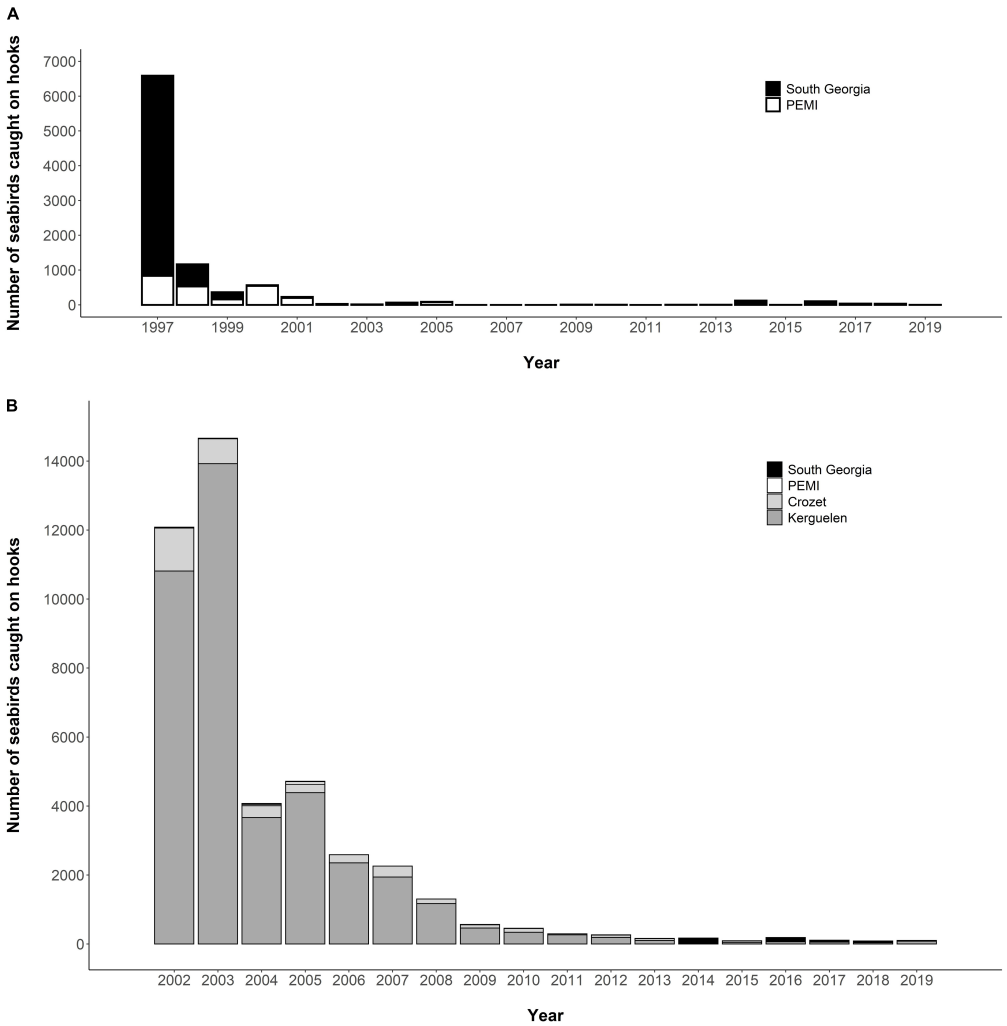


FIGURE 5 | Bycatch of seabirds in the Patagonian toothfish fisheries of **(A)** South Georgia and Prince Edward/Marion Islands ("PEMI") from 1997 to 2019; and **(B)** South Georgia, PEMI, Crozet and Kerguelen from 2002 to 2019 (Source: CCAMLR, 2010, 2019b). Seabird bycatch around Heard Island is excluded as it has amounted to <20 individuals per year since the start of toothfish longlining in 2003 in this region (CCAMLR, 2018c).

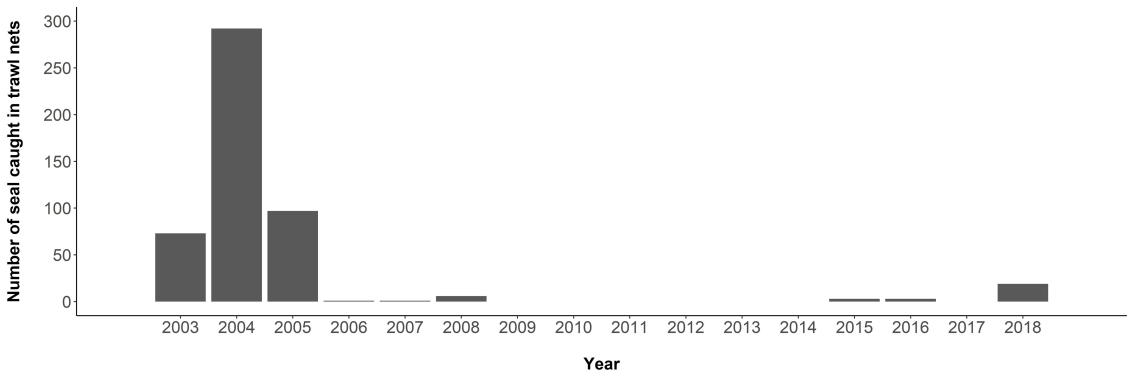


FIGURE 6 | Bycatch of Antarctic fur seals in the krill trawl fishery from 2003 to 2018 in the South Atlantic sector of the Southern Ocean (CCAMLR Area 48). Numbers were not reported between 1973 and 2002 (Source: CCAMLR, 2018a).

This, and inconsistencies in the data collection and quality, prompted CCAMLR to recommend improved observer coverage and the mandatory use of Marine Mammal Exclusion Devices (MMEDs) by all vessels (Hooper et al., 2005). Trawling systems all require nets fitted with marine predator entanglement mitigation measures to be towed at slow speeds (∼4 knots). Fur seal bycatch dropped to <10 per year between 2006 and 2017 (CCAMLR, 2018c), but uncertainty around the real extent of these events remains high, as observer coverage is <100%. In 2018, 19 fur seals were incidentally captured by one krill trawler, which was attributed to a malfunction in the MMED (CCAMLR, 2019b).

Marine mammals are rarely bycaught in toothfish longline fisheries. Antarctic fur seals, southern elephant seals and, to a lesser extent, leopard seals, have been either hooked or entangled in the South Atlantic and South Indian Ocean sectors but these events have remained anecdotal (<10 individuals/year across all fishing areas since 2003; CCAMLR, 2018a,b). Sperm whales (*Physeter macrocephalus*) entanglements in longlines have occurred 8 times since 2007 (5 dead and 3 released alive; CCAMLR, 2009c, 2011, 2012; Richard et al., 2020). Only one killer whale has been recorded hooked and dead on a longline (CCAMLR, 2009a).

Depredation. Depredation, i.e., species feeding on catches directly on the fishing gear, is an operational interaction that has emerged in all Patagonian toothfish longline fisheries over the past 30 years (Kock et al., 2006; Söffker et al., 2015; Tixier et al., 2019a). While Antarctic fur seals and southern elephant seals are involved occasionally (Roche et al., 2007; Söffker et al., 2015; van den Hoff et al., 2017), killer whales and sperm whales most frequently take toothfish from hooks across the Southern Ocean (Kock et al., 2006). Catch depredation by these two species has been reported in all the EEZs of the Southern Ocean (Crespo et al., 1997; Nolan et al., 2000; Hucke-Gaete et al., 2004; Purves and Agnew, 2004; Tixier et al., 2016, 2019a,c; Boonzaier et al., 2012; Janc et al., 2018) and in international waters within the CCAMLR and Southern Indian Ocean Fisheries Agreement areas (Gasco et al., 2019a,b).

Interactions can occur during >50% of the fishing operations and result in fish removals equivalent to >30% of the total catch (Gasco et al., 2015; Tixier et al., 2020), hence depredation can lead to substantial socio-economic and ecological impacts. While entanglement or bycatch occur sporadically (Kock et al., 2006; Richard et al., 2020), the major threat is the use of firearms or explosives by illegal, unreported and unregulated (IUU) fishing vessels to repel depredating individuals (Guinet et al., 2015). At Crozet, such lethal responses contributed to the 60% decline of the local killer whale population in the 1990s (Poncelet et al., 2010; Tixier et al., 2017). While IUU fishing activities were greatly reduced after 2003, evidence of a bullet injury on a killer whale at Crozet in 2019 indicates that depredating individuals are still being shot from IUU vessels (C. Guinet, *pers. comm.*). Depredation may also alter the predatory role of killer and sperm whales in ecosystem functioning through changes in distribution and diet, and artificial provisioning effects on populations (Tixier et al., 2015; Towers et al., 2019).

Discards. Discards (uneaten bait, offal, unwanted non-target fish) from fishing vessels are consumed by many albatrosses and petrels in the Southern Ocean (Cherel et al., 2017; McInnes et al., 2017b), and in more northerly waters during the non-breeding season (Jiménez et al., 2017). In CCAMLR waters, discarding is currently banned in all fisheries south of 60°S. In toothfish fisheries in the EEZs around subantarctic islands, discarding is prohibited during setting and can only take place during hauling on the opposite side of the vessel. For some species, particularly black-browed albatross, greater consumption of discards has been linked to more extensive overlap with fisheries or higher discard availability around colonies, and also to higher breeding success or breeding frequency among colonies, or across years within the same colony (McInnes et al., 2017b; Pardo et al., 2017).

Fishing gear, and other debris discarded or lost from fishing vessels. Fishing gear (mainly hooks and snoods) lost or deliberately discarded by fishing vessels is ingested in large quantities by albatrosses and large petrels, particularly wandering albatrosses at South Georgia, which frequently scavenge behind vessels especially off South America (Nel and Nel, 1999; Phillips et al., 2010; Cherel et al., 2017). Many hooks fed to chicks are completely digested, but there is no information on possible long-term toxicological effects. A substantial proportion of the non-fishing marine debris (mainly plastics) ingested by wandering albatrosses and southern giant petrels (*Macronectes giganteus*) at South Georgia also originate from fishing vessels operating outside CCAMLR waters, which has impacts at least at the individual level (Phillips and Waluda, 2020). Discarding is monitored carefully in the toothfish fishery around South Georgia, and marked, vessel-specific hooks are required. Controls are generally weaker elsewhere, and ingestion of anthropogenic items remains a problem for several subantarctic seabirds (Phillips et al., 2010; Phillips and Waluda, 2020).

Food web effects of fishing

The Antarctic krill fishery currently operates in three distinct locations in the Southern Ocean and is driven primarily by the environmental conditions and local catch limits. During the summer, fishing occurs primarily off the west coast of Coronation Island (South Orkney Islands). Toward the summer's end, the fleet moves into the Bransfield Strait until the catch limit is achieved, and then moves to the waters around South Georgia in winter. The move into the Bransfield Strait coincides with a large influx of male Antarctic fur seals, presumably coming from South Georgia after the summer breeding season, though any potential interactions with the fishery remain unknown (A. Lowther, *pers. comm.*). In this region, the fishery is extending its activities until the beginning of winter, thus overlapping with the fledging period of three pygoscelid species (during summer, Hinke et al., 2017) as well as with feeding activities of large numbers of humpback whales present in the area until winter (Weinstein et al., 2017).

In areas that experience natural variability in krill abundance, robust evidence exists for an impact on penguin foraging performance (Reid et al., 2005; Waluda et al., 2012, 2017) and baleen whale reproductive success (e.g., Seyboth et al., 2016). Currently catches in the Antarctic krill fishery are <0.5% of the estimated regional biomass. However, in recent

years the fishery has concentrated over specific hotspots where krill dependent predators forage (Santa Cruz et al., 2018). While spatial and temporal overlap has been demonstrated (Santora et al., 2010; Ratcliffe et al., 2015; Hinke et al., 2017; Weinstein et al., 2017) direct evidence that current levels of biomass extraction alter life histories of predators has not been clearly demonstrated. Conversely, Watters et al. (2020) argue there is no evidence that simply having a small catch relative to estimated krill biomass indicates precaution (see section "Integrated Conservation Under Uncertainty and Change"). Only few studies have investigated the overlap between flying seabirds and Antarctic krill fisheries, but one recent study for Antarctic petrels from Dronning Maud Land concluded that competition was negligible (Descamps et al., 2016). CCAMLR has previously recognized that the existing monitoring design would be insufficient for distinguishing between ecosystem changes due to commercial harvesting and changes due to environmental variability (physical or biological; CCAMLR, 2019b,c).

The importance of Antarctic (*Dissostichus mawsoni*) and Patagonian toothfish in the diet of many predators – and subsequently population-level effects of toothfish biomass removal – remains unclear and understudied. Patagonian toothfish are eaten by both wandering and black-browed albatrosses at Indian Ocean colonies, but only by wandering albatrosses at South Georgia where they overlap with fisheries during the breeding season (Cherel et al., 2000, 2017; Mills et al., 2020); this suggests that toothfish is rarely a natural prey for albatrosses, even if they can be made available by deep-diving seals or cetaceans returning to the surface. Both Patagonian and Antarctic toothfish are natural prey of sperm whales (Yukhov, 1972; Kawakami, 1980), and Patagonian toothfish is important for Crozet killer whales, composing >30% of their diet (Tixier et al., 2019b). The extent to which populations of these species were affected by the illegal overexploitation of stocks across the Southern Ocean in the 1990s is not known. In the Ross Sea, Antarctic toothfish is a natural prey of Weddell seals (Ainley and Siniff, 2009) and type-C killer whales (Pitman and Ensor, 2003; Ainley and Ballard, 2012), but spatial and seasonal variation in its importance in diets remain unclear. This uncertainty has generated much debate around the impacts of the toothfish fishery on these species. For example, while overfished toothfish stocks were proposed as responsible for local declines in killer whale sightings (Ainley et al., 2017), to date fine-scale bottom-up effects of fishery extraction on populations have not been evidenced (Pinkerton and Bradford-Grieve, 2014; Pitman et al., 2018).

Large-scale fishing by Soviet fleets from the late 1960s to early 1970s depleted mackerel icefish stocks, as well as marbled (*Notothenia rossii*) and gray (*Lepidonotothen squamifrons*) notothenia around subantarctic islands, which had not recovered by the early 2000s (Kock, 2007). These fish were, and mackerel icefish remain, key prey for predators that may have been impacted by the much-reduced stocks of the small notothens after the fisheries collapsed (Waluda et al., 2017). Given the currently low fishing effort for mackerel icefish, and its offshore location, any effects on predators are now very likely to be minor.

Future Threats

There is growing interest in large mesopelagic organisms (mainly fish and squid) as potentially harvestable resources (e.g., FAO, 2011) and krill fisheries are expanding (Johnston et al., to be published within this research topic) to meet with growing concerns over food security. Lantern fishes (*Myctophidae*) represent huge resources (estimated between 2 and 19.5 gigatons) available for potential future exploitation for direct human consumption and for aquaculture feed (Hidalgo and Browman, 2019) but their ecology and life histories are little known (St John et al., 2016). As myctophid and krill fisheries use midwater trawl fishing gear (Prellezo and Maravelias, 2019), the threats (direct and indirect interactions) are expected to be expanding in magnitude, as well as extending impact to a different suite of mesopelagic marine predators. However, there is currently no knowledge of how a myctophid fishery would be distributed spatially or temporally, nor what level of biomass extraction would lead to significant food web effects or ecosystem perturbation.

Pollution

Pollution is broadly defined as the contamination of the environment by substances or compounds that cause harmful health effects. Globally, 1 million new chemicals are formulated annually (Burton et al., 2017), with a proportion of emissions inevitably destined for the polar regions. Despite the remoteness, and the "shielding" nature of oceanic and atmospheric systems surrounding Antarctica (Bengtson Nash et al., 2010, 2017), pollution from lower latitude source regions represents a growing but largely unmonitored threat due to an absence of routine surveillance and measuring systems in Antarctica. In the context of rapidly changing polar climates, pollution is clearly a co-stressor to wildlife (Fossi and Panti, 2018) with for example, the impacts of poor body condition and pathogens expected to be compounded by accumulated pollutant burdens (Routti et al., 2018). Pollutant categories known to impact Antarctic biota from remote global sources include, but are not limited to synthetic chemicals, heavy metals and macro, micro and nano-plastic debris. Key input pathways of these to the Antarctic region include the atmosphere, ocean currents, *in situ* usage and biological transport (Bengtson Nash, 2011).

Persistent Organic Pollutants

Persistent Organic Pollutants (POPs) are a sub-group of organic chemicals that satisfy four criteria: persistence, toxicity, tendency to accumulate in wildlife over time, and magnify between trophic levels; as well as a propensity for long-range transport. While most POPs reach polar regions via the atmosphere, as a function of their persistence and semi-volatility (Wania and Mackay, 1993), perfluoroalkylated substances are proteinophilic (Prevedouros et al., 2006) and hydrophilic, favoring accumulation in surface waters and dispersal via oceanic pathways (Yamashita et al., 2008). In addition, Antarctica supports a number of highly migratory species that can serve as biological "vectors" of chemical transport to the region (Cipro et al., 2018). Finally, increasing human polar activity represents a pollution hazard, with Antarctic research stations identified as

local emitters of modern POPs (Bengtson Nash et al., 2008; Hale et al., 2008; Wild et al., 2015).

Persistent Organic Pollutants have been identified in Antarctic biota since the 1960s (George and Frear, 1966), including in top predators (Aono et al., 1997; Bustnes et al., 2006, 2007; Waugh et al., 2014; Dorneles et al., 2015; Das et al., 2017). The POP profiles of Antarctic foraging species are typically distinct from northern hemisphere and lower southern latitude counterparts (Bengtson Nash, 2011), reflecting unique, pesticide-dominated, hemispheric usage trends, as well as the long-range transport capabilities of individual chemicals (Bengtson Nash et al., 2010). For example whilst ubiquitous in the Southern Ocean, polychlorinated biphenyls (PCBs) do not dominate chemical profiles of predators but Hexachlorobenzene (HCB) and para, para-Dichlorodiphenyldichloroethane (p,p'-DDE) do (Corsolini et al., 2003; Bengtson Nash et al., 2008), with some indication of legacy POP burdens declining in baleen whales over the past three decades (Bengtson Nash, 2018).

As most known POPs accumulate in the lipid reserves of animals, body condition is an important consideration when evaluating POP burden in wildlife, in terms of target tissues, timing for exposure assessment (sampling) and evaluation of toxic effects (Bengtson Nash, 2018). Several studies have investigated potential toxic effects of POP exposure to Antarctic top predators, although this area of research remains challenging due to the uncontrolled nature of testing on larger, free-roaming species. In snow petrels, circulating levels of legacy POPs were positively correlated with levels of the stress hormone corticosterone (Tartu et al., 2015). Similarly, a humpback whale fibroblast cell line has been applied for the *in situ* investigation of toxicological effect of HCB and p,p'-DDE via immunotoxic, genotoxic and cell integrity endpoints (Burkard et al., 2015, 2019; Maner et al., 2019). Further investment into *in vitro* approaches is suggested for advancing our understanding of the toxicological sensitivity of Antarctic predators.

Mercury

Methylation of inorganic mercury Hg (II), mainly by bacteria, produces methylmercury (MeHg), an organic form of mercury that readily biomagnifies in aquatic food webs. MeHg contributes 50% of total Hg (HgT) in Antarctic bottom waters compared to just 5% of surface waters (Cossa et al., 2011). Accordingly, benthic feeding species (e.g., gentoo penguins) or species consuming benthopelagic species (e.g., wandering albatross) have accumulated some of the highest HgT levels of 21 seabirds from the Kerguelen Islands (2.42 and 4.45 μg/g dw, respectively) (Blevin et al., 2013). Similar findings were made for penguin communities on King George Island (Polito et al., 2016). Further, levels of HgT varied between 0.004 and 0.8 μg/g dw in Southern Ocean squid with the pelagic *Slosarczykovia circumantarctica* and the deep-water species *Fillipovia knipovitchi* demonstrating the lowest and highest levels, respectively (Seco et al., 2020).

Generally, HgT levels increase with decreasing latitude, with lower levels found in Antarctic phocid species and albatross compared to their temperate or tropical counterparts (Aubail et al., 2011; Cherel et al., 2018). To date Antarctic minke whales are the only Antarctic-foraging cetacean species in which Hg burdens have been reported, harvested in Japanese commercial whaling operations and Japanese Whale Research Under Special Permit from 1980 to 1999. Considering the bioaccumulative nature of MeHg, the trophic position occupied by cetaceans, and the known Hg contamination of lower trophic levels (Sontag et al., 2019), this remains a significant research gap. Hg is a known neuro-, immune- and genotoxin (Kershaw and Hall, 2019). Hence, there is significant interest in elucidating the impacts of Hg exposure to Antarctic biota. For instance, heat shock protein transcription in Weddell, Ross and crabeater seals from the Amundsen and Ross Seas negatively correlates with Hg concentrations in blood (Lehnert et al., 2017). Finally, the endocrine-disrupting and behavioral effects of Hg were investigated in snow petrels in relation to Hg burdens, with the notable finding that egg-neglect was higher in males with higher Hg burdens (Tartu et al., 2015).

Plastic

The entanglement of animals in flotsam plastics decreases the survival of individuals by restricting breathing, movement and the ability to successfully feed. Globally, 36% of seabird species have been documented as entangled by plastic debris (Ryan, 2018). In the Southern Ocean, plastic entanglement has been reported in at least 18 flying seabird (Kühn et al., 2015; Ryan, 2018) and seven penguin species (Ropert-Coudert et al., 2019). Of the world's marine mammal species, 45% have been documented with cases of entanglement (Gall and Thompson, 2015) highlighting the pollution pressures faced by migratory and resident Antarctic species (e.g., García-Godos et al., 2013).

Plastic debris is ingested by a wide range of marine animals, including top predators (Phillips and Waluda, 2020). There is a lack of data on the exposure to and impacts of plastic ingestion and entanglements on animals in the Southern Ocean (Gall and Thompson, 2015; Provencher et al., 2019). The risks posed by plastics on these species is determined by a variety of life history and environmental drivers such as foraging area or feeding strategy (Fossi et al., 2012; Tavares et al., 2017; Germanov et al., 2018). Seabirds are the vertebrate group for which there is most information on ingestion of marine plastics. For some species, records of plastic ingestion date back almost 30 years (e.g., short-tailed shearwaters *Ardenna tenuirostris;* Puskic et al., 2020). Albatrosses and petrels present the highest risk (Roman et al., 2019). The high amounts of debris collected by these birds (Phillips and Waluda, 2020) may be linked to their reliance on scent to detect prey that leads them to target bio-fouled plastics (Nevitt et al., 2006; Savoca et al., 2016). Flotsam plastic acts as a matrix that aids in the dispersal of rafting organisms. Biofilms on marine plastics absorb environmentally present chemical pollutants, such as metals and POPs (Johansen et al., 2018; Richard et al., 2019). Additionally, chemical additives used in the manufacturing of plastics can contribute to increased pollutant burden in animals (Lu et al., 2019). For many marine vertebrates, the digestive tract provides a favorable environment for chemical pollutants to leach from ingested plastics (Tanaka et al., 2013, 2015; Coffin et al., 2019). There is growing concern for the combined pressures of plastics and their associated chemical pollutants upon marine wildlife health (Bakir et al., 2016).

Health and Disease

Diseases can be introduced to Southern Ocean top predators through human and animal vectors, changing climate, stress and pollutants. On their own, each of these drivers can potentially cause unpredictable effects to predator health; in combination, effects are very likely multiplicative.

Despite much of Antarctica still being considered pristine (Tow and Cowan, 2005; Convey, 2011; Grimaldi et al., 2015), there has been vastly increased human activity in the last two centuries (Frenot et al., 2005; Kerry and Riddle, 2009) including recent exponential increases in Antarctic tourism (see section "On-land Disturbance, Human Impacts and Non-indigenous Species," IAATO, 2019). There is opportunity for disease introduction into relatively naïve populations via anthropogenic introduction of organisms (Lewis et al., 2004; Frenot et al., 2005; Tow and Cowan, 2005; Walton, 2012), in addition to migratory species coming into contact with fauna in more developed regions; a high risk likelihood presents from either (or both) of these threats. It is therefore imperative to address the paucity of data concerning diseases in Antarctic and sub-Antarctic populations.

Data are lacking on how altered species distributions and interactions due to climate change (Turner et al., 2013) can facilitate the introduction and spread of infectious diseases in the Antarctic. However, the effects of climate and changing species distributions and densities on wildlife disease has already been well-recognized in the Arctic (e.g., Van Hemert et al., 2014; VanWormer et al., 2019) where multiple outbreaks of phocine distemper virus (PDV) were associated with reduction in the extent of sea ice leading to PDV exposure and infection across species of sympatric marine mammals (VanWormer et al., 2019). In Antarctica, extensive research on sea-ice distribution and shifts in top predator movement ecology (e.g., McMahon and Burton, 2005; Massom and Stammerjohn, 2010) now needs to be partnered with investigations into how these changes affect disease prevalence, expression, and transmission.

Introduced Disease and Expanding Range

Human facilitated movement of pathogens is one of the main contributing causes behind the rise of emerging infectious diseases globally (Voyles et al., 2015). Since the first Antarctic explorations in 1899 birds and mammals have been introduced (see section "On-land Disturbance, Human Impacts and Non-indigenous Species"), as well as human food and body waste products (Kerry and Riddle, 2009) with all the risk for non-indigenous organism introduction this entails (Convey, 2011). While non-native species are no longer wilfully brought to Antarctica, the sub-Antarctic islands are not subject to the environmental protocols of the Antarctic treaty, with quarantine measures and invasive species management enacted by the administering country. This can result in inconsistent and unstandardized management protocols (Jabour, 2009; Walton, 2012).

Current knowledge of diseases in Antarctic species has been largely limited to isolation of viral and bacterial agents in seabirds, at distinct locations and investigations of mass mortality events, rather than any large scale coordinated effort to collect baseline data across multiple spatial scales and species. A review on Antarctic seabirds concluded further research is required to assess pathogen (and parasite) presence, geographical and temporal variation, how this could influence host species and the management required in the event of outbreaks (Barbosa and Palacios, 2009). Two outbreaks of Avian Cholera (*Pasteurella multocida*) have occurred on the Antarctic peninsula (Leotta et al., 2006), and more recently on subantarctic islands (Gamble et al., 2019). The presence of an evolutionarily distinct lineage of avian influenza virus' (AIVs) in Adélie penguins was discovered in 2013 at the Antarctic Peninsula (Hurt et al., 2014). A new study discovered the presence of 107 viral species in Antarctic penguins; the majority was associated with host diet and ticks (Wille et al., 2020). However, it is unknown whether any of these viruses cause disease in penguins. In 2014, phylogenetic analysis revealed genomic segments of AIVs from both Eurasian and North American lineages in two seabird species (Hurt et al., 2016). These studies demonstrated not only the presence of potentially highly pathogenic agents in just one section of Antarctica, but also a combination of endemic and introduced disease agents. Highlighted by these knowledge "gains" are the unknown consequences that future disease introductions might hold and the huge knowledge gaps remaining to be filled across the continent and its associated islands.

There remain many knowledge gaps on host-parasite relationships in Antarctic faunal assemblages. In seabirds and in marine mammals, ectoparasites and gastrointestinal parasites are the most documented groups (Barbosa and Palacios, 2009; McFarlane et al., 2009). Biting lice, feather mite, flea, tick and helminthes are most frequently recorded among seabirds (Barbosa and Palacios, 2009); amongst mammals, the main organisms are sucking lice, nasal mite, flea and helminths (Murray et al., 1965; Pugh, 1993; McFarlane et al., 2009). The first report of a blood parasite in Antarctica was published recently, when a *Babesia* sp. was detected in chinstrap penguins (Montero et al., 2016). The only tick species identified in Antarctica, *Ixodes uriae*, is the probable vector of this *Babesia* sp., although it has not been confirmed (Montero et al., 2016). Outside Antarctica, *I. uriae* may also be a potential vector of different protozoans (Peirce and Prince, 1980) and bacteria, as *Rickettsia* spp. (Chastel et al., 1993). The lack of several blood parasites in Antarctica (e.g., *Plasmodium and Haemoproteus*) is explained by the absence of appropriate vectors (e.g., mosquitoes, Culicidae) that cannot mature in the region due to the harsh climate conditions (Laird, 1961; Merino et al., 1997). However, environmental changes can modify the context of vectors, parasites and hosts in relation to their development and disease transmission (Patz et al., 2000). A slight temperature increase may be directly related to the augmentation of tick feeding, as found on parasitized penguins at the Antarctic Peninsula in warmer years (limited evidence) (Benoit et al., 2009), and allow the proliferation of potential vectors (Jones et al., 2002) accidentally introduced in the Antarctic ecosystem.

Animal Stress and Consequences for Health

Serological evidence of potential disease agents, be they viral, bacterial, protozoal or parasitic, is only one aspect of disease ecology. Human activity, in addition to the potential spread of pathogens (indigenous and translocated), results in increased stress in wildlife populations, which contributes to disease outbreaks (Lafferty and Holt, 2003) and threatens immunocompetence (Tarszisz et al., 2014) via its often-devastating consequences on the immune system (e.g., Dhabhar, 2009) and can be a significant factor in disease expression. Anthropogenic induced stress occurs through a variety of means, including (but not limited to): physical proximity (tourists and researchers); pollution of the Antarctic environment; nutritional stress; and habitat alteration and fragmentation. Nutritional stress occurs in Antarctic animal populations due to alterations in the abundance and distribution of prey and/or from direct depletion of fish stocks (Grimaldi et al., 2015). Direct anthropogenic-induced stress also occurs from physical proximity to humans (e.g., Engelhard et al., 2001, 2002), which has hastened the rate of non-native microorganism introduction, particularly in ice-free coastal areas where human activities are most prevalent (Tow and Cowan, 2005; Jabour, 2009; Grimaldi et al., 2015). Disease ecology of predator populations, particularly those that fall within the ever-increasing sphere of human activities, requires increasing attention to successfully predict and manage outbreaks.

Migratory Animals as Vectors for Disease Transmission

Disease and the potential for far-ranging migratory species to act as vectors among different animal populations is a very real risk within MEASO areas. While most Southern Ocean wildlife has evolved in relative seclusion, a number of top predators are migratory species. Seals, cetaceans and albatrosses are wide ranging species (Hindell et al., 2020). The Arctic tern breeds in the Northern hemisphere, but migrates to Antarctica for the austral summer, with the reverse occurring for Wilson's storm petrel (*Oceanites oceanicus*) (Kerry and Riddle, 2009). Southern elephant seals travel several thousand kilometers during their 10 months at sea (Hindell et al., 2016), and can encounter a range of hosts of common diseases. In several northern phocid species the canine distemper virus (CDV), a morbillivirus with high prevalence throughout the world's dog population (McCarthy et al., 2007), spread throughout populations leading to mass mortalities (Grachev et al., 1989; Kennedy et al., 2000). Serological evidence of CDV has been found in several Antarctic seal species, although no clinical disease has yet presented (Bengtson et al., 1991). Far-ranging migration can therefore increase the risk of disease exposure at distant sites, with the potential for disease transmission to large sections of the population in areas where other species congregate e.g., haul-out sites for southern elephant seals, breeding colonies for seals and birds. Couple these with the ability of diseases to spread more rapidly in marine as opposed to terrestrial populations (McCallum et al., 2003), and the potential for both increased expression of endemic disease and the emergence of new infectious diseases becomes a highly credible threat.

On-Land Disturbance, Human Impacts and Non-indigenous Species

Species' tolerance to disturbance vary, and disturbance timing and duration are relevant when evaluating impact. For example, disturbance effects can be different during highly sensitive stages in the breeding cycle (e.g., egg laying in seabirds, pre-weaning in marine mammals) making it complex to study. A major challenge is to quantitatively link behavioral and physiological responses to demography and population size. Relying on observations of behavioral changes may be insufficient, as they may not reveal cryptic and long-term effects on populations (Coetzee and Chown, 2016). Here, we broadly discuss land-based impacts and consequences of human-related disturbance mainly on seabirds and seals.

Direct Site Disturbance on Land Including Station Facilities and Tourism

Disturbance at breeding sites, attacks by natural predators or fights amongst conspecifics are part of life. Human presence, on the other side, is not, and several studies showed a stronger reaction to human disturbance than to natural predators (de Villiers et al., 2005, 2006). For example, repeatedly disturbed penguins experience a reduction in their breeding success (Giese, 1996; Ellenberg, 2017). Also, colonially breeding species are more prone to abandon their nests than solitary breeders. Site disturbance can be transient (e.g., visitations) or physical (destruction of habitat); both can have long-term consequences for populations (Christiansen and Lusseau, 2015). Colonially breeding seabirds and seals are particularly susceptible as they attract attention of both researchers and tourists.

In the Antarctic context, this is particularly important where ice-free, terrestrial habitat suitable for vertebrates is limited and concentrated in coastal regions. It is here where most human activities also occur (Shaw et al., 2014). Across Antarctica, the footprint of all infrastructure and buildings now exceeds 390,000 m^2, with an additional disturbance footprint of $>$5,200,000 m^2 just on ice-free land (Brooks et al., 2019). This footprint is similar in size to the total ice-free area of Antarctica and affects over half of all large coastal ice-free areas, disproportionately concentrating human impacts in some of the most sensitive areas as many species rely on ice-free ground to breed. While the Antarctic Treaty System (ATS) forbids the destruction of colonies, a research station brings with it a variety of disturbance sources ranging from noise of generators, vehicles (terrestrial and marine), aircraft and people to increased visitation of wildlife in the station surrounds. Station personnel and tourists visit concentrations of wildlife near the stations frequently (e.g., Tin et al., 2014) and often throughout the breeding period.

In Antarctica, mainly at the Antarctic Peninsula, visitor numbers (tourists, staff and crew) have been increasing over the last two decades (Liggett et al., 2011; Woehler et al., 2014) to nearly 55,500 people in the 2018/19 summer resulting in over 852,600 individual visits (IAATO, 2019). While not all reported

visits were to wildlife sites, areas free of human visitation are becoming rarer (Hughes et al., 2011; Liggett et al., 2011), and tourists tend to visit breeding colonies in large groups at a higher frequency than researchers, commonly throughout the breeding season. Although tourists do not always interact with animals directly, both kinds of activities – research and visitation – are types of disturbance but the long-term impact is difficult to measure and is rarely examined (Carey, 2009). A 21-year study of tourist interactions with gentoo penguins has revealed a decline in the Goudier Island population and a reduction in breeding success (Dunn et al., 2019). It also showed a significant link with higher numbers of tourist visitors (from 262 in 1996/1997 to 19,688 in 2016/2017). However, given the complexity of possible drivers, including a significant negative effect of increasing air temperature and shifts in sea ice variables on breeding pairs, the authors recommended both improved management strategies to protect this penguin population, and the initiation of similar studies at other frequently visited penguin sites. Detailed site- and species-specific research can support effective guidelines to develop and implement visitor management; well-managed ecotourism can contribute to wildlife conservation (Ellenberg, 2017).

In contrast to tourists, researchers typically work in small teams and may need to capture and handle animals. However, these interactions tend to be time limited and individual animals are typically manipulated once or twice in a season (Wilson and McMahon, 2006; McMahon et al., 2012). Few studies address the consequences of repeated handling, but one investigation of southern elephant seal pups showed no measurable short-term (survivorship) or long-term (fitness) consequences of handling intensity (McMahon et al., 2005). Non-lethal disturbance impacts are often reported as not detrimental with only minor effects, but long-term studies on apparently minor effects of transient disturbance are rare. For example, for eco-physiological studies blood samples are frequently collected, but the long-term effects of this procedure on other aspects of the animals' lives are rarely examined (Angelier et al., 2011). When assessing impacts of researcher disturbance on wildlife, it is important to consider whether previous exposure influences animals' responses. Colonies of some species subjected to long-standing research efforts may over time become less sensitive to human presence than naïve colonies. Cumulative exposure to non-lethal disturbance has been estimated using spatially explicit capture–recapture models (Christiansen et al., 2015) applied to whale-watching boat interactions. Similar approaches could be useful for wildlife populations influenced by the cumulative effects of either a repeated disturbance factor or experiencing several disruptive factors (natural and anthropogenic) simultaneously, as it is important to consider all relevant stress factors that affect animals at the time of study.

Noise Disturbance

Noise created by human activities occurs both on land and at sea. Fixed wing aircraft and helicopters have increased the range of accessible sites, thereby increasing the human footprint; but few studies have investigated the long-term effects of anthropogenic noise on land. Studies evaluating the immediate impact of helicopters approaching wildlife demonstrated that animals changed behavior, but there was no distinction between visual/acoustic effects (van Polanen Petel et al., 2006 and references therein). The use of wheeled and tracked vehicles on and near stations as well as in the field is widespread but the effects on wildlife are largely unknown. Weddell seals reduced the number of calls they made when over-snow tracked vehicles passed them (van Polanen Petel et al., 2006). While a single event of this nature causes only transient disturbance, the situation is unclear where vehicle operations occur frequently in the same area. The distance between vehicles and wildlife is also important, as is the breeding stage.

Assessment of underwater noise impacts in the Antarctic is an increasingly important issue, primarily related to ship traffic (from tourism, fisheries, and research), but also geophysical research (e.g., seismic surveys) and research station support activities (including construction). A recent review identified marine mammals to be most vulnerable, having the highest auditory sensitivity and using sound for communication, navigation and foraging; reported noise effects included avoidance responses, behavioral changes, disruption of foraging, changes in communication, and death in extreme cases (Erbe et al., 2019 and references therein). Priority research needs to include improved data on marine mammal distribution, hearing sensitivity (e.g., a mysticete audiogram) and assessment of the effectiveness of noise mitigations options. These data can aid refinement of noise exposure criteria for management, assisting the standardization of reasonable noise threshold requirements across countries.

Remote Monitoring via Unmanned Aerial Vehicles

The use of new technologies such as unmanned aerial vehicles (UAVs) is spreading rapidly and is expected to make wildlife monitoring less disruptive and more cost effective (e.g., Muller et al., 2019; Nowak et al., 2019). However, research on the potential impact of UAVs on wildlife is still preliminary (e.g., Rümmler et al., 2018; Weimerskirch et al., 2018) and potential long-term effects remain poorly understood. UAVs have quickly become a mainstream activity (Šimek et al., 2017). IAATO introduced a moratorium on recreational UAV flights in coastal areas (IAATO, 2015) and recorded the number of flights on IAATO registered vessels. In 2014/15, some 89 UAV flights were reported and in 2018/19 the number had risen to 1984 (IAATO, 2019) of which 95% were of commercial nature and less than 2% were for scientific purposes.

Currently, logistical and operational activities benefit from the use of UAVs, but information of UAV use in non-IAATO linked tourism and other commercial or scientific operations is largely absent. Issues near wildlife include the risk of accidents, aircraft flying too low over wildlife concentrations, and the potential number of UAVs flying under no limitations. Therefore, in 2018, comprehensive environmental guidelines for UAV usage in Antarctica were drafted and adopted by the ATS Parties to help avoid and/or reduce disturbance to wildlife while allowing for beneficial use (Harris et al., 2019). To our knowledge there are no equivalent guidelines for operation of unmanned underwater

vehicles used for observing wildlife (e.g., Clarke and Tyler, 2008) or other purposes.

Non-indigenous (Introduced and Invasive) Species

Antarctica and the sub-Antarctic islands have no native land mammals; deliberate or accidental introductions occurred when the islands were exploited for their natural resources (Russ, 2007; Convey, 2011). The response of island fauna was complex and variable. While non-native predators caused extinction of some endemic species (e.g., Taylor, 1979; Holdaway et al., 2010), not all introductions increased the mortality of local wildlife populations. For example, at New Island, Falkland Islands, introduced rodents and cats appear to coexist without a major impact on the local seabird populations; the cats (*Felis catus)* prey mainly on rodents (Quillfeldt et al., 2008).

Most commonly, increased mortality among native vertebrate populations has been caused directly or indirectly by rats (*Rattus rattus*), mice (*Mus musculus*), cats and rabbits (*Oryctolagus cuniculus)*. Rodents inflict significant injury and mortality among seabirds, including albatross chicks (Wanless et al., 2007; Jones and Ryan, 2010; Dilley et al., 2016). As the birds evolved without the presence of natural terrestrial predators, they are ill suited to defend themselves (Frenot et al., 2005). For critically endangered species such as the Tristan albatross (*Diomedea dabbenena*; Wanless et al., 2007, 2009) chick mortalities compound the albatross deaths in longline fisheries and worst-case scenario modeling predicts species extinction in ∼30 years; effective mitigation of both fishery mortality and mouse predation impacts is required (Wanless et al., 2009).

Mice adapted well to local conditions on many sub-Antarctic islands. At Marion Island, they reached densities of >150 mice ha^{-1} (Matthewson et al., 1994). Cats were eradicated here in the 1990s (Jones and Ryan, 2010; Jones et al., 2019). Since 2003, mouse attacks on albatrosses (including fatally) have been noted. Mice also predated incubating adults at Gough Island where mouse densities are ∼280 mice ha^{-1} (Parker et al., 2016; Jones et al., 2019).

At Macquarie Island, rabbits significantly reduced breeding habitat of burrowing seabirds whose populations declined markedly. In 2010–12, rabbits and rodents were eradicated, and many seabird populations improved (Springer, 2018). Similarly, at the Kerguelen Archipelago, seabird populations rebounded post-eradication of rabbits some increasing 4- to 8-fold (Brodier et al., 2011).

Introductions of non-native mammals to the Antarctic continent are currently unlikely as the environmental conditions are unsuitable for most non-native species (Woehler et al., 2014).

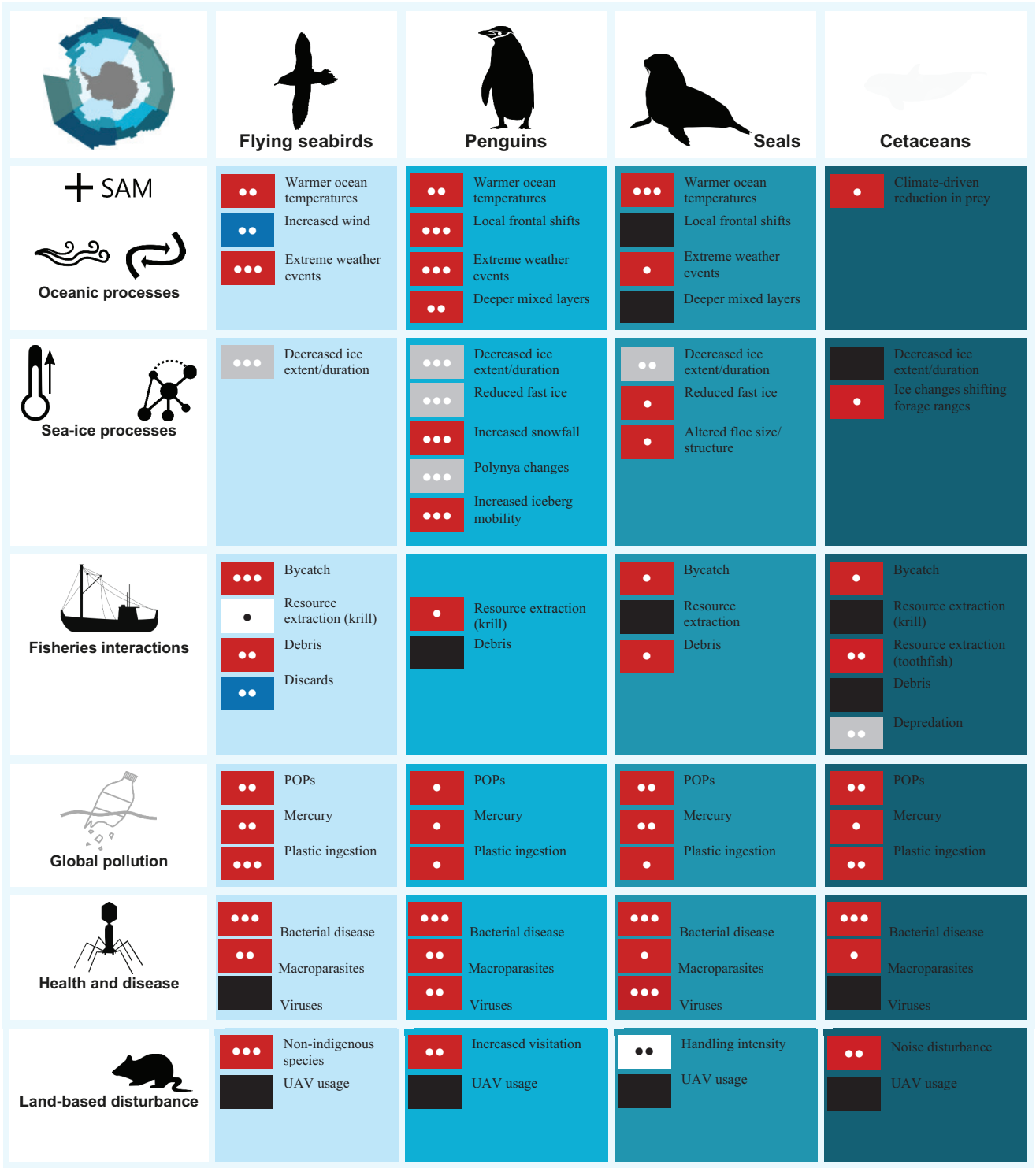
INTEGRATED CONSERVATION UNDER UNCERTAINTY AND CHANGE

Many factors directly or indirectly threaten top predators (**Table 3**) and substantial gaps in information and governance capacity remain (**Box 2** and **Table 4**). For example, population estimates for many predator species are imprecise, or out of date, in some cases by several decades (e.g., Phillips et al., 2016; Trathan et al., 2019). Estimates of population trend might exist at some of the better-known breeding sites, but regional or global estimates for many species are insufficient for accurate assessment of change driven by factors threatening predators. To inform management in the face of these threats, a better understanding of the potential causative mechanisms that shape population size, demography, phenology, distribution, diet and behavior is urgently needed along with more comprehensive and integrated management. This section explores the challenges and opportunities that scientists and policymakers face in the implementation of adequate measures for conserving top predators (**Table 5**).

Governance of Southern Ocean top predators occurs through a wide suite of legal instruments and associated regulatory bodies (**Table 4**) and through regional fisheries management organizations (RFMOs) adjacent to the CCAMLR area. While the IWC, CCAS and RFMOs primarily take a single-species approach in the management of predators, CCAMLR has a unique ecosystem and precautionary mandate toward conservation (see section "Southern Ocean Fisheries Interactions"). The Madrid Protocol (1991) also establishes an obligation to provide suitable protection to top predators as species-specific or system-wide measures. Other international bodies have a remit that covers the Southern Ocean and may provide opportunities for developing measures to support top predator conservation, such as ACAP.

Climate change related threats to Southern Ocean top predators are global in nature, thus requiring coordination across management bodies (Rintoul et al., 2018; Chown and Brooks, 2019). While the global threats are managed by the United Nations Framework Convention on Climate Change, an opportunity exists for CCAMLR and the Antarctic Treaty Parties to incorporate recommendations coming out of United Nations bodies such as the IPCC. For example, the SROCC (IPCC, 2019) highlights several urgent issues of significance to managing Southern Ocean ecosystems, including changes in sea-ice advance/retreat and related impacts on ice-dependent top predators, as well as potential effects of climate related drivers on food web structure and function, biodiversity and fisheries. Furthermore, the report emphasized that governance arrangements in the polar regions are currently not sufficient to adequately address the projected risks (IPCC, 2019). In light of this report, during the CCAMLR annual meeting in 2019, some members recalled CCAMLR Resolution 30/XXVIII on climate change (CCAMLR, 2009b), noting that it was timely to update the 2009 resolution, yet despite extensive discussions no agreement followed (CCAMLR, 2019a; paras 8.11 to 8.16). Over recent years, some CCAMLR parties have pursued related initiatives, such as a Climate Change Response Work Program that specifies actions to manage the Southern Ocean ecosystem more effectively under climate change. However, despite having a dedicated agenda item toward discussing climate change, these initiatives have been stalled by difficulties in reaching consensus (Rayfuse, 2018). The Committee for Environmental Protection – which provides recommendations to the Antarctic Treaty Parties for carrying forward provisions regarding the Environmental Protocol – has also developed a similar program and is progressing (CEP, 2019), but at a pace much slower than that of climate-related changes. The issues identified here and

TABLE 3 | Graphical table summarizes effects of high-level drivers on Southern Ocean top predators (red: negative, blue: positive, gray: mixed effects, white: no change, black: data required) with confidence indicated as ● ● ● high, ●● medium, ● low.



See text for commentary on the capability of current monitoring to be able to detect effects.

throughout this paper need to be urgently factored into CCAMLR and the Antarctic Treaty Consultative Parties precautionary approaches (Hughes et al., 2018).

The management of indirect interaction and effects on top predators is undertaken in two ways: a systems approach and an approach to reduce resource competition. One systems

BOX 2 | Research gaps and priorities.

Data coverage

Top predators receive considerable study effort and arguably represent the taxa for which the most ecological information is available. Yet, significant gaps remain at geographic (away from the main study sites and in vast Southern Ocean expanses), species (cryptic cetacean species) or life stage (juveniles) levels. Routine population censuses are spatially very limited, and population estimates for many predator species are imprecise, or out of date. Observational data remain sparse and difficult to collect during winter, especially within the sea-ice, hampering understanding of processes shaping predator-prey interactions in polynyas or under the ice. In oceanic areas, we are improving our understanding of the role of physical oceanic structures (eddies, filaments, fronts) in shaping the prey field distribution and hence predator foraging success. Further work should prioritize quantifying relationships (and their uncertainty) between key biological parameters (population growth rate, mortality, breeding success, migration phenology) and their biophysical drivers, to improve predictive capacity.

Given that top predators integrate signals over various spatiotemporal scales, we can take advantage of this through use of bio-logging and bio-monitoring technologies. Scaling up from such observations to synoptic predictive modeling represents an important strategy to overcoming monitoring limitations.

Projections of future change

Our understanding of current ocean/climate – prey – predator links and dependencies is inadequate. This is especially important for projecting how environmental changes will affect predator populations, but also for disentangling changes related to climate from changes with other causative mechanisms, such as fisheries. Meso- and fine-scale ocean features and biological coupling are not well-resolved in most earth system models. This limits the realism in modeling and projecting biotic interactions. Notably it is also complex to project socio-economic components.

Over the coming decade, we can expect higher resolution forecasting, and improved coupling (ocean-ice, physics-biology), which can better resolve features influencing predators and their prey. Alongside, we need to improve our characterization of linkages between ocean/climate, prey and predators. While a lot of attention has been given to krill-predator interactions, the importance of other prey, like toothfish or myctophids, deserves increased attention, as these become potential targets for commercial fisheries. Other key habitat requirements, notably fast ice (critical for some species life stages), remain poorly represented within both observational and modeled products.

Identification and management of current and future risks

While outside the direct scope of MEASO, gaps in understanding the connectivity of the Southern Ocean with the rest of the planet (Murphy et al., to be published in this research topic) pose major threats to our ability to protect it. Management bodies like CCAMLR have made extensive efforts to limit by-catch for example, but these best practices stop at the CCAMLR administrative boundaries, while some species distribute far beyond them. Governance for conservation of top predators requires coordination across management bodies. Also, a renewed commitment to progressing work programs specifying actions to manage the Southern Ocean ecosystem more effectively under climate change, and adequately addressing the projected risks for species and the ecological systems upon which they depend.

Similarly, administrative boundaries are porous to invasive species, introduced pathogens and their possible role in emerging diseases, or pollution. These increasingly influential and multiplicative threats deserve specific attention, as little is known, for instance, on the toxicological sensitivity of Antarctic predators to POPs and mercury, but also the real extent of plastic pollution and its impact. Growing human presence and activities, e.g., through tourism, requires studies to carefully investigate how disturbance, including exposure to a diversified and amplified soundscape, may affect predators long-term.

So, how to address these gaps and challenges? Clearly, additional funding is always a benefit, but this could be targeted toward goals that are often not at the core of funding schemes. Long-term monitoring has proved an invaluable requirement to examine the inter-connected climatic and anthropogenic effects. However, this cannot solely be maintained by limited research resources. To this end, and in parallel to researcher positions, dedicated long-term positions for "monitoring scientists" should be created – a commitment that would also increase work opportunities for many talented early career scientists. With such a task force, long-term monitoring sites could be expanded. The continued improvement in remote technologies (including satellite censusing, drones, underwater moorings, animal-borne environmental samplers), should also form an efficient and core part of continuous monitoring, implemented wherever needed to upgrade monitoring programs. It is also crucial to promote the recent trend in scaling up from individual projects toward multi-site, multi-species synthesis studies, as these are the only possibility to obtain synoptic views and understanding of these ecosystems.

approach to managing for multiple stressors is through the establishment of marine protected areas (MPAs). CCAMLR has established two MPAs to date – one near the South Orkney Islands (∼94,000 km^2) and one of the world's largest in the Ross Sea (>1.55 million km^2). There are also multiple large MPAs in subantarctic island Exclusive Economic Zones (see Brooks et al., 2020), established partly to provide protection for top predators (see Trathan et al., 2014; Trathan and Grant, 2020). However, Hindell et al. (2020) assessed the locations of predator hot spots in the Southern Ocean and examined how these are expected to change under climate scenarios. They compared these locations to the established and proposed marine protected areas in the region and concluded that further MPAs are needed to provide for the long-term requirements of these predators, including the existing proposals before CCAMLR as well as other areas. The protected areas system remains largely unsystematic and underdeveloped (Hughes and Grant, 2017; Brooks et al., 2020).

Beyond CCAMLR, Annex V of the Environmental Protocol to the Antarctic Treaty enables the Parties to designate Antarctic Specially Protected Areas (ASPAs) to protect environmental values, including areas with important or unusual assemblages of species, like major breeding colonies of seabirds or mammals (Environmental Protocol, 1991). ASPAs are primarily on land; some include a limited at-sea portion, for which CCAMLR is consulted, and comprise all colonies of one or more bird species (Wauchope et al., 2019). Given the threats to top predators, MPAs and ASPAs provide an important tool to help mitigate impacts. A stronger connection between ASPAs (Antarctic Treaty) and MPAs (CCAMLR) is desirable to enhance protection of species that use both domains.

Under Annex II to the Protocol, vulnerable species can be designated as Antarctic Specially Protected Species (SPS) (Environmental Protocol, 1991). Designating species facilitates protection across all life history stages and eventually of all genetically distinct meta-populations (Trathan et al., 2020). Currently, no species has yet been designated an Antarctic SPS; however, designation should in theory mitigate any human activities that might harm candidate species. The relationship between CCAMLR and the Antarctic Treaty would also ensure consistency in the application of such measures by CCAMLR. Work to consider possible designation of emperor penguins

TABLE 4 | Regulatory bodies with responsibility for conserving Southern Ocean marine predators, particularly with respect to the main threats shown in **Table 3**, i.e., climate change, fisheries interactions, global pollution, health and disease and land-based disturbance.

Legal Instrument	Regulatory body	Responsibility	Approach	Information needs and gaps
International Convention on the Regulation of Whaling	International Whaling Commission	Conservation of whales	Historical catch quotas; modern moratorium; Southern Ocean Whale Sanctuary; population assessments.	Status of Southern Ocean whales (including abundance, trend and past catches), including under environmental change (and fisheries indirect interactions).
Antarctic Treaty and the Protocol on Environmental Protection to the Antarctic Treaty	Antarctic Treaty Consultative Meeting and Committee for Environmental Protection	Environmental protection of the Antarctic continent and the seabed	Antarctic Specially Protected Areas/Species; Prohibitions of taking or harming Antarctic species; Prohibitions of introducing non-native species; Environmental impact assessments for science bases.	Population status and trends of many species unclear; biodiversity assessments needed; insufficient regulations for managing some threats (e.g., pollution from global sources, disease and tourism).
The Convention for the Conservation of Antarctic Seals (CCAS)	N/A (currently no commercial sealing)	Conservation of Antarctic seals	Catch regulations (and prohibitions), protected species and protected areas.	Population status, including under environmental change.
Agreement on the Conservation of Albatrosses and Petrels	Meeting of the Parties	Conservation of Albatrosses and Petrels	Coordination of international activities; Recommendations for seabird mitigation measures, management and protection of breeding sites.	Accurate population status of many species unknown; Effective seabird mitigation lacking in a number of RFMOs leaving Southern Ocean albatross and petrel populations at risk.
Convention on the Conservation of Antarctic Marine Living Resources (CAMLR Convention)	Commission for the Conservation of Antarctic Marine Living Resources	Conservation of Antarctic marine living resources, including fished species as well as the ecosystem more broadly	Catch quotas; Ecosystem approach to management; Mitigation measures to avoid birds and mammals; Protected areas; Climate change resolutions/measures.	Lacking adequate knowledge of ecosystem impacts (direct/indirect) from fishing as well as impacts from climate change.
Conventions related to Tuna and other fished species	Regional Fisheries Management Organizations (RFMOs)	Conservation of marine living resources (including ecosystems) adjacent to the CCAMLR Area	Mitigation measures to avoid birds and mammals.	Lacking adequate compliance mechanisms to mitigate seabird bycatch.

The table shows the legal body, their responsibility, approach, and information needs and gaps with regards to Southern Ocean birds and mammals.

TABLE 5 | Key messages arising from this chapter.

Key Messages
1. In the Southern Ocean, top predators provide some of the best long-term datasets and, hence, capacity to address issues dealing with climate change.
2. Climate change is an overarching threat that acts independently and/or in combination with other threats, especially fisheries, but disentanglement of effects remains key to defining and evaluating conservation measures.
3. Many subantarctic seabird populations remain threatened despite existing fisheries mitigation measures, requiring improved practices beyond CCAMLR waters (high confidence).
4. Global pollutants increasingly impact Southern Ocean biota, and long-range migrations by top predators can favor transport of pollutants, invasive species and diseases (low confidence).
5. Emerging health and stress indices show promising capacity for top predators to provide monitoring of ecosystem change (medium confidence).
6. As human activities – tourism and research – increase so does the potential for direct disturbance impacts particularly in ice-free coastal regions (high confidence); management mechanisms must continue to evolve to mitigate these.
7. Risk-assessment frameworks that explicitly account for predator consumption, including recovering baleen whale populations, are a critical new tool for allocating spatial (krill) catches.
8. Similar approaches integrating across differing Southern Ocean management responsibilities are necessary to coordinate responses to the accelerated pace of climate-related change.

is underway (Trathan et al., 2020), given its vulnerability to environmental changes and related dire population projections (e.g., Jenouvrier et al., 2019).

One ongoing major threat, especially to flying seabirds, is incidental mortality in industrial fisheries. While CCAMLR has successfully eliminated, or at least reduced to very low levels, the mortality of seabirds in longline fisheries, this issue remains a challenge for longline and trawl fisheries outside of the CCAMLR Convention Area. One solution might be more outreach and coordination from CCAMLR to adjacent RFMOs. This could include sharing strategies on seabird bycatch mitigation measures and encouraging more direct action or coordination with ACAP.

Beyond threats of direct interactions, a challenge in implementing true ecosystem-based management is to reduce the effects of resource competition between a fishery and top predators, particularly for the krill fishery. While a requirement under CCAMLR, fisheries are still managed under a single-species stock assessment approach. This approach has thus far only provided for predators in setting the catch limits of krill. It has not yet been able to effectively and directly incorporate spatial impacts on predator and prey and environmental changes. This latter need has been demonstrated by a hierarchical model using 30 + years of penguin monitoring data, which revealed that penguin performance was reduced when local harvest rates exceeded relatively low thresholds (Watters et al., 2020). This effect was similar in magnitude to that of poor environmental conditions, suggesting that even relatively small catch limits may not be precautionary for their predators. Measuring these impacts are a tremendous challenge and wrought with uncertainty. Predators respond to many drivers, including but not limited to environmental conditions and predators' interactions. However, lack of evidence does not mean lack of impact.

The commission for the Conservation of Antarctic Marine Living Resources has made strides in the last year by agreeing to an advanced management strategy for krill that would include not only a stock assessment, but also regular updates of biomass estimates and a risk assessment framework to inform the spatial allocation of catch (CCAMLR, 2019c, para 5.17). The risk assessment framework would include consideration of the spatial foraging needs of predators, including accounting for the ongoing recovery and modeling.

The development of the risk framework, while demonstrating progress in CCAMLR's ecosystem approach, exemplifies the need for integration, in this case between the Scientific Committees of CCAMLR and the IWC. The krill risk assessment framework (SC-CAMLR, 2016, 2019) will necessarily incorporate up-to-date whale density and abundance data into models of krill consumption by predators (e.g., Kelly et al., 2018; Trathan et al., 2019; Warwick-Evans et al., 2019a,b). The IWC's Scientific Committee oversees the population assessments of whales, recording data on abundance and trends, validating statistical analyses of whale abundance and recovery, and assessing environmental and anthropogenic threats. Both CCAMLR and IWC Scientific Committees recognize that improved engagement between these intergovernmental organizations could support CCAMLR in achieving ecosystem assessment objectives. Initiatives in planning to assist with this include a Cetacean Subgroup within CCAMLR's Scientific Committee, a joint workshop on Southern Ocean ecosystem modeling (IWC, 2017 p56; SC-CAMLR, 2018 p7.12) and a joint IWC-CCAMLR workshop (IWC, 2018). For populations of conservation concern, the IWC implements Conservation Management Plans, providing a framework to protect and rebuild depleted populations through coordinated collaboration of countries spanning their range. Two such populations (southeast Pacific and southwest Atlantic right whales) can also range into the Southern Ocean (the Bellinghausen/western Antarctic Peninsula region, and Scotia Arc/northern Weddell Sea, respectively). Antarctic blue whales are also classified as Critically Endangered on the IUCN Red List. Explicit consideration of possible impacts on these depleted populations should be considered within CCAMLR's ecosystem management framework.

Efforts to reduce interactions with land-based colonies have been occurring throughout the Antarctic Treaty System.

For example, SCAR and IAATO are currently leading a systematic conservation planning project, to inform on how to optimally manage biodiversity, science and tourism. Antarctic tourism has increased dramatically in the last two decades. The decline in Goudier Island gentoo penguins (see section "Direct Site Disturbance on Land Including Station Facilities and Tourism") is in contrast to less visited sites elsewhere in the region (Dunn et al., 2019) and to the core objectives of IAATO, i.e., ensuring that tourism has no more than a minor or transitory impact on the Antarctic environment (IAATO, 2019). In 2019, the Netherlands and the United Kingdom convened a workshop on Antarctic tourism, attended by many parties and IAATO, and produced multiple recommendations to the Antarctic Treaty Consultative Meeting (ATCM, 2019) which were agreed. These recommendations included work between Parties, COMNAP, SCAR and IAATO to ensure that current Antarctic visitor guidelines are in line with best practice, levying of an administrative fee which could be used to support environmental monitoring of areas visited by tourists, development of a standard framework for assessing the safety and environmental impact of new tourism activities, and to improve and standardize rules compliance among the parties involved in Antarctic tourism.

Overall, the institutions with responsibility for conserving Southern Ocean top predators must manage for those priority species with a listed status of concern, as well as more broadly for direct and indirect (including food web) effects on predators. However, the paucity of information on the status of many species coupled with ongoing threats poses a significant management challenge. Further, the Southern Ocean lacks institutions that are directly responsible for the control of pollution, disease, tourism and other threats highlighted above. All the above-mentioned tools and approaches, and others (**Table 5**), need to be used swiftly and in creative ways given the accelerated pace of climate-related change in the world's oceans (Tittensor et al., 2019).

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SoB and YR-C coordinated the project, and assembled and edited the manuscript. All authors wrote the content, with specific contributions as outlined below, provided review and edits across the manuscript, and approved the final version. YR-C and SoB: sections "Abstract" and "Introduction". RR, YR-C, and JJ: section "Data, Methods and Tools". PPi, CC, MW, SL, and AF: section "Influence of Climate Change on Marine Predators". AL, PT, and RP: section "Interactions With Commercial Fisheries and Resource Extraction". SuB and PPu: section "Pollution". MD, CM, AR, and ET: section "Health and Disease". BW and SoB: section "On-Land Disturbance, Human Impacts and Non-indigenous Species". CB, PT, JJ, and MS: section "Integrated Conservation Under Uncertainty and Change".

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.566936/full#supplementary-material

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frontiers in Marine Science

REVIEW
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Global Drivers on Southern Ocean Ecosystems: Changing Physical Environments and Anthropogenic Pressures in an Earth System

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The manuscript assesses the current and expected future global drivers of Southern Ocean (SO) ecosystems. Atmospheric ozone depletion over the Antarctic since the 1970s, has been a key driver, resulting in springtime cooling of the stratosphere and intensification of the polar vortex, increasing the frequency of positive phases of the Southern Annular Mode (SAM). This increases warm air-flow over the East Pacific sector (Western Antarctic Peninsula) and cold air flow over the West Pacific sector. SAM as well as El Niño Southern Oscillation events also affect the Amundsen Sea Low leading to either positive or negative sea ice anomalies in the west and east Pacific sectors, respectively. The strengthening of westerly winds is also linked to shoaling of deep warmer water onto the continental shelves, particularly in the East Pacific and Atlantic sectors. Air and ocean warming has led to changes in the cryosphere, with glacial and ice sheet melting in both sectors, opening up new ice free areas to biological productivity, but increasing seafloor disturbance by icebergs. The increased melting is correlated with a salinity decrease particularly in the surface 100 m. Such processes could increase the availability of iron, which is currently limiting primary production over much of the SO. Increasing CO_2 is one of the most important SO anthropogenic drivers and is likely to affect marine ecosystems in the coming decades. While levels of many pollutants are lower than elsewhere, persistent organic pollutants (POPs) and plastics have been detected in the SO, with concentrations likely enhanced by migratory

species. With increased marine traffic and weakening of ocean barriers the risk of the establishment of non-indigenous species is increased. The continued recovery of the ozone hole creates uncertainty over the reversal in sea ice trends, especially in the light of the abrupt transition from record high to record low Antarctic sea ice extent since spring 2016. The current rate of change in physical and anthropogenic drivers is certain to impact the Marine Ecosystem Assessment of the Southern Ocean (MEASO) region in the near future and will have a wide range of impacts across the marine ecosystem.

Keywords: Southern Annular Mode, ozone hole, cryosphere and climate change, biogeochemsitry, carbon dioxde, non-indigenous species, warming, freshening

INTRODUCTION

The Southern Ocean (SO) physical environment is shaped by permanent cold and predictable seasonal cycles. However, despite its relative isolation within the Antarctic Circumpolar Current (ACC) inter-annual variation of the SO is strongly influenced through atmospheric and oceanic teleconnections. In an era of rapid climate change it is vital to identify the global drivers of the SO marine ecosystems. It is important to understand the regions within the SO where their effects are greatest, the expected impacts of any changes in these drivers, and crucially their interactions. For the working group, Marine Ecosystem Assessment of the SO (MEASO), global drivers are classified as those that influence the whole of the SO, even though their affects may manifest more strongly in some regions than others. Local drivers are defined as those that influence a particular location or series of locations within the SO (Grant et al., to be published in this research topic). While there is a global demand for protein to feed the ever increasing human population, southern ocean fisheries have regional impacts on stocks and ecosystems. A key difference is that local drivers can be managed with local interventions, e.g., regional regulation of fisheries. Yet, global drivers can only be managed externally to the region, e.g., climate change, ozone and plastic. Global tourism is driven by global drivers such as increasing wealth and demand for wilderness experiences. However, the regional impacts of tourism can also be managed through local regulation. Tourism therefore appears as both a global and local driver.

The manuscript outlines the global phenomena that impact the SO now and are expected to continue to impact it in the future. Atmospheric drivers considered here include changes in ozone, trends in Southern Annular Mode (SAM), variability in El Niño Southern Oscillation (ENSO), elevated air and ocean temperatures and ongoing increases in atmospheric CO_2. Global oceanic connections considered here include the global thermohaline (overturning) circulation as well as changes in the SO, including eddies currents and the exchange of water masses (**Figure 1**). Other global anthropogenic drivers include pollution and tourism.

These drivers, and their interactions, affect a range of attributes of the SO environment. Those considered here are: the cryosphere including marine ice, ice shelves and glaciers as well as salinity. For the purposes of MEASO the SO is separated into five sectors and three zones (**Figure 2**)

The majority of the biological consequences within pelagic and benthic marine ecosystem are discussed in the specific MEASO biota papers (as described in Constable et al., 2014 to be published in this research topic), but the impact of changes in the biogeochemical cycles, including the impacts of CO_2 and ocean acidification are included. The increased risk of non-indigenous species establishing in the SO (range extensions in **Figures 1**, **2**, **4**) and the external influences on species that migrate in and out of the SO are also discussed as external drivers in this manuscript.

There have been several recent attempts to assess the dynamism of stressors impacting the Southern Ocean and its inhabitants (Constable et al., 2014; Gutt et al., 2015; Rogers et al., 2020). Where the current work differs is in taking a detailed look at large scale, global, influences on the physical environment, and to set these into a MEASO context. Where appropriate, the level of confidence in a conclusion is given according to the approach of the IPCC (Mastrandrea et al., 2011). These are given in italics in parentheses, with an appropriate reference where the confidence level has been judged elsewhere. When not accompanied by a reference, we judged confidence from the levels of agreement we observe in the scientific literature and the amount of evidence presented to support the conclusion, including consideration of any contrary evidence. Sometimes, we only report on the scope of the evidence in terms of agreement and amount. The levels of confidence are not to be used as the inverse of confidence for alternative hypotheses, as those alternatives may not be addressed in the literature. The future prognosis of these drivers is assessed and gap analysis is used to define future priorities.

PHYSICAL DRIVERS

SAM/ENSO

Stratospheric ozone concentration in the middle and high latitudes of the southern hemisphere has been decreasing in spring, summer and winter since the 1970s (e.g., WMO, 2011). Termed stratospheric ozone depletion, it is considered the single largest driver of change in summer, tropospheric (atmospheric) circulation in the southern high latitudes (Polvani et al., 2011). Normally, ozone absorbs UV radiation, radiatively warming the stratosphere. Its depletion, caused by chlorofluorocarbon (CFC) emissions, that began in the 1970s, means reduced absorption when sunlight returns to the southern high latitudes in the southern spring, and results in radiative cooling of the

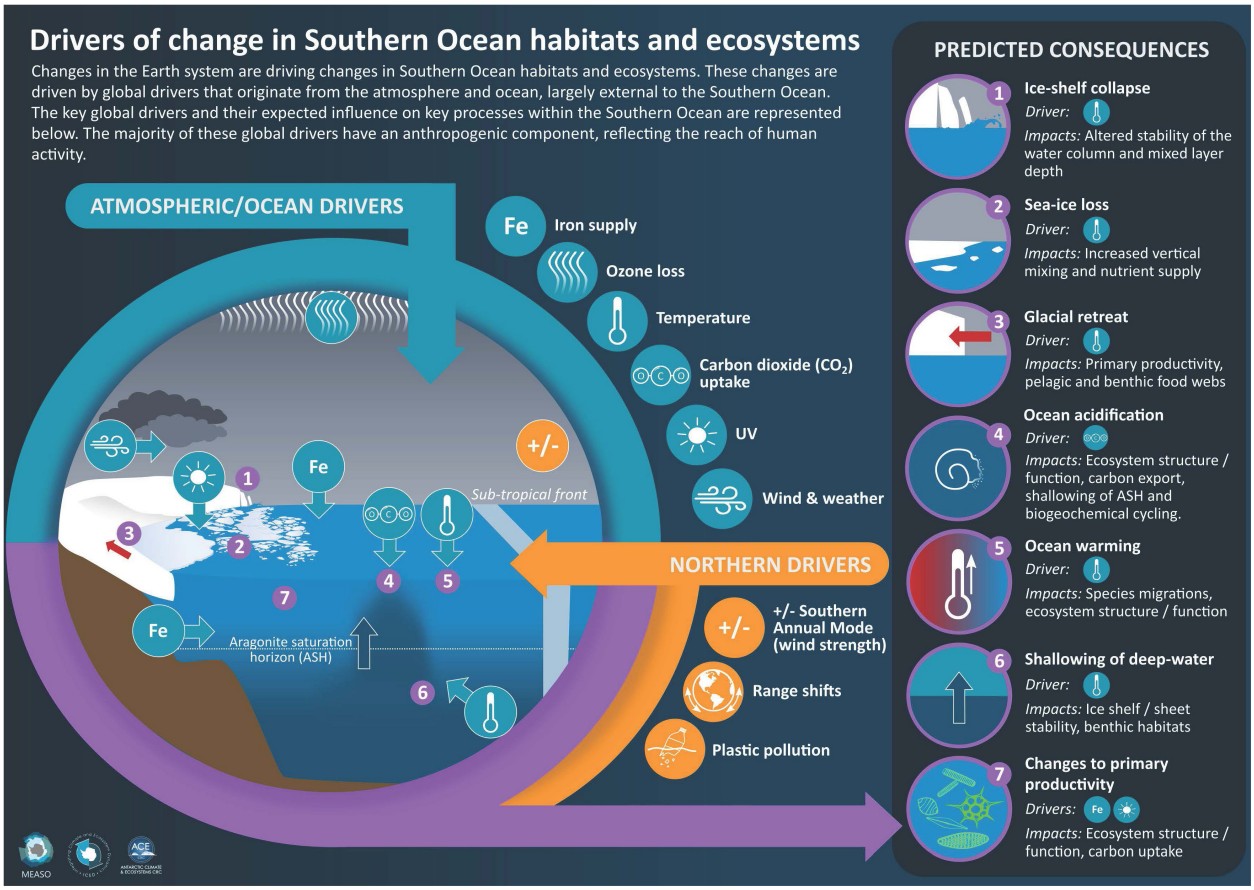

FIGURE 1 | Description of the global drivers affecting the Southern Ocean. Northern drivers are global drivers whose influence reaches from North of the Southern Ocean.

stratosphere over Antarctica. The dynamic response is increased shear in the zonal wind field and a strengthened stratospheric polar vortex as the atmosphere moves to restore the thermal wind balance (Thompson and Solomon, 2002). These changes in the stratosphere propagate to the troposphere, in approximately 2 months. The tropospheric effect is therefore observed in summer and is seen as a poleward shift of the mid-latitude jet and the accompanying storm track (Thompson and Solomon, 2002).

The tropospheric effect is an indication that stratospheric ozone depletion directly influences the leading mode of atmospheric circulation variability in the southern extratropical regions, the Southern Annular Mode (SAM). A measure of the SAM is an index calculated as the pressure gradient between mid-latitudes and Antarctica (Marshall, 2003), which when strongly positive, results in westerlies that are stronger than average and shifted poleward (e.g., Swart et al., 2015). Since 1957 there has been a significant increase in positive SAM in the austral summer and autumn (Marshall, 2003, 2007). The summer trend is thought to be forced primarily by stratospheric polar ozone depletion (Perlwitz et al., 2008). The variability of the SAM has a significant impact on Antarctic surface temperature (Marshall and Thompson, 2016), precipitation (Marshall et al., 2017), and sea ice (e.g., Hobbs et al., 2016; Doddridge and Marshall, 2017). The strong circumpolar westerlies associated with a positive SAM contributes to a cooler, drier, continental plateau (Eastern Antarctica) as they prevent the southward penetration of warmer air. Conversely, the Antarctic Peninsula warms because of warm air advection by the northwesterly flow, which also induces orographic precipitation on the western slopes and a rain shadow on the eastern slopes (Thompson and Solomon, 2002; Marshall and Thompson, 2016; Marshall et al., 2017). The increase in sea ice extent observed in the satellite era is attributed, in part, to increased northward Ekman drift associated with stronger westerlies over the Southern Ocean, facilitating the spread of the ice.

The SAM interacts with ENSO during the austral summer, particularly in the Pacific sector (e.g., Carleton, 2003; L'Heureux et al., 2006; Lim et al., 2019). When a La Niña phase in the tropical Pacific (cooler than average sea surface temperatures in the central and eastern tropical Pacific Ocean) co-occurs with a positive SAM phase at mid-high latitudes, this condition amplifies the effect of stratospheric ozone depletion. SAM and the high latitude ENSO both exert an influence on the Amundsen Sea Low (ASL), a climatological low pressure system centered off the coast of West Antarctica, the central pressure of which has deepened in recent years in response to an increase in the number

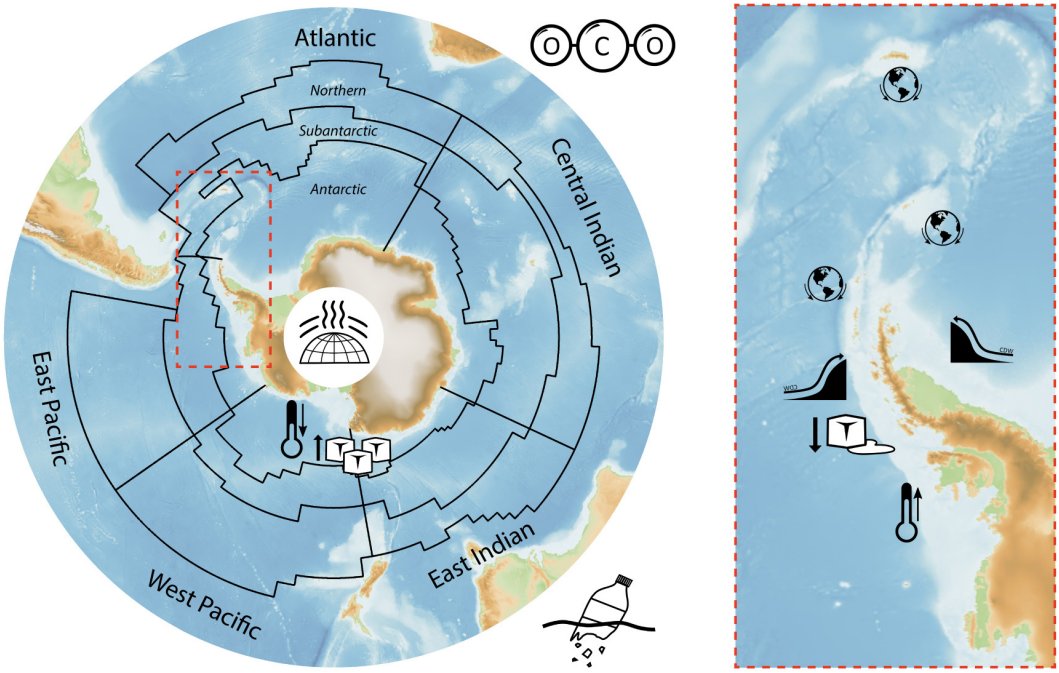

FIGURE 2 | Areas for assessing effects of global drivers in the Marine Ecosystem Assessment of the Southern Ocean (black lines) with the Antarctic Peninsula highlighted (red dashed box). The five sectors (Atlantic, Central Indian, East Indian, West Pacific and East Pacific) and zones (Antarctic, Subantarctic and Northern) are labeled. Zonal boundaries are the Southern ACC Front between Antarctic and Subantarctic zones, and the Subantarctic Front between Subantarctic and Northern zones, with the Subtropical Front to the north. Icons indicate currently identified critical locations for increase and decrease in temperature and sea ice, potential for invasive species, and where circumpolar deep water is increasingly shoaling onto the continental shelf. They also illustrate general effects of ozone depletion, pollution and ocean acidification.

of cyclones entering the region. This increase is primarily due to the more positive SAM driven by ozone depletion (Grieger et al., 2018). This effect on the ASL may have far reaching consequences since the ASL plays a role in altering ocean currents, allowing warm Circumpolar Deep Water (CDW) to reach more frequently under the Pine Island and Thwaites glaciers that drain much of West Antarctica (Thoma et al., 2008). This has coincided with a period of thinning of these glaciers (Thoma et al., 2008).

Temperature

Atmospheric Warming

Intensifying warm and moist westerly winds during more frequent positive phases of the summer SAM cause pronounced atmospheric warming of the Northern and central sectors of the West Antarctic Peninsula (WAP). Strong interannual variations of atmospheric warming/cooling patterns are strongly related to climatic modes of SAM and ENSO (Bers et al., 2013). The strengthening of the westerly winds has also resulted in the warm air passing over the mountains of the Antarctic Peninsula, which has contributed to the melting of the east Antarctic Peninsula ice shelves (Cape et al., 2015).

Oceanic Warming

The SO has been a stable cold environment for millions of years, shaping unique ecosystems of cold adapted Antarctic biota. Within this stable regime there have been 100's to 1000's year time scale variations of 2–4°C on the WAP, which are associated with reconstructions of the SO westerly winds (Shevenell et al., 2011). The increased intensity of positive summer SAM events are correlated with significant changes in seawater temperature that have been recorded in recent decades (*high confidence*; Hellmer et al., 2017; Moffat and Meredith, 2018). Circumpolar deep water (CDW), the temperature maximum layer of Antarctic Continental Shelf Bottom Water (ASBW) is warming (0.1°C decade^{-1}) and shoaling (−30 m decade^{-1}) in most regions around the Antarctic (*high confidence*; Schmidtko et al., 2014) and both hydrographic and climatic forcing, modify the atmospheric and ocean heat transport.

Regional Patterns

At the northwestern tip of Bransfield Strait and the South Shetland Islands (East Pacific), ocean temperatures are cooled by water entering from the Weddell Sea, while mean air temperatures increased by 0.4°C per decade between 1991 and 2012 (Schloss et al., 2012). Melt events at the Northern WAP are regional and episodic, and thus amplify environmental and ecological variability in coastal and shelf systems (Meredith et al., 2018). In contrast, the central/south WAP is influenced by atmospheric warming and by upwelling of warm CDW onto the shelf, which has driven thinning of about 75% of the ice shelves of the AP and the Amundsen Sea. Mean atmospheric temperatures increased by 3°C (0.6°C per decade) and sea surface temperatures

by 1°C (SST in the upper 100 m) between 1955 and 2004 (Moffat and Meredith, 2018). In spite of a recent superimposed cooling phase recorded since the early 2000s, which appears to be associated with shifts in decadal forcing in this region (Turner et al., 2016), net warming of the WAP atmosphere is still significant and the ocean has continued to warm (Martinson et al., 2008). Similarly, increases in seawater temperature have been reported for the Atlantic Sector, with warming averaging over 2°C in the upper 150 m over the past 81 years (Whitehouse et al., 2008) and 0.3–1.5°C in subsurface temperature (50–400 m) at the Eastern Antarctic Peninsula (Etourneau et al., 2019).

Other regions of the SO either remained stable or cooled in the last two-three decades. These differences originate from varying patterns in the ocean heat transport around the Antarctic (Schmidtko et al., 2014) and shoaling of warm deep water (WDW) up onto the continental shelf. For instance, relatively warm CDW entering the eastern Weddell Sea gyre causes shoaling of WDW (+0.8°) flowing along the continental shelf break in the Southern Weddell Sea. Models project intrusion of WDW into the Filchner-Ronne Ice Shelf cavity as part of a tipping point scenario, which would dramatically increase basal melt rates, threatening the stability of the largest floating ice mass fringing the Antarctic continent (Timmermann and Hellmer, 2013; Hellmer et al., 2017). The warming has been observed in most sectors, but the vertical displacement of the CDW core shows a more complex pattern, with deepening in the Cosmonaut and Northern Weddell Seas and shoaling elsewhere (Schmidtko et al., 2014). It is interesting to note that while the general trend of CDW also persists in the Ross Sea, no shoaling and intrusions of CDW onto the shelf have been observed so far (H. Hellmer, pers. communication). In contrast to the warming of the AP and CDW in the Weddell and Ross Seas/gyres, the Eastern sections of the continental SO have shown a cooling trend (Rogers et al., 2020). With continued warming of the earth's atmosphere, future warming between now and 2100, is expected across the whole of the SO (Rogers et al., 2020).

Many SO marine ectotherms are adapted to a narrow annual thermal range of only 2–4°C, and are therefore vulnerable to the effects of warming (*medium confidence*). Increasing ocean temperature is also correlated with the secondary effects of warming on summer sea ice dynamics and glacial melting in coastal and near-shore regions (*high confidence*). Increasing temperature is therefore projected to shape open ocean ecosystems and affect coastal communities down to the level of species ecological performance and molecular composition (*high confidence*, Ashton et al., 2017; Peck, 2018).

Currents and Eddies

The SO circulation forms a major horizontal connection between ocean basins as well as a vertical link between shallow and deep water masses. The ACC consists of a strong, multi-jet, and turbulent eastward flow around Antarctica, transporting approximately $173.3 \pm 10.7 \times 10^6$ $m^3.s^{-1}$ (Donohue et al., 2016). The ACC, driven by westerly winds and surface buoyancy fluxes, is also identified by three main circumpolar fronts, separating distinct water masses, which contribute to the isolation of the SO (Sokolov and Rintoul, 2009).

As indexed by the SAM, a clear trend in strengthening of westerly winds has been observed in recent decades (Swart et al., 2015), yet there is no evidence of a significant increase in the ACC transport (*medium confidence*; Chidichimo et al., 2014). Although the response of the ACC transport and eddy field to wind forcing is still uncertain (*low confidence*), the presence of active ocean eddy dynamics, and its saturation suggested by modeling (Munday et al., 2013), buffers the oceanic response to atmospheric changes. This apparent cascade of energy into small scale eddies is supported by the satellite derived measurements, which indicate an increase in eddy kinetic energy over the last two decades. This is especially significant in the Pacific and Indian Ocean sectors of the SO (*medium confidence*; Hogg et al., 2015).

The use of sea surface temperature (SST) and sea surface height (SSH) contours to track front locations has suggested there has been a latitudinal change in the mean location of the ACC. This could have major impacts on marine ecosystems by modifying the environmental conditions experienced by numerous marine organisms (Bost et al., 2015; Cristofari et al., 2018; Meijers et al., 2019). However, this approach was challenged because these parameters are affected by the large-scale thermal expansion and steric sea-level rise occurring as a result of the warming of this circumpolar region. Recent studies found no significant long-term trend in either the annual mean latitude of zonal wind jets between 1979 and 2009 (Swart et al., 2015) or the zonally averaged latitude of ACC transport, which seem insensitive to changes in the SO's broad-scale structure (Gille, 2014; Chapman et al., 2020). The location of the ACC may be constrained by sea floor and land mass topography, particularly close to narrow gaps between land masses, such as Drake's Passage (*high confidence*; Moore et al., 1999).

The assessments of trends in the overturning circulation is challenging due to the high inter-decadal variability related to wind stress (*low confidence*; Waugh et al., 2013; DeVries et al., 2017; Ting and Holzer, 2017). While the production and export of Antarctic Bottom Water in the global ocean has decreased (medium confidence; Purkey and Johnson, 2013; Desbruyeres et al., 2017), this may reflect the same inter-decadal variability (low confidence; Abrahamsen et al., 2019).

Future projections for the SO under different warming scenarios from CMIP5 and CMIP6 models suggest that the trends observed over the last few decades will continue in the coming century at a rate that depends on future emission scenarios (Meredith et al., 2019). Projections include the strengthening of the westerly winds for all scenarios, except under stringent mitigation (Bracegirdle et al., 2020), and as a response, increased eddy activity (Downes and Hogg, 2013). Warming of the ACC and the freshening of surface water from increasing precipitation is projected to continue for all emission scenarios (Sallée et al., 2013; Bracegirdle et al., 2020). Due to their inability to explicitly resolve eddy processes (Gent, 2016; Downes et al., 2018) and increased water input from melting ice (Bronselaer et al., 2018), the projections from CMIP5 or CMIP6 models have low confidence. Evidence from other models suggests that glacial meltwater from ice sheet might continue in the future (*medium confidence*; Levermann et al., 2020; Seroussi et al., 2020), with important impacts on ocean circulation, including cooling of

surface subpolar ocean (Bronselaer et al., 2018; Rye et al., 2020) and warming of subsurface subpolar waters (Sadai et al., 2020).

Seawater Circulation and Exchange

The observed changes in ocean properties and circulation in Antarctica reveals the central role that regional variability plays in understanding the evolution of this system (Thompson and Solomon, 2002). At depth, warm waters around Antarctica supply heat and nutrients to the continental shelf. This supply to the coastal ocean varies greatly around the continent. Circumpolar Deep Water (CDW) has both warmed significantly since the late 70s and its core has shallowed by about 30 m per decade (Schmidtko et al., 2014). The expression of these changes in open ocean properties is not straightforward, however, as strong shelf currents, the Antarctic Slope Front (ASF) in particular, act as a barrier for cross-slope exchange. In the regions where the ASF is weak or absent, i.e., the Bellingshausen and Amundsen Seas, the warming of shelf waters more closely follows the changes in the open ocean (Schmidtko et al., 2014; Thompson et al., 2018).

The rapid warming of the WAP (Meredith and King, 2005) has impacted ocean properties as a result of increased freshwater input to the coast (Meredith and King, 2005; van Wessem et al., 2017) altering the structure of the upper layers of the ocean (Martinson et al., 2008; Welhouse et al., 2016). This region also shows strong impacts from ENSO and its interaction with SAM variability, which has been shown to modulate wind forcing, which in turns modulates the depth of the mixed layer and marine productivity on interannual scales (Venables and Meredith, 2014). Warming of the subsurface layers of the Peninsula is representative of similar trends along the Bellingshausen and Amundsen Seas, where the weak presence or absence of the Antarctic Slope Front, found along the shelf break elsewhere in Antarctica, facilitates the flooding of the shelf by the warming CDW (Thompson et al., 2018). Deep, steep canyons and other topographic features play a key role in the across-shelf exchange of properties along this and other Antarctic shelves (Moffat et al., 2009; Martinson and McKee, 2012). This exchange is strongly modulated by small ocean eddies that play a role on both the supply of heat and nutrients to the shelf (Moffat et al., 2009) as well as the export of shelf-modified waters to the open ocean (Brearley et al., 2019). Eddy-driven exchange is a key modulating factor of ocean properties around the continent, and this process is modulated by wind forcing (Thompson et al., 2014; Stewart and Thompson, 2015). The WAP shelf has experienced a build-up of subsurface heat (Martinson et al., 2008), and while full attribution of this change remains unresolved, both the changes in open ocean water properties and the increase of coastal stratification as a result of increased freshwater discharge from the coast likely play a role in this process.

The combination of strong regional and temporal variability in observed ocean properties, combined with what are still relatively limited datasets, result in significant challenges when trying to attribute the origin of the changes. Elsewhere in Antarctica, teasing out anthropogenic change from natural variability has proven challenging for many variables, suggesting that the observed change is consistent with the pattern expected from natural variability (Jones et al., 2016). This implies that process studies to understand the underlying mechanisms of variability as well as continued efforts to improve the observational records around Antarctica are critical to understand the nature of change around the continent and the impacts on marine ecosystems.

SOUTHERN OCEAN ATTRIBUTES

Marine Ice

Every year Antarctic seasonal sea ice undergoes a sixfold change in ice-covered area; it is one of the largest seasonal signals on Earth, with consequent effects on air-sea exchanges of heat, momentum and gases (most notably CO_2), water mass properties and finally, on marine ecosystems. Antarctic sea ice is, however, highly variable and frequently exposed to strong storms, high winds and waves. These factors affect Antarctic sea ice growth and melt processes, thickness evolution and drift, and impart high regional and seasonal variability.

Over the past four decades there has been a modest increase in spatially averaged Antarctic sea ice extent. However, this Antarctic-wide average hides important regional and seasonal details, as Antarctic sea ice is not increasing everywhere and shows high seasonal and regional variability (e.g., Parkinson, 2019). The two regions showing the strongest but opposing sea ice trends are the east Pacific, Bellingshausen-Amundsen Sea, sector (where sea ice decreased over 1979–2015) and the west Pacific, Ross Sea Sector (where sea ice increased over 1979–2015). Although the changes in sea ice were opposite, the rates were comparable to those observed in the Arctic (Cavalieri and Parkinson, 2012; Parkinson and Cavalieri, 2012; Stammerjohn et al., 2012).

These contrasting regional sea ice distributions can in part be explained by the SAM and ENSO changes detailed previously. The westerly winds have strengthened mostly in austral summer and autumn, i.e., when SAM shows the strongest positive trends (Marshall, 2003, 2007), thus impacting sea ice distributions mostly in summer and autumn (Stammerjohn et al., 2008; Hobbs et al., 2016). ENSO also effects regional and seasonal sea ice distributions, with the strongest signal being an Antarctic Dipole between the Amundsen/Ross and Bellingshausen/Weddell sea regions, consisting of positive/negative sea ice anomalies during a La Niña, and vice-versa for El Niño (e.g., Yuan, 2004). Together, strong phases in SAM and ENSO can either amplify or dampen the effect on sea ice distributions, along with other atmospheric perturbations, e.g., Pacific Decadal Oscillation, the Atlantic Multi-decadal Oscillation, greenhouse gas increases, not to mention ocean changes in heat and freshwater content and stratification, making attribution quite challenging.

This last decade, 2010–2020, has been most notable for showing the strongest changes in Antarctic-wide sea ice. During 2012–2014 numerous records were broken for Antarctic-wide high sea ice extent (based on satellite observations since 1979) (Turner et al., 2013; Reid and Massom, 2015; Reid et al., 2015). There appeared to be no one dominant factor behind the record maxima, but instead, for each of these 3 years (2012–2014), there were different regions and seasons contributing to the record high sea ice extent (Reid and Massom, 2015). Then, just as abruptly,

Antarctic-wide sea ice extent since spring 2016 has shown numerous record lows, for which several explanations have also been proposed, including anomalies in both the atmosphere and ocean, with a possible deep ocean driver acting on decadal or longer timescales (e.g., Stuecker et al., 2017; Turner et al., 2017; Schlosser et al., 2018; Meehl et al., 2019; Wang et al., 2019). Whether this recent decline in Antarctic sea ice extent will continue or not is still unknown, and once again points to the challenges in attributing and predicting Antarctic sea ice changes.

Previous work has highlighted the effects of changes in sea ice and how they can transform shallow water benthic ecosystems associated with changes in light regimes (Clark et al., 2013) and also by producing longer phytoplankton blooms and increased iceberg disturbance (Barnes et al., 2018a). Importantly for SO foodwebs, biodiversity and nutrient cycling and the abundance of Antarctic krill (*Euphausia superba*) all depend on the extent of winter sea ice, which is varying between sectors within the SO (Atkinson et al., 2019). Sea ice is one of the major drivers of energy flow into the SO and the effects of future sea ice extent on SO productivity are difficult to predict (*low confidence*).

Ice Shelf Disintegration

The floating ice shelves shape unique conditions in the SO for marine life living below them. Ice shelves are floating masses of ice slowly advancing from the glaciers of the interior toward the ocean, at least regionally and temporarily since the late Oligocene (Hochmuth and Gohl, 2019). They range from 100 to 1,400 m thick. The distance between the grounding line, where they lose contact with the land and the edge facing the open ocean, ranges from a very short distance to approximately 600 km. By far the largest two, which are each roughly the size of Spain are the Ross and Filchner-Rönne Ice shelves in the Pacific and Atlantic Ocean, respectively. With a total area of 1.63×10^6 km^2 ice shelves cover 36% of the continental shelf being equivalent to 11% of the size of the continent (Clarke and Johnston, 2003). Their existence and dynamics demand a replenishment of ice from the hinterland, permanently low air and water temperatures and depend on specific geomorphological structures. Ice shelves also seem to stabilize glacier draining velocity (Miles et al., 2018) and interact with sea-ice and ocean dynamics (Jourdain et al., 2017). The Larsen A ice shelf in the North of the Antarctic Peninsula most likely disintegrated more than once during the Holocene due to natural temperature changes (Domack et al., 2005). Further south the Larsen B on the east coast of the Peninsula (2002) as well as Wordie (2009) ice shelves on the west coast of the Peninsula, collapsed due to recent regional atmospheric and ocean warming, respectively (Massom et al., 2018). Ice shelves shape almost 50% of the coastline and icebergs as large as the size of Jamaica calve from the seaward edges. Despite this dynamism, the long-term mass balance currently seems to remain stable. However, large-scale long-term disintegration and melting is predicted under ongoing climate-change scenarios (*high confidence*; Naughten et al., 2018).

Besides impacts on ocean physics the disintegration of large ice shelves causes one of the most effective changes in marine ecosystems (*medium confidence*). The covering of ice acts as a barrier to energy exchange between the water and the atmosphere. Once this barrier is gone then there will be increased transfer of wind, heat and light energy, affecting the stability of the water column and the mixed layer depth. When light penetrates into the water it initiates the production of algal biomass (*medium confidence*, Bertolin and Schloss, 2009; Peck et al., 2010), which is the basis for almost all life in the oceans, in a previously totally dark and, thus, food-poor environment (Raes et al., 2010; Gutt et al., 2011). Icebergs calving naturally and more frequently under climate-change scenarios from ice shelves (*high confidence* for the next decades; e.g., Rack and Rott, 2004) drift in the ACC, scour the sea-floor (see e.g., Post et al., 2020) and eventually run aground before they disintegrate. These processes also have local to regional impact on pelagic and benthic systems (*medium confidence*; Gutt and Piepenburg, 2003).

Glacier Retreat

A third, smaller but important area of marine ice loss is glacier retreat. Like sea ice and ice shelves, glaciers are also showing decreases, and in fairly complex geographic patterns. Nearly 90% of glaciers along the WAP are now retreating, and their retreat rates are also increasing (Cook et al., 2016). CDW upwelling has driven frontline retreat of nearly all glaciers South of the Bransfield Strait (Cook et al., 2016; Etourneau et al., 2019). There is also evidence of thinning in southern glaciers around the East Pacific Sector (Hogg et al., 2017 and references therein). Until they reach grounding lines this glacier retreat generates icebergs and therefore coastal ice scouring and is opening up new fjordic habitats and carbon sinks (see Barnes et al., 2020). Although the high sedimentation in such environments can be harsh for new colonists (Sahade et al., 2015), they could be important for a number of reasons. Unlike elsewhere in the world, Antarctica has no other low wave energy-high productivity habitats, e.g., salt marshes, seagrass meadows and mangrove swamps, that provide hotspot potential for fast track from carbon capture to burial and sequestration. However, they also provide a, previously missing, key habitat which may provide opportunity for invasion of these newly exposed areas by non-indigenous species.

Meltwater and Freshening

Seawater salinity in the whole SO has decreased during the last 60–70 years (e.g., Jacobs et al., 2002; Jacobs and Giulivi, 2010; Hellmer et al., 2011; Durack et al., 2012). Surface waters (i.e., above 100 m depth) south of the ACC have shown stronger freshening rates, 0.0011 ± 0.0004 yr^{-1} (de Lavergne et al., 2014), than intermediate waters, 0.0002–0.0008 yr^{-1} (Skliris et al., 2014), or bottom waters, 0.0004 ± 0.0001 yr^{-1} (*medium confidence*; Menezes et al., 2017). Higher freshening rates have been recorded over Antarctic continental shelves, although there are large spatial differences with the Ross and Cosmonaut Sea displaying intense freshening, whereas the Bellingshausen and Amundsen Sea (East Pacific sector) are showing the opposite trend, i.e., increasing salinity, (Schmidtko et al., 2014). The latter may be the consequence of more frequent and shallower intrusions of CDW (Schmidtko et al., 2014), a saltier and warmer water mass (*high confidence*; Moffat et al., 2009). Despite the high melting rates of glaciers in west Antarctica (Paolo et al., 2015),

enough CDW intrusions seem to reach the shelf in order to prevent a steady freshening of these shelf waters. This may be the consequence of changes in large scale atmospheric and ocean circulation patterns (e.g., the increasing frequency and strength of SAM), since these drive the intrusions of CDW, rather than shelf hydrographic conditions (Nakayama et al., 2018). Similarly, a relationship between positive SAM and increased freshening has been registered for other areas (e.g., Atlantic sector: eastern Antarctic Peninsula and Weddell Gyre) although atmospheric warming seems to drive this relationship instead of hydrographic conditions (Dickens et al., 2019). Although similar freshening trends have been registered in different Antarctic regions, the drivers and mechanisms involved vary spatially (*high confidence*). For example, except for the WAP, positive SAM has increased northward Ekman drift of sea ice that is formed close to the continent (Holland and Kwok, 2012), increasing the transport of freshwater to the open ocean and promoting the freshening recorded for offshore waters in the SO (Haumann et al., 2016).

Freshening has other effects besides salinity. Stratification has a key controlling influence on phytoplankton blooms as do sources of iron from glacial meltwater and icebergs (De Baar et al., 1995; Loscher et al., 1997; Dierssen et al., 2002; Höfer et al., 2019; Hopwood et al., 2019). These inputs may, however, be more restricted to coastal waters than previously thought (Hopwood et al., 2019). In contrast, there is limited evidence that meltwater inputs can dilute the macronutrient concentrations of seawater (Henley et al., 2017; Höfer et al., 2019). Meltwater may also carry a high amount of inorganic suspended matter (e.g., glacial flour) that may kill, or impair the functions of, pelagic (Pakhomov et al., 2003; Fuentes et al., 2016; Giesecke et al., 2019) and benthic organisms (high agreement, limited evidence; Torre et al., 2014; Sahade et al., 2015). Finally, although there is medium confidence that the volume of Antarctic Bottom Water has decreased (Purkey and Johnson, 2013; Desbruyeres et al., 2017), there is almost no direct record of freshening hindering the formation of Antarctic Bottom Water (Silvano et al., 2018). Besides, recent studies suggest that the formation and northward export of Antarctic Bottom Water depends on several processes varying on multi-annual time scales (Abrahamsen et al., 2019), which need longer time series in order to detect any long term trend.

Biogeochemistry

CO_2 Uptake and Ocean Acidification

One of the most important functions of the SO in the Earth System is its uptake of atmospheric CO_2 by physical and biological processes and its release of oceanic CO_2 to the atmosphere (Sarmiento and Le Quere, 1996; Marinov et al., 2006; Gruber et al., 2009, 2019; Lenton et al., 2013; Henley et al., 2020 this volume). However, this uptake is leading to changes in ocean biogeochemistry, which could have devastating consequences for the ecosystem. Ocean acidification driven by oceanic uptake of atmospheric CO_2 is expected to occur earlier in the SO than most other ocean regions, due to enhanced solubility of CO_2 at low temperature and upwelling of deep waters with high CO_2 concentrations (Orr et al., 2005; McNeil and Matear, 2008; Feely et al., 2009). Ongoing changes in upper ocean temperature and salinity are very likely to impact the solubility of CO_2 in SO surface waters, and projected increases in the Revelle factor are expected to increase the biologically mediated uptake of CO_2 over the twenty-first century (Hauck and Völker, 2015; Hauck et al., 2015; Henley et al., 2020).

At the global scale, oceans have absorbed ∼30% of the anthropogenic atmospheric CO_2 and this has already caused shifts in seawater carbonate chemistry by reducing seawater pH, carbonate ion concentrations and therefore saturation states of the carbonate minerals aragonite and calcite (Ω, where values < 1 indicate undersaturated conditions that result in the dissolution of carbonate structures; Doney et al., 2009; Orr, 2011; McKinley et al., 2017; IPCC, 2019). Prior to the industrial period, atmospheric CO_2 was approximately 280 μatm with global average surface seawater pH of 8.17 and Ω_{arag} ∼3.5. Atmospheric pCO_2 has now reached 380–400 ppm, which has reduced surface seawater pH to 8.01–8.05, equivalent to a 100-fold increase in hydrogen ion concentration (Guinotte and Fabry, 2008; Doney et al., 2009; IPCC, 2019). Associated decreases in carbonate saturation have led to a shallowing of the saturation horizon by 30–200 m (Feely et al., 2002, 2004; Sabine et al., 2004). These trends are likely to continue and to accelerate in the coming decades, based on the current RCP 8.5 worst case "business as usual" emissions scenario. Further reductions of 0.3–0.4 pH units and Ω_{arag} ∼1.2 are projected (*high confidence*) at atmospheric pCO_2 of 851–1,370 by the year 2100 associated with further shallowing of both aragonite and carbonate saturation horizons (ASH and CSH) (Houghton et al., 2001; Caldeira and Wickett, 2003; IPCC, 2019).

The SO has taken up around 40% of the total oceanic uptake of anthropogenic CO_2 (Orr et al., 2001; Fletcher et al., 2006; Devries, 2014). The Ω_{arag} is in SO surface waters is largely below 1.5, with particularly low values in winter (Jones et al., 2017; IPCC, 2019). Trends of ocean acidification have already been observed in many of the MEASO areas, such as the east Pacific Antarctic and Subantarctic zones, Atlantic Antarctic zone, west Pacific Antarctic zone and across the East Indian sector (Hauck et al., 2010; van Heuven et al., 2011; Midorikawa et al., 2012; Takahashi et al., 2014; Munro et al., 2015; Williams et al., 2015; Lencina-Avila et al., 2018). The ASH resides at ∼730 m depth southwards of 60'S, cross-cutting the steep Antarctic continental shelf (McNeil and Matear, 2008; IPCC, 2019), whilst the CSH resides at approximately 3,000 m (Sewell and Hofmann, 2011). The ASH is expected to shoal to the surface during winter periods from ∼2,030 and across all seasons by 2100 (Orr et al., 2005; McNeil and Matear, 2008; McNeil et al., 2010; IPCC, 2019). This is likely to impact upon phytoplankton abundance, growth rates and species composition as well as zooplankton growth, reproductive success and survival, especially of ecologically important species of pteropods and krill (Tortell et al., 2008; Kawaguchi et al., 2013; Trimborn et al., 2013; Gardner et al., 2018; Henley et al., 2020). Mg-calcites are more soluble than aragonite and Southern Ocean surface waters are already undersaturated for ≥ 12 mol% $MgCO_3$ and are predicted to become undersaturated for 4–5% mol% $MgCO_3$ by 2100 (Andersson et al., 2008). Areas of upwelling CDW (from 2 to 3 km depth) can bring seawater with low Ω_{arag}

(∼0.9–1.08, ∼490–570 μatm pCO_2) toward the upper ocean in the ACC, leading to conditions that are corrosive for aragonite-secreting organisms such as pteropods (Bednaršek et al., 2012). Models suggest that upwelling could become stronger in the near future but the severity and timeframe with respect to carbonate undersaturation remain poorly constrained (Constable et al., 2014; Rintoul, 2018). Potential impacts of ocean acidification on microbial communities could lead to faster recycling of organic matter and overall declines in carbon export (Maas et al., 2013; Deppeler et al., 2018; Westwood et al., 2018), with implications for large-scale biogeochemical cycling and potentially climate, but more research is required.

The coastal regions around Antarctica are characterized by highly variable topography, bathymetry, hydrodynamics and carbonate chemistry, which leads to highly variable seawater pH, pCO_2 and Ω. Present day variations include Ross Sea surface pCO_2 values ranging from ∼100 to 450 μatm, equivalent to aragonite saturation of 3–4, between the autumn and summer, which then decline > 4-fold during autumn/winter to near-undersaturation of aragonite at 1.1–1.2, with an associated reduction of pH by 0.6 units (McNeil et al., 2010). Summer periods are characterized by high primary production, whilst entrainment of carbonate-depleted CDW occurs onto the Ross Sea Shelf during winter (Sweeney, 2004; McNeil et al., 2010). Similar seasonal patterns have been observed in surface waters at coastal sites of McMurdo Sound, McMurdo Jetty and Cape Evans with changes in seawater pH of 0.3 units (Kapsenberg et al., 2015) and in Prydz Bay with changes of 0.6 pH units (Gibson and Trull, 1999). Continued ocean acidification is projected to show large and uncertain regional and local variations, particularly in coastal regions (*high confidence*; IPCC, 2019). Nevertheless, model simulations have projected a pronounced increase in aragonite undersaturation around 2030, affecting around 30% of Southern Ocean surface waters by 2060 (Hauri et al., 2016). There is also medium certainty that the current rates of change are the fastest observed for at least 300 million years and high confidence that these changes will continue to rise at an accelerating rate (Canadell et al., 2007; Hönisch et al., 2012; IPCC, 2019), making ocean acidification likely to become one of the most important drivers of Southern Ocean ecosystem structure and functioning in the near future (Gutt et al., 2015).

Increasing Iron Inputs and Freshwater Flux From Glacial Ice Melting

The Southern Ocean is a large high nutrient low chlorophyll (HNLC) zone where primary production is not limited by the availability of macronutrients, as in other oceans, but of the essential micronutrient, iron (e.g., De Baar et al., 1990; Moore et al., 2013). As such, iron supply to Southern Ocean surface waters has a profound impact on primary production and ecosystem functioning, and is changing in response to changes in Earth's climate, large-scale ocean circulation and regional environmental conditions (Henley et al., 2020 and references therein). Increases in iron supply are expected due to increases in dust flux from lower latitudes (IPCC, 2019), oceanic iron transport to the sub-Antarctic in strengthening western boundary currents (Bowie et al., 2009) and enhanced release of terrigenous iron sources from glacial ice and the Antarctic continent (Lin et al., 2011; Gerringa et al., 2012; Sherrell et al., 2015; Winton et al., 2016; van Der Merwe et al., 2019). However, these may be offset to an extent by increased stratification of the upper ocean linked to a weakening overturning circulation, which could lead to a reduction in iron delivery from underlying waters (Tagliabue et al., 2009; Rintoul, 2018), and the ongoing declines in sea ice, which can store iron (Lannuzel et al., 2016). Changes in iron speciation, solubility, scavenging, internal cycling and remineralization—as well as phytoplankton dynamics, iron requirements and the impacts of ocean acidification—further complicate the net effect of climate and environmental changes on iron availability to phytoplankton blooms (e.g., Planquette et al., 2013; Blain and Tagliabue, 2016; Hutchins and Boyd, 2016; Andrew et al., 2019). Nevertheless, there is good agreement amongst CMIP5 models that Southern Ocean NPP will increase overall as a result of increased iron supply, changes in mixed layer depth, declining sea ice cover, increasing SST and altered westerly winds (Bopp et al., 2013; Leung et al., 2015; Fu et al., 2016; Moore et al., 2018). Increased iron supply and temperature could also lead to a floristic shift to diatoms and potentially *Phaeocystis antarctica*, with consequences for benthic and pelagic consumers as well as nutrient uptake, carbon export and large-scale biogeochemical cycling (Henley et al., 2020).

Impact of Climate-Induced Physical Changes on Nutrient and Carbon Supply and Distribution

The ongoing and projected increase in wind speeds and storminess over large parts of the Southern Ocean is likely to increase upwelling and upper ocean mixing, thus micro- and macronutrient flux from the CDW source waters into the mixed layer (Moore et al., 2018; Rintoul, 2018). As regional warming continues, anticipated sea ice losses would also increase vertical mixing and nutrient supply by removing the barrier to wind-driven mixing of the surface ocean, as has been observed at the Antarctic Peninsula (Venables et al., 2013; Henley et al., 2017). The increased vertical flux of iron would be more important than that of macronutrients for biological productivity in the iron-limited open Southern Ocean (e.g., Leung et al., 2015). Increasing wind speeds, storminess and ice losses may also increase the outgassing of oceanic CO_2, as has occurred in the past (Le Quere et al., 2007; Lenton et al., 2013). Shoaling of carbon- and nutrient-rich CDW in most regions around Antarctica (Schmidtko et al., 2014) is also likely to increase the flux of nutrients and carbon toward the ocean surface. In contrast, projected increases in glacial meltwater inputs may increase stratification around Antarctica with the potential to reduce vertical nutrient fluxes and availability to phytoplankton blooms (see section on freshening). This could limit primary production in locations and at times of year when surface macronutrients are drawn down to limiting concentrations (Henley et al., 2017, 2018; Höfer et al., 2019). Ice shelf disintegration could have complex effects on upper ocean mixing and vertical carbon and nutrient fluxes depending on the relative forcing of increased exposure to winds and altered strength and position of the buoyant meltwater plume (e.g., Randall-Goodwin et al., 2015). Projected increases in

eddy activity within the ACC and the anticipated changes in ocean currents and frontal positions will influence the transport and distribution of nutrients and carbon around the Southern Ocean, as well as air-sea exchange of CO_2 (Sallée et al., 2012; Rintoul, 2018; Chapman et al., 2020).

Biogeochemical Consequences of Climate-Driven Changes to Pelagic and Benthic Food Webs

The large-scale climatic and environmental drivers of changes in the abundance and distribution of marine organisms will also have important consequences for Southern Ocean biogeochemistry through export fluxes, carbon storage in pelagic and benthic food webs, and for benthic-pelagic coupling (Henley et al., 2020). For instance, the southward contraction of krill populations in the Atlantic sector and linked increases in salp abundance may reduce carbon transfer through the pelagic food web, with implications for carbon storage and export (Atkinson et al., 2004, 2019; Murphy et al., 2016). Phytoplankton, zooplankton and higher organisms also play an important role in benthic-pelagic coupling and the transport of nutrients and carbon vertically and horizontally (e.g., Lavery et al., 2010; Belcher et al., 2017; Cavan et al., 2019), which could be interrupted by shifts in abundance, distribution or trophic interactions. In contrast, increases in primary production and benthic biomass in response to reduced sea ice duration and longer growing seasons on the Antarctic Peninsula (Peck et al., 2010; Moreau et al., 2015) have the potential to increase carbon storage and invigorate benthic nutrient and carbon cycling as well as benthic-pelagic coupling (Barnes et al., 2018a). Benthic-pelagic coupling and water column transport are key to the (re)distribution of nutrients in the Southern Ocean, such that climate-forced changes in these mechanisms could hold severe consequences for the entire ecosystem. Because the microbial loop plays a decisive role in the fate of organic carbon in pelagic and benthic food webs (Azam et al., 1991; Sailley et al., 2013), climate-driven shifts in microbial communities and processes are very likely to have a strong impact on ecosystem carbon storage, benthic-pelagic coupling and regional biogeochemistry (Henley et al., 2019 and references therein).

ANTHROPOGENIC DRIVERS

Tourism

Antarctic Tourism started over 100 years ago (Headland, 1994) but the modern trend for ecotourism started in 1950's and the first dedicated expedition cruise ship for the Southern Ocean was the Lindblad Explorer launched in 1969[1]. There was a steep increase in shipborne tourism in Antarctic from around 100 visitors in the late 1950's to a peak in the 2007–2008 season of 46,000. Visitor demographics are heavily affected by global socio-economic factors and the sharp decline following 2008 is attributed to the world economic crisis and the International Maritime Organization (IMO) ban on the use and carriage of heavy fuel oil in Antarctica. Traditionally Antarctic tourism is seen as an emerging market due to increasing global wealth. The industry began growing again steadily after 2011, reaching a new peak of 55,000 visitors in 2018–2019, mostly within the East Pacific and subAntarctic zone of the Atlantic MEASO areas, with most passenger landings and traffic concentrated at a few locations (Bender et al., 2016). Expedition cruising is the fastest growing market within the entire cruise industry, with new expedition cruise ships being built at the fastest rate in history, suggesting that, unless disease outbreaks pause the industry in the long term, this trend in visitor numbers is expected to continue (*high confidence)*.

The nature of Antarctic ecotourism is also changing with the increased number of itineraries expanding the market to attract more active tourists, with options to kayak, camp on the ice, dive and snorkel with wildlife as well as skiing, including heli-skiing[2]. Additionally, fly cruising options are increasing with passengers flying into King George Island and starting their trip from there (Bastmeijer, 2009), spending more of their trip within the Southern Ocean. New vessels with the latest X-bow design are expected to increase the ability to push into ice and therefore expected to open up the West Pacific MEASO area (Ross Sea) to more tourism (*medium confidence*).

Today the large majority of all tour operators operating in Antarctica are members of the International Association of Antarctic Tour Operators (IAATO), a self-governing body, including all commercial SOLAS passenger ship operators (see footnote). The association's membership comprises 105 companies and organizations from all over the world. The future protection of Antarctica from the impacts of human activity requires collaboration on a global scale. To promote effective visitor management, IAATO annually shares detailed information on its activities with Antarctic Treaty Parties. Without further regulation the geographic spread of visits is virtually certain to increase.

All of these developments are highly likely to increase the footprint of Antarctic tourism, potentially increasing the impact on marine ecosystems, particularly through the risk of the introduction of non-indigenous species. There are also concerns about the risk of tourists transferring anthropengic diseases to Antarctic seabirds. However, the greatest health concern for the cruise ship industry are over human disease transmission within the close quarters of cruise ships (Hill, 2019). These concerns have been amplified by the COVID-19 pandemic and the trajectory of SO tourism is now much less certain.

Pollutants

Many anthropogenic pollutants are resistant to environmental degradation and can be transported from human population sources to remote regions of the world, such as the Southern Ocean. Heavy metals have been detected in ice core samples, with, for example, lead from Australian mining operations appearing at concentrations of up to 6 $pg.g^{-1}$ after the start of the industrial revolution (McConell et al., 2014). Radioactive isotopes of elements such as chlorine (^{36}Cl) are, also, still being released

[1] www.iaato.org

[2] https://www.adventuresmithexplorations.com/cruises/antarctica/new-expedition-ships/

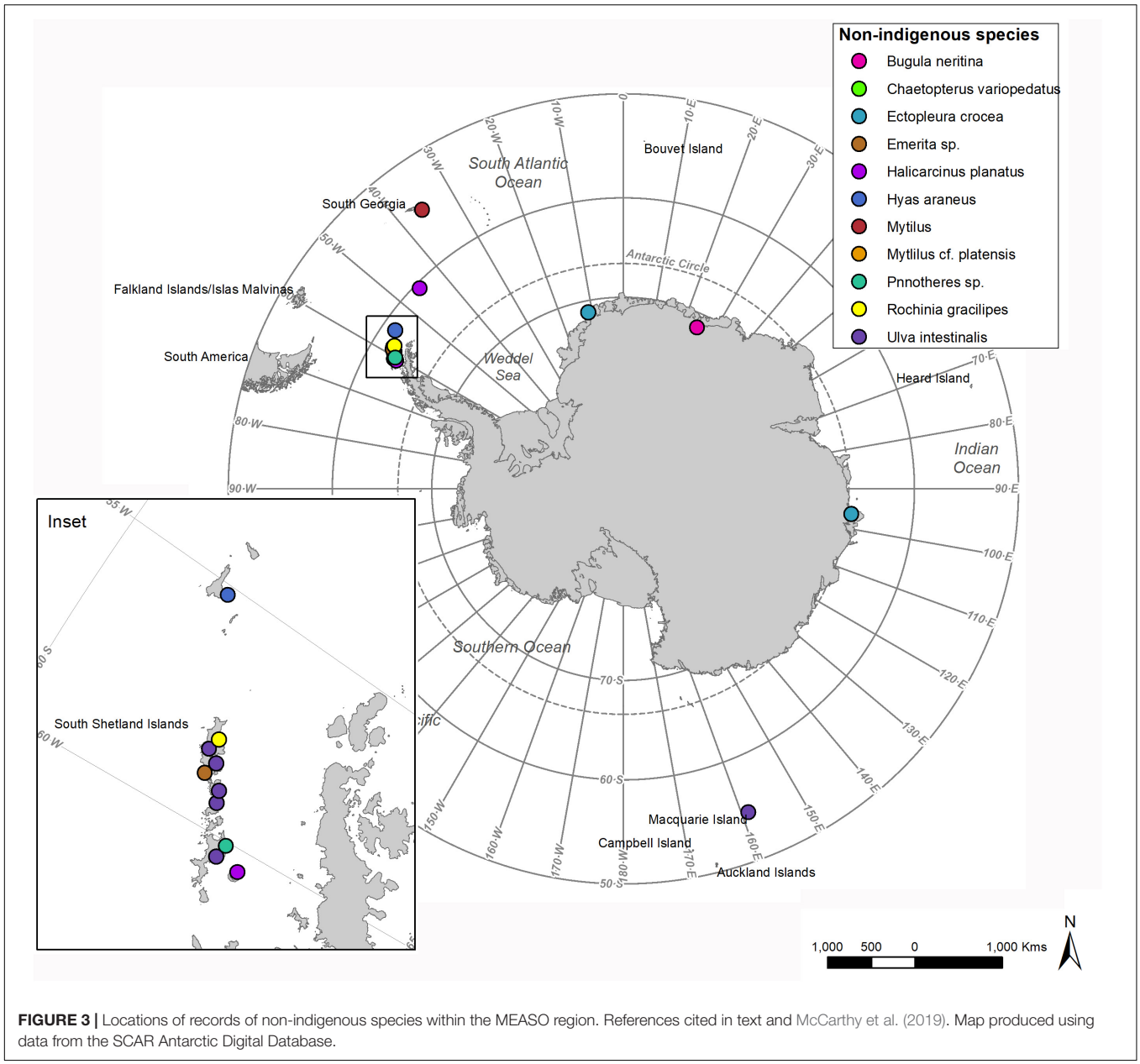

FIGURE 3 | Locations of records of non-indigenous species within the MEASO region. References cited in text and McCarthy et al. (2019). Map produced using data from the SCAR Antarctic Digital Database.

from the cryosphere after nuclear bomb tests in the 50's and 60's (Pivot et al., 2019). The persistent organic pollutants (POPs; Krasnobaev et al., 2020) and marine debris, amongst which the plastics have become a focus for policy makers and the public alike (Rochman et al., 2016), will be discussed in detail here. Increase in atmospheric CO_2 is covered within the previous biogeochemistry section and the impact of CFCs are covered in discussions about SAM/ENSO.

POPs consist of a number of different chemicals, including polychlorinated biphenyls (PCBs), organochloride pesticides (O) and polybrominated diphenyl ethers (PBDEs). A recent study of these compounds in the East Pacific region found comparable PCB and OCP concentrations to those detected 10 years earlier, but detected PBDEs for the first time (Krasnobaev et al., 2020). In contrast to some previous studies, there was no indication of local sources for this pollution, e.g., from research stations (Wild et al., 2015), rather that the pollution was highly likely to have come from atmospheric sources (Krasnobaev et al., 2020). This atmospheric origin is supported by the highest concentration of POPs being recorded in the surface phytoplankton, early in the summer, soon after the sea ice, and any snow cover has melted (Casal et al., 2018, 2019; Krasnobaev et al., 2020). With changes in the cryosphere, particularly the reduction in sea ice duration, and the associated changes in phytoplankton bloom dynamics, the seasonal pattern of POPs is projected to become less pronounced (*high confidence*). Global legislation, such as the Montreal protocol can only control chemicals that are widely used and once their effects are clearly demonstrated.

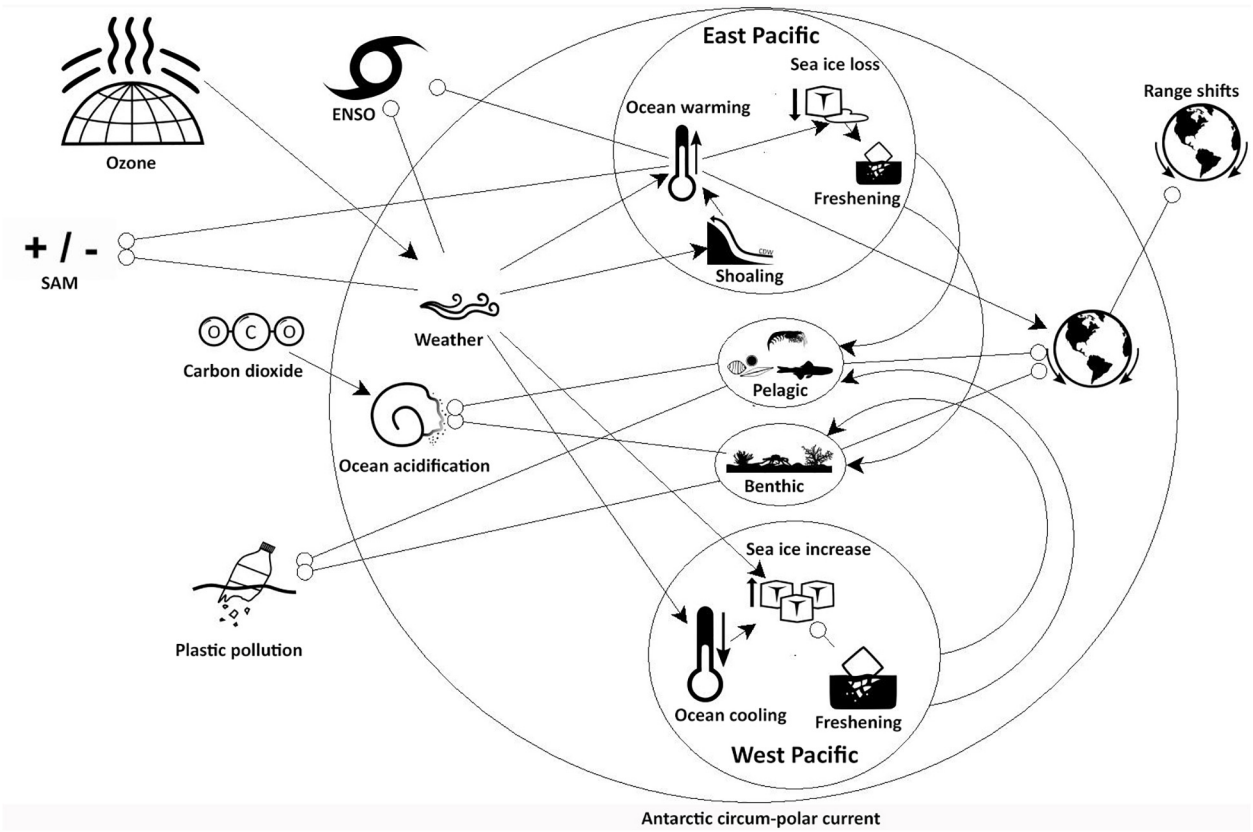

FIGURE 4 | Qualitative network diagram describing the linkages between the global drivers and the benthic and pelagic Southern Ocean assemblages. Northern drivers are global drivers whose influence comes from North of the Antarctic cirucm-polar current (ACC). Contrasting effects are highlighted by separate west Pacific (western Antarctic Peninsula) and east Pacific regional networks. Range shifts from north of the ACC (Non-indigenous species) and within the Southern Ocean are indicated separately. An arrow head indicates a positive influence, an open circle indicates a negative influence.

TABLE 1 | Assessment of the current direction of each of the identified global drivers within the MEASO sectors, in recent times (R) and in the future (F).

Region	Zone	Ozone		SAM		ENSO		Temperature		Tourism		Pollution		Sea Ice		Ice Shelves		Salinity		pH		NIS	
		R	F	R	F	R	F	R	F	R	F	R	F	R	F	R	F	R	F	R	F	R	F
Atlantic Ocean	A	+	+	+		+	+		+	+	?	+	+	–	?	–	–	–	–	?	–	No	+
	S	+	+	+		+	+	+	+	+	+	+	+	–	?	N/A	N/A	–	?		–	+	+
	N	+	+	+		+	+	+	+	+	+	+	+	N/A	N/A	N/A	N/A	–	+		–	+	+
Central Indian	A	+	+	+		+	+		+	N/A	?	+	+	–	?	No	No	–	–	?	–	No	+
	S	+	+	+		+	+		+		+	+	+	N/A	N/A	N/A	N/A	–	?		–	+	+
	N	+	+	+		+	+		+		+	+	+	N/A	N/A	N/A	N/A	–	+		–	+	+
East Indian	A	+	+	+		+	+	–	+			+	+	+	?	No	No	?	–	?	–	No	+
	S	+	+	+		+	+	–	+			+	+	+	?	N/A	N/A	–	?		––	No	+
	N	+	+	+		+	+	–	+			+	+	N/A	N/A	N/A	N/A	–	+		–	?	+
West Pacific	A	+	+	+		+	+	–	+			+	+	+	?	No	No	–	–	?	–	No	+
	S	+	+	+		+	+	–	+			+	+	+	?	N/A	N/A	–	?		–	No	+
	N	+	+	+		+	+	–	+			+	+	N/A	?	N/A	N/A	–	+		–	?	+
East Pacific	A	+	+	+		+	+	+	+	+	?	+	+	–	?	–	–	–	?	?	–	No	+
	S	+	+	+		+	+	+	+	+	?	+	+	–	?	N/A	N/A	–	+		–	No	+
	N	+	+	+		+	+	+	+	+	?	+	+	N/A	?	N/A	N/A	+	+		–	No	+

*The assessment is drawn from the reviews in the previous text and the citations therein. + indicates an increase,– indicates a decrease, No indicated no change, ? indicates a known uncertainty. N/A means the category is not applicable in that zone. The MEASO regions and sectors are defined in **Figure 2**. Full explanations behind the assessment and references are cited in the text. Currents and eddies are not included due to large uncertainties over their future projections.*

BOX 1 | Research Gaps and Priorities.

Modeling the trajectories of climate change is one of the biggest challenges to understanding the future impacts of drivers on the Southern Ocean and a key limitation to future projections. Whereas arctic environmental responses to climate over the last decade have been continuous and homogeneous, Antarctic and SO changes are regional and variable (Stammerjohn et al., 2012; Parkinson, 2019), resulting in ambiguous effects when looking at the global scale.

There is also a degree of uncertainty over when tipping points will be reached (e.g., Timmermann and Hellmer, 2013; Hellmer et al., 2017). Current model predictions for sea ice extent and duration have been poor despite the mechanisms driving sea ice formation/melting having such a profound impact on the SO (Reid and Massom, 2015). This is typified by the retreat of tidewater glaciers and floating ice shelves and the number of icebergs that will be present to scour the sea floor. At a certain point the trend will move from increasing to reducing numbers of icebergs being present, starting to reverse the trends in ice scour (Barnes et al., 2020). Whether this will happen before irrecoverable change has occurred within benthic communities is hard to predict.

The very limited availability of long-term time series hinders our ability to discern between interannual/interdecadal changes and long-term trends in ecosystem shift. It is difficult to inform policy and decision makers without a clear distinction between natural variability and global change impacts. Funding agencies must allocate money to maintain long-term sampling programs. Continued and improved data collection through international effort to obtain standardized datasets, developments in modeling and integrated work programs, such as the Southern Ocean Observing System (Newman et al., 2019) are allowing improved coverage and better predictions of future drivers across the Southern Ocean. Only through funding of extended time series can trajectories of change be monitored and tipping points be better constrained.

As with all remote regions, data coverage is better near locations with the greatest human footfall. This footfall is also higher in summer than winter. Remote sensing from satellites and remote monitoring stations are key tools to increase the spatio-temporal coverage and improve the reliability of projections that can significantly reduce the cost of long term sampling programs. The increase in continuous observing systems will be key to improving data coverage. Innovation, technological advancements on autonomous vehicles and other platforms (e.g., oceanographic moorings), including the ability to measure under the seasonal ice cover and floating ice sheets should contribute towards improving our understanding of processes occurring during the winter, and how they change in longer time-scales.

Understanding if human behavior will change, and how international treaties will limit the pace of climate change, will be key. Industrial process are developing novel chemicals, some of these are designed to replace substances that are currently controlled, such as CFCs. However, some of these replacements, such as SF_6, are known to be potent climate gases (Widger and Haddad, 2018) which could markedly change rates of atmospheric warming. The fate of new industrial chemicals needs to be tracked and understood so that their impacts can be determined and impacts controlled before they have major impacts.

History shows that novel industrial chemicals will continue to be developed with a considerable time lag before they are recognized as POPs.

Plastics are a global problem with levels in remote regions of the Atlantic. There has been a 10 fold increase in the quantity of plastic debris on beaches in the remote Falkland, Tristan da Cunha, St Helena and Ascension Islands in the last decade (Barnes et al., 2018b). The number of items increasing from approximately 1 to 10 per meter of beach (Barnes et al., 2018b). Large items of plastic drifting onto the Antarctic Peninsula were first reported nearly 20 years ago (Barnes and Fraser, 2003). These were first recognized as vectors for the introduction of non-indigenous species but in more recent times, the break down products of waste plastic, the micro- and nanoplastics have become a major concern as they can affect suspension and deposit feeders which are dominant members of the Antarctic benthos (Waller et al., 2017; Horton and Barnes, 2020), even affecting the immune system, as recently described in the sea urchin, *Sterechinus neumayeri* (Bergami et al., 2019). A recent study has also demonstrated effects of nanoplastics on keystone species such as the Antarctic krill (Bergami et al., 2020). The local sources of microplastics are discussed in the local drivers manuscript but there is also recent evidence of global transport of microplastics to the SO in the ocean currents and precipitation (Åslund, 2018).

BIOLOGICAL DRIVERS

Non-indigenous Species

The shallow seas of the SO and its outer lying archipelagos have high levels of endemism in the region; up to 70% in some taxa (David and Saucède, 2015). Here we term species not native to the region as non-indigenous species – NIS. Its relative historic isolation, means that it still has an almost entirely native biota (Convey et al., 2014; de Broyer et al., 2014), and is the only large surface environment on the planet where this is still the case (Bax et al., 2003; Early et al., 2016). There are thought to be many factors causing this, including its large size, historic geographic and environmental isolation by the ACC, and long periods of relatively constant environment (Ruiz and Hewitt, 2009). These attributes mean that NIS that are able to establish are likely to outcompete or prey upon native biota and entire native communities could be disrupted.

However, there are "barriers" to species movement. The Polar Front is both semi-porous and migratory over time (Clarke et al., 2005). Species can cross the Polar Front in short ecological time frames in eddies and rafting as well as over longer time frames with glaciation-interglacial shifts of ocean fronts and crawling along the seafloor (Sands et al., 2015; Fraser et al., 2018). Recent human activity, including increasing tourist visitation and more widespread national Antarctic operator logistical and research activity (Tin et al., 2014; Bender et al., 2016; Pertierra et al., 2017), have increased the types of vectors and opportunities, including ship hulls and plastic in the sea (Barnes, 2002; Lewis et al., 2003, 2004). Furthermore changes in the cryosphere and sea temperatures described above have also changed the potential survivorship of NIS propagules in transit to the region, their establishment and spread (Clarke et al., 2007; Turner et al., 2009; McCarthy et al., 2019). Risk of NIS transport and establishment in marine environments is not evenly spread around the southern polar region (Barnes et al., 2009) and threat levels are strongly coincident with human transport routes and

destinations (Hughes et al., 2019; McCarthy et al., 2019). One of the main threats is seen as the bivalve mollusc genus *Mytilus* which are already well documented NIS elsewhere in the world (Hughes et al., 2019).

Preventative/biosecurity measures have been considerably ramped up and enforced within the last decade, including with the production of a Non-native Species Manual by the Committee for Environmental Protection (CEP, 2017) and biosecurity checklists by the Council of Manager of National Antarctic Programs (COMNAP/SCAR, 2010). Some steps have been taken to address NIS within ballast water, with the Antarctic Treaty Consultative Meeting and International Maritime Organisation (IMO) having agreed ballast water exchange protocols for ships entering the Southern Ocean (ATCM, 2006; International Maritime Organisation Marine Environment Protection Committee [IMO], 2007) and more stringent internationally applicable ballast water regulations, having entered into force in 2017, which require ships to treat or exchange ballast water (International Maritime Organisation [IMO], 2004). However, there is still little progress to reduce marine NIS risk associated with hull fouling, possibly due to the perceived expense and impact on itineraries of hull cleaning activities. There may also be the perception that traveling though sea ice will scour the hulls free of NIS, thereby removing the risk, but research has shown fouling species persisting in sea chests and water intakes ports on the ship hull (Lee and Chown, 2007; Hughes and Ashton, 2017) and many vessels operating in polar water actively avoid sea ice, removing any potential biosecurity benefit (McCarthy et al., 2019). Marine invasions are harder to detect and much harder (if not impossible) to reverse (Ojaveer et al., 2014) and effective biosecurity practices depend more on national operator measures rather than the action of individuals (e.g., the cost and coordinated effort required to clean a ship's hull).

The majority of NIS records have been in the Atlantic and East Pacific regions where the majority of boat transits into the Southern Ocean occur (**Figure 3**). For example, a NIS marine algae (*Ulva intestinalis*) arrived and established at Deception Island (Clayton et al., 1997). It has also been reported from other frequently visited locations, Half Moon, Livingston, Robert, Nelson, King George, Penguin and Elephant Islands and sub-Antarctic Macquarie Island (**Figure 3**). There have been concerted efforts to bring experts together for NIS risk assessment, to identify most likely invader species and vectors and to provide stronger prevention and management advice (Key, 2018; Roy et al., 2019), which could be usefully undertaken within other regions of Antarctica.

New approaches to threats to native species (Morley et al., 2019) and most likely invaders (Hughes et al., 2019) have been through risk analysis. More than a hundred likely potential invaders were considered, mainly likely to come from southern South America and establish in the northern Antarctic Peninsula and Scotia Arc locations. Mytelid mussels were highest on the NIS risk, because they are abundant in ports, widely successful invaders elsewhere, have survived journeys to the SO (Lee and Chown, 2007) and tend to smother coastal life on establishment (Hughes et al., 2019). The strength of these approaches has been illustrated by the recently discovered population of *Mytlilus cf. platensis* which settled in a shallow subtidal habitat of the South Shetland Islands (Cárdenas et al., 2020).

Poleward movement of species to bottlenecks such as Patagonia, South Africa and Australasia is likely to intensify over the coming decades, increasing propagule pressure of potential NIS (Ruiz and Hewitt, 2009). The number of vessels, people and water-born debris set to reach the region also seems likely to continue to increase, as does climate-mediated environmental change (Barnes, 2002; Barnes et al., 2018b; McCarthy et al., 2019). Consideration of the problem and preventative action have both been stepped up for some pathways, but the challenge is considerable and the impacts and costs of NIS can clearly be seen in every other major non-polar environment.

Migratory Species and External Impacts

Migratory species in Southern Ocean ecosystems include pinnipeds, cetaceans and seabirds. Many of these species travel long distances to Antarctic and sub-Antarctic waters during the austral summer to forage on low-trophic level prey. Migratory species are uniquely vulnerable to changing environmental conditions due to their long-distance travel and reliance on a number of unique integrated factors (Leaper et al., 2006; Tulloch et al., 2017). These include whole suites of discrete sites remaining intact, the resources they require at those sites being available at the right time, and the connections between sites remaining within reach given a species' movement capability (Newson et al., 2009).

Migratory species moving through Southern Ocean ecosystems face numbers of direct and indirect pressures from changing physical environments and human activities across their range. Within Antarctic waters, changing climate drivers will alter productivity regimes, which will very likely affect low trophic prey such as krill (Flores et al., 2012), with possible flow-on effects to dependent migratory fur seal (*medium confidence*; Croll and Tershy, 1998), baleen whale (*high confidence*; Tulloch et al., 2019) and seabird (*medium confidence*; Barbraud et al., 2012) predators that travel to Antarctic waters to forage. Many of these species are particularly vulnerable due to low abundances and slow population growth. Historical commercial exploitation of migratory fur seals and whales across the Southern Oceans pushed many species almost to extinction. Although some heavily depleted populations of seals and whales have begun to recover (Hucke-Gaete et al., 2004; Tulloch et al., 2017), populations of whale species including blue, fin and Southern rights are still well below their pre-exploitation numbers despite international protection. Some populations of Southern Ocean seabirds are very low numbers due to historical fisheries interactions, and are likely vulnerable to changes in adult mortality given their life history characteristics (high confidence; Phillips et al., 2016).

The long distance movements of Southern Ocean migratory species make them susceptible to other external anthropogenic impacts, such pollution, ship strikes fishing gear interactions diminishing food supplies, and reduced breeding habitats, all of which can reduce population numbers or negatively affect the fitness of an animal (Rosenbaum et al., 2014; Clapham, 2016).

While pollutant exposure is generally low within the SO, pollutants pose a serious risk to SO migratory species. Migratory seabirds such as south polar skuas (*Catharacta maccormicki*) and brown skua (*Catharacta skua lönnbergi*) have up to 20 times higher levels of the persistent organic pollutant (polybrominated diphenyl ethers) than endemic species that live year round within the SO, likely due to exposure to contamination events at lower latitudes during the non-breeding season when they migrate northward (*high confidence*; Yogui and Sericano, 2009; Corsolini et al., 2011).

Due to this exposure when outside of the SO, migratory species likely act as vectors for transporting pollutants into the SO (*medium confidence*; Yogui and Sericano, 2009; Corsolini et al., 2011). Marine debris can also enter the Antarctic ecosystem carried by nektonic animals such as seabirds and seals (Barnes et al., 2004). Fur seals can become entangled on the South American continental shelf or along populated shores (Laist, 1997; do Sul et al., 2011). During the austral winter migratory marine biota reach lower latitudes, when seabirds ingest floating plastics in the open ocean; on nesting areas, plastics may then be regurgitated to chicks (*medium confidence*; Fry et al., 1987; van Franeker and Bell, 1988; Wilcox et al., 2015). Greater quantities of plastics traveling in the SO likely increase the possibility of transport of colonists to Antarctica (*medium confidence;* Barnes, 2002). Terrestrial threats such as disease and predation may affect migratory seabirds nesting on land (Phillips et al., 2016). Introduced mammals are the foremost land-based threat to seabirds on sub-Antarctic islands (*high confidence*; Jouventin and Weimerskirch, 1991; Baker et al., 2002).

Since the early 90s, efforts conducted by the Committee for the Conservation of Antarctic Living Marine Resources (CCAMLR), via a series of conservation measures, have been very successful in addressing the problem of incidental mortality, especially seabirds, in the Convention area. However, during migrations outside of the SO bycatch and entanglement in fisheries gear are recognized as the most significant threat to the survival of cetacean and seabird species and populations globally (Read, 2008; IWC, 2010; Barbraud et al., 2012). Continued industrialization of fisheries have led to intensification of fishing effort in many regions (Pauly, 2009), including increased presence of fishing gear in whale habitat (Lewison et al., 2004; Read et al., 2006), increasing the risk of interactions with such gear (Cassoff et al., 2011). Binding legal requirements to reduce bycatch exist in the national legislation of many countries. However, despite new technologies and industry recognition of the issue, monitoring and management can be costly, and/or ineffective, and bycatch remains a major global problem (Tulloch et al., 2020). Unregulated or increased longline and trawl fishing in key breeding areas for vulnerable species of albatross (e.g., *Thalassarche melanophrys, Diomedea* spp.) is likely to lead to continued population declines (*high confidence*; Tuck et al., 2003; Phillips et al., 2016). Some baleen whale populations (e.g., southern right whales in the southeastern Pacific off Chile and Peru) are small and endangered, and, for them, even small numbers of fisheries gear entanglements are potentially significant (low confidence; Reeves et al., 2013).

Other external drivers affecting SO migratory species include vessel traffic and mining activities. Ship strike/collision can result in injury, displacement, disturbance, and behavioral modification (*high confidence*; van der Hoop et al., 2015; Pirotta et al., 2019). The number of reported vessel strike incidents has increased over the last 2 decades (Peel et al., 2018), but reporting biases exist related to species identification, spatial coverage of reports and type of vessels involved, and quantifying the rate of occurrence of these collisions is difficult because many incidents are not detected. Southern right whale (*Eubalaena australis*) populations off South Africa and off eastern South America (Brazil, Uruguay and Argentina) have historically suffered high mortality due to vessel strikes (56 reported cases before 2007, *high confidence*; van Waerebeek et al., 2007). Studies show likely behavioral modifications of migratory whales including southern right and humpback whales (*Megaptera novaeangliae*) with reduced foraging and shifting of traditional use areas in response to noise from human activities such as shipping and seismic surveys (*high confidence*; Parks et al., 2007; Dunlop et al., 2010; Blair et al., 2016).

Some migratory animal populations may also be susceptible to diminishing food supplies in regions where fisheries are poorly managed, or where climate change impacts may affect lower trophic prey populations. Overfishing can have profound implications for higher-order predators. Population-level impacts on seabirds such as albatrosses and petrels may occur through direct competition with fisheries for prey (*medium confidence*; Croxall and Gales, 1998; Baker et al., 2002). The level (and the effects) of competition for food resources between seabird populations and fisheries, however, is uncertain. Lower trophic prey such as krill are expected to be affected by future warming oceans given climate change (*high confidence*; Flores et al., 2012). It is uncertain how climate change may facilitate or hinder the recovery of species that forage heavily on krill or rely on stable sea-ice conditions in rapidly warming regions of the SO (Simmonds and Isaac, 2007). Blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*) and humpback whales that forage in mid-latitudes may be the most at risk from climate-induced impacts on their prey (*medium confidence*; Tulloch et al., 2019).

ASSESSMENT

Main Drivers and Their Interactions

The global physical and human drivers, along with their interactions, were summarized from the proceeding text into a qualitative network diagram (**Figure 4**). The Northern drivers, those whose influence on the SO comes from North of the region, dominate the changes happening within the SO. The major effect of the ozone hole on atmospheric circulation and wind strength which, in turn, have had contrasting regional effects on the cryosphere of the West Pacific (Ross Sea) and East Pacific (western Antarctic Peninsula) sectors of the SO, were a consistent theme throughout the assessment. The importance of the additive interactive effects of SAM and ENSO were

also repeated. The other key human driver is the increase in CO_2, which is not only linked to warming, and its impact on the cryosphere, but will also lead to ocean acidification and affect the carbon cycle (*high confidence*). This is expected to have an impact on both benthic and pelagic ecosystems (*high confidence*). Unless human emissions are controlled, the comparatively limited current impact of pollution and non-indigenous species is expected to increase into the future (*high confidence).*

Future Prognosis and Priorities

The future projections of the global drivers highlighted in the proceeding literature review are summarized through the assessment in **Table 1**. One of the main themes running through this assessment are the large uncertainties in the models that are used to make these projections. Only a concerted international effort will enable these uncertainties to be reduced (**Box 1**). International frameworks, working groups and grants, such as the Antarctic Treaty System and CCAMLR, the Southern Ocean Observing System (SOOS) and MEASO, and the EU Rise network project CoastCarb, are essential to ensure consistent approaches are applied across the region.

Many of the changes in global drivers that have affected SO marine ecosystems over recent decades were strongly linked to the loss of atmospheric ozone since the 1970s (*very high confidence*; **Table 1** and **Figure 4**). One of the key future uncertainties about how global drivers of SO marine ecosystems will change, therefore, relates to the impact of the expected reversal of the ozone hole. Will this start to reverse some of the recent physical changes, or will global and regional increases in temperature override this? The best estimates suggest that within decades the global increase in temperature is highly likely to override any cessation of warming in the Eastern Pacific sector, particularly the Antarctic Peninsula (*high confidence*; Turner et al., 2016; Rogers et al., 2020). Depending on the trend in SAM, the reversal of the stronger winds may reduce the cooling influence in the East Indian and West Pacific zones, ultimately leading to warming across the whole of the SO (*medium confidence*).

While the reversal of the winds may slow the shoaling of warm water onto SO shelves (*medium confidence*), the increase in global air temperatures is very likely to continue the disintegration (giant iceberg formation) and melting of ice shelves. The number or glaciers in retreat and their retreat rate will further increase and many will soon reach ground lines (*very high confidence*). To make predictions for sea ice change is much less clear. The mechanisms underlying the recent drop from near recent maximum to minimum sea ice extent since spring 2014 including the time-scale over which these drivers are operating, is uncertain (*low confidence*). As one of the key drivers for SO marine ecosystems, and crucial for key SO species such as krill and some top predators, this leaves a large area of uncertainty around the future of sea ice.

Some pollutants such as CFC's, are subject to global agreements, their levels are controlled and their impacts are reversing (*medium confidence*). As the impact of other industrial climate gases are identified (e.g., sulfur hexafluoride, SF_6; Widger and Haddad, 2018) research on which pollutants need to be controlled will need to keep pace with technological developments. However, even under the best case future emission scenarios atmospheric CO_2 will continue to increase (*high confidence*), adding to global increases in temperature. CO_2 will continue to dissolve into the ocean, lowering the pH. Year round measurements from a wider variety of locations, are required to constrain uncertainties in the models.

Other anthropogenic drivers also have degrees of uncertainty. Until very recently global tourism was expected to increase in parallel with economic prosperity, however, growing health concerns over mass tourism (Hill, 2019) have been amplified by the COVID-19 pandemic and the trajectory of near future SO tourism is now highly uncertain. There are also concerns about the risk of tourists transferring anthropengic diseases to Antarctic seabirds which may become reflected in future recommendations of IAATO and the Antarctic Treaty (Cerdà-Cuéllar et al., 2019).

In particular the necessity of determining between trends that are the result of natural variability and those that are anthropogenic or the result of climate change requires an increased number of extended time series. Process studies, to understand the underlying mechanisms of this variability, must be a priority. Efforts to improve the observational records around Antarctica are critical to understand the nature of change around the continent and to predict the impacts on marine ecosystems.

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Future Risk for Southern Ocean Ecosystem Services Under Climate Change

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The Southern Ocean supports ecosystem services that are important on a global scale. Climate change and human activities (tourism, fishing, and research) will affect both the demand for, and the provision of, these services into the future. Here we synthesize recent assessments of the current status and expected future climate-driven changes in Southern Ocean ecosystems and evaluate the potential consequences of these changes for the provision of ecosystem services. We explore in detail three key services (the 'blue carbon' pathway, the Antarctic krill fishery, and Antarctic tourism), tracing the consequences of climate change from physical drivers through biological impacts to the benefits to humans. We consider potential non-climatic drivers of change, current and future demands for the services, and the main global and regional policy frameworks that could be used to manage risks to the provision of these services in a changing climate. We also develop a formal representation of the network of interactions between the suite of potential drivers and the suite of services, providing a framework to capture the complexity of this network and its embedded feedback loops. Increased consideration of the linkages and feedbacks between drivers and ecosystem services will be required to underpin robust management responses into the future.

Keywords: Southern Ocean, Antarctic krill, blue carbon, ecosystem services, climate change, Antarctic tourism, Antarctic Treaty System, IPCC (Intergovernmental Panel on Climate Change)

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INTRODUCTION

Ecosystem services are the benefits that people obtain from ecosystems (Costanza et al., 1997; Millennium Ecosystem Assessment [MEA], 2005). Despite ongoing debate about the concept, this area of research continues to grow, with the recognition that incorporating measures of ecosystem services into assessments of change provides a useful means of integrating environmental, economic and social factors, and the development of comprehensive frameworks to help achieve this (Costanza et al., 1997; UNEP, 2010; United Nations et al., 2014[1]; Guerry et al., 2015; Seddon et al., 2016; Townsend et al., 2018; IPBES, 2019; Bateman and Mace, 2020). The extent to which people benefit from ecosystem services depends on both the ecosystem's capacity to supply them and society's demand for, and use of, them. The capacity to supply ecosystem services is a function of both ecosystem structure and process (**Figure 1**). For example, the capacity to supply harvestable fish depends on

[1]https://seea.un.org/content/seea-experimental-ecosystem-accounting-revision

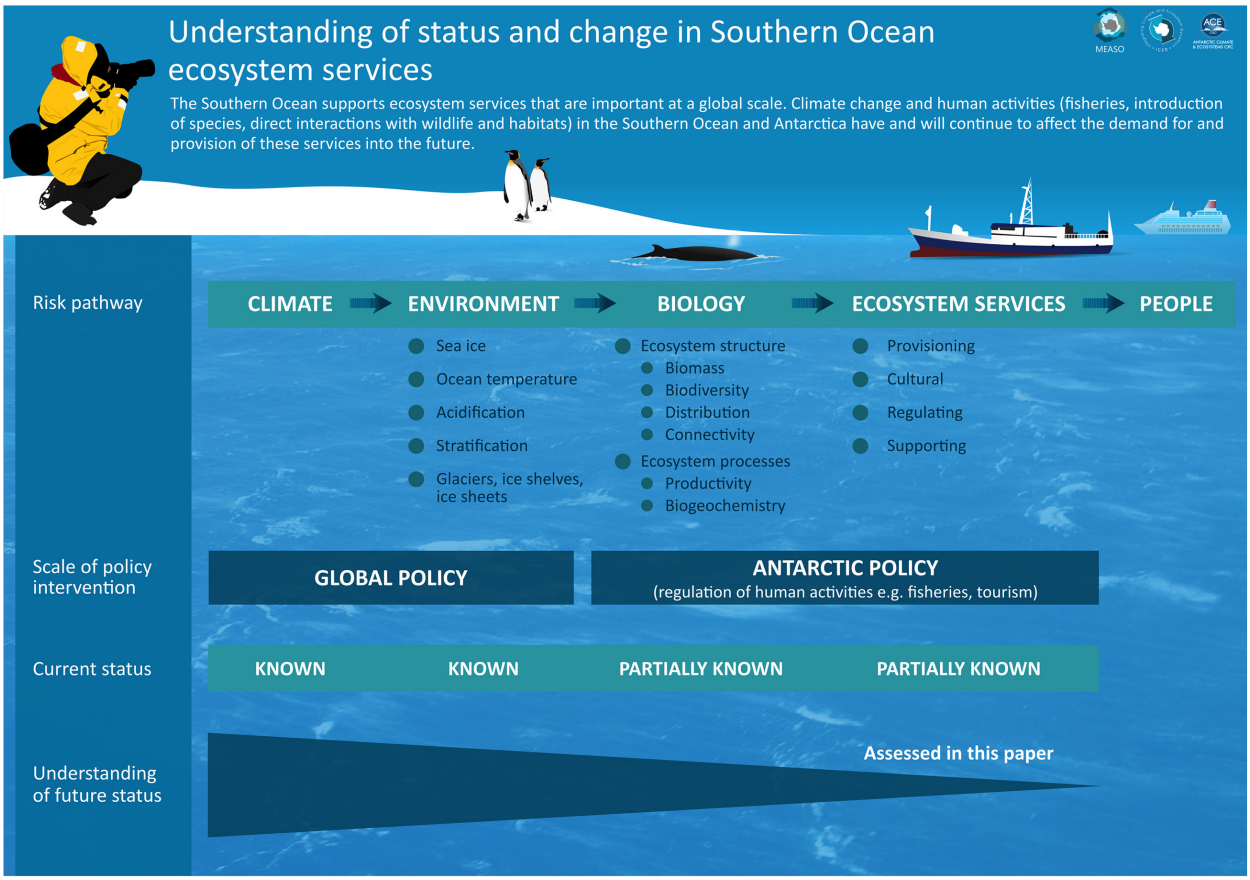

FIGURE 1 | Key risk pathways affecting Southern Ocean ecosystem services, from climate change impacts on physical drivers through to biological impacts and on to the benefits obtained by humans. The variables listed under 'Environment' and 'Biology' are examples of the wider suite of variables that could be affected.

the existence and availability of those fish (structure), and the production of new biomass (process). Both the capacity to supply ecosystem services and the demand for them may be influenced by a variety of drivers, with climate-driven environmental change potentially a key driver of both. Information on how supply and demand may change in future is thus a critical requirement for decision-making in relation to the conservation of ecosystems, the management of human activities that affect these ecosystems and for planning the response to climate-driven change. However, despite an increasing body of research on the impacts of climate change on ecosystem services (Mooney et al., 2009; Montoya and Raffaelli, 2010; Pedrono et al., 2016), quantitative syntheses are limited (Runting et al., 2017).

The focus of this study is on that part of the Southern Ocean overseen by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) ([2]hereafter we refer to this as the Southern Ocean for simplicity). The Southern Ocean is amongst the most rapidly changing oceans of the world, with consequences for global-scale storage and cycling of heat, carbon and other climatically- and ecologically-important properties. For example, the circulation and properties of Southern Ocean water masses are changing due to atmospheric effects including the loss of stratospheric ozone and increasing greenhouse gas concentrations, and are, in turn, affecting the physical and biological carbon pumps. Ocean temperatures are increasing; sea ice duration and extent is changing; and ocean acidification is advancing markedly in polar waters (Mayewski et al., 2009; Turner et al., 2009, 2014; Constable et al., 2014; Meredith et al., 2019; Morley et al., 2020). Such changes exert influences on biota and thence ecosystem services (**Figure 1**). The instruments of the Antarctic Treaty System (ATS) recognise the importance of Antarctic ecosystems to people in terms of their living resources, their value to scientific research, and their "wilderness and aesthetic value." The entire area south of 60°S is protected under the Antarctic Treaty[3], while the Convention on the Conservation of Antarctic Marine Living Resources extends further north to the Polar Front (Grant et al., in preparation), and underpins the management of fishing activities in the Southern Ocean. The Convention entered into force in 1982, and established CCAMLR[4] as its decision-making body. Information on how

[2]http://www.ccamlr.org/en/organisation/convention-area, accessed September 2020.

[3]https://www.ats.aq/index_e.html, accessed September 2020.

[4]http://www.ccamlr.org/en, accessed September 2020.

Southern Ocean ecosystems are changing, and what this means for their conservation and management, is becoming increasingly important for CCAMLR and the wider ATS (Grant and Penhale, 2016; Hughes et al., 2018).

Over the last decade extensive research has been undertaken to understand the effects of change on Southern Ocean ecosystems, with increasing recognition of the need for interdisciplinary approaches to integrate traditionally separate scientific disciplines such as climate science and ecology (Smetacek and Nicol, 2005; Murphy et al., 2008). In addition to national research programmes, there are a number of initiatives to coordinate international observation and research efforts, for example Scientific Committee on Antarctic Research (SCAR) programmes and initiatives such as the Southern Ocean Observing System (SOOS); the Integrated Climate and Ecosystem Dynamics in the Southern Ocean (ICED) Programme [co-sponsored by SCAR and the Integrated Marine Biosphere Research (IMBeR) project], which includes the MEASO (Marine Ecosystem Assessment for the Southern Ocean); and the United Nations Decade of the Ocean which includes a Southern Ocean contribution (Murphy et al., 2008; Meredith et al., 2013; Hofmann et al., 2020; Constable et al., in preparation). Key research questions include how climate change affects critical environmental variables, and how these changes impact Southern Ocean biota (e.g. see: Constable et al., 2014; Gutt et al., 2015; Rogers et al., 2020). Much of this work is synthesised and assessed in the recently published United Nations' Intergovernmental Panel on Climate Change (IPCC) Special Report on the Ocean and Cryosphere in a Changing Climate (SROCC) (IPCC, 2019).

While various exercises have assessed ecosystem services in most regions of the globe (Millennium Ecosystem Assessment [MEA], 2005; Guerry et al., 2015; Dunford et al., 2018), similar comprehensive assessments are lacking for the Southern Ocean and Antarctica (Grant et al., 2013b; Pertierra and Hughes, 2019). A number of studies have, however, considered Southern Ocean ecosystem services using a range of approaches. These include an attempt to catalogue the main services at the circumpolar scale (Grant et al., 2013b), regional assessments (Deininger et al., 2016; Neumann et al., 2019) and studies considering the potential effects of change (Murphy et al., 2016; Rogers et al., 2020; Trebilco et al., 2020). However, at present, although it is evident that the Southern Ocean provides globally important ecosystem services, information is sparse on their current status, and how they may change into the future. Such information would improve understanding of the wider consequences of change in Southern Ocean ecosystems (Cavanagh et al., 2016a), and help to ensure that the range of services are adequately recognised in decision-making at regional and global scales (Hill and Grant, 2013).

While the SROCC assessment (and the studies it draws upon) provides a central source of information on the effects of climate change on the Antarctic marine environment, the potential impacts of these changes on Southern Ocean biota, and the level of agreement about, or confidence in, these impacts, it includes only limited information on the implications for ecosystem services. Here, we use the SROCC as our primary source of information on the key drivers of change, and how they are projected to affect the biological components that underpin the suite of Southern Ocean ecosystem services, to undertake a risk assessment regarding the impacts of climate change on the capacity of the ecosystem to deliver the services in the future. Our assessment of risk translates qualitative projected change in drivers to qualitative consequences for ecosystem elements underpinning ecosystem services. This qualitative approach is pragmatic in the absence of specific information on the magnitude of impact to ecosystem services. We acknowledge non-climatic influences, including the large-scale historical perturbation of the Southern Ocean ecosystem as a result of sealing and whaling (discussed in detail in Grant et al., in preparation), and the difficulties of disentangling these impacts and their associated recoveries from the effects of environmental change, particularly in establishing baselines against which future change and risk can be assessed (Smetacek and Nicol, 2005). Our risk assessment also implicitly assumes that other influential factors, including the scale and distribution of ongoing human activities (e.g. fishing, tourism) in the Southern Ocean, remain unchanged, and does not account for regional differences in these factors (e.g. accessibility). We note, however, that the effects of these other drivers, as well as future changes to their scale or geographic reach, could be as important as those of climate change, particularly at local or regional scales (Grant et al., 2013b; Klein et al., 2018; Morley et al., 2020; Grant et al., in preparation). We therefore explore in more detail the potential effects of combined drivers for three case studies focused on key ecosystem services: the 'blue carbon' pathway (i.e., the process of carbon capture and fixation by marine organisms, through storage in organism bodies to sequestration), the Antarctic krill fishery, and tourism. We identify key areas of demand and use of these services where relevant, noting that there are considerable regional differences (identified in more detail in Grant et al., in preparation). We also consider future demand for services, and identify the main global and regional policy frameworks that could be used to manage risks to the provision of these services in a changing climate. We use the information in our assessment to develop a formal representation of the network of relationships between this suite of ecosystem services and their drivers. This provides an accessible framework for understanding the complexity of this network, as well as a basis for future modelling to underpin robust management responses into the future.

MATERIALS AND METHODS

We extracted information from the SROCC (IPCC, 2019), predominantly Chapter 3 (Meredith et al., 2019) regarding drivers of change that have a clear connection to Southern Ocean ecosystem services. This includes information about future changes in these drivers; the level of confidence in this information (see Abram et al., 2019); the biological significance of this information (and level of confidence if stated); and the ecosystem services to which it relates (**Supplementary Table S1**). We then used this information to assess understanding of how future climate change might impact the ecosystem services. Following Grant et al. (2013b), we described each ecosystem service, categorised as either provisioning, regulating,

supporting and cultural (Millennium Ecosystem Assessment [MEA], 2005). Our study focuses on provisioning, regulating and supporting services, and one cultural service, namely tourism (**Supplementary Table S2a**), but we did not evaluate other cultural services nor those services that existed either in the past (e.g., the harvesting of the now overfished marbled rockcod *Notothenia rossii*) and those that might become important in the future (e.g., harvesting of mesopelagic fish). These additional services are listed in **Supplementary Table S2b**. Note that we did not include the ecosystem services of water or air quality regulation., i.e., the uptake of chemicals and pollutants from the ocean and atmosphere, or waste treatment, i.e., decomposition of organic wastes by bacteria and microorganisms. These are underpinned by a complex network of interacting ecosystem processes and merit separate studies. We also briefly described the biological components that underpin each of the services. We then summarised the projected impacts of climate-related drivers of change on these biological components, acknowledging other drivers, anticipated changes in demand for the service (i.e., the societal need for the service, ranging from the demand for fish as a food source to the reliance on the role of the blue carbon pathway in climate regulation), and whether the service (and/or its biological components) are considered in theory and/or practice by instruments of the ATS (**Supplementary Table S2**). Our assessment focuses on the circumpolar scale, with regional-scale differences, including the distribution of human activities, discussed in the case studies.

We used this information to undertake a risk assessment regarding the impacts of climate change on the capacity of the ecosystem to deliver each service (in **Supplementary Table S2a**) in the future. Specifically, we assessed the risk of negative climate-driven impacts on ecosystem services given the conditions in the 2100 forecast for the IPCC Representative Concentration Pathway (RCP) 4.5 scenario (Abram et al., 2019).

The level of risk was determined based on the likelihood of change in each driver (derived from the level of confidence for directional change in these drivers), and the potential consequences for each ecosystem service (derived from the nature of the impact of each driver on biological components underpinning ecosystem services). Negative impacts of climate change are assumed to carry higher risk for ecosystem services. We then assigned confidence to these risk ratings based on the level of confidence regarding the impact of drivers on biological components (as stated in the SROCC, **Table 1**). A combined assessment of risk across all climate-related drivers for each ecosystem service is presented in the results (**Table 2**). In determining an overall risk rating for the capacity of the ecosystem to deliver each service in the future we assumed that the drivers do not exacerbate each other, such that the maximum risk for any driver is the overall risk. This assumption is unlikely to be true in all cases, but information regarding the relationship between impacts of drivers (i.e., whether they are antagonistic, neutral or synergistic) is not currently available. Confidence levels are presented for each individual risk pathway (i.e., for each driver-ecosystem service combination).

We have focused in detail on three key services: the blue carbon pathway, the Antarctic krill fishery, and Antarctic tourism. These were chosen based on their global as well as regional importance (Grant et al., 2013b; Deininger et al., 2016; Murphy et al., in preparation), and because they are clearly distinct from each other, differing in terms of the ecological underpinning, benefits they provide to humans, and how they are managed. Each case study provides a description of the ecosystem service, including its importance to people and the biological components essential to provision of the service. Through the case studies we traced the consequences of climate change from physical drivers through to biological impacts and subsequently to the benefits obtained by people. We relate these to current and future demand for the services, consider other relevant (non-climatic) drivers, and identify the main global and regional policy frameworks that could be used to manage risks to them in the future.

Based on the connections between services, biota and drivers identified in our assessment, we developed a formal network representation of these interactions to better elucidate how the capacity of the ecosystem as a whole to deliver each service may be affected (**Figure 2**). We used the established symbology for signed digraphs that is used in qualitative network modelling (Melbourne-Thomas et al., 2012; see also Trebilco et al., 2020). Connections between ecosystem services and drivers are identified as positive, negative, positive and/or negative (i.e., direction variable or dependent on context) and weak

TABLE 1 | Look-up risk table for ecosystem services.

		Consequence for ecosystem service		
		Nature (direction) of impact of driver on biological components underpinning ecosystem services		
	Level of confidence for change in driver	**Negative**	**Mixed**	**Positive**
Likelihood of change in driver	Low	Intermediate risk	Intermediate risk	Low-level risk
	Medium	High-level risk	Intermediate risk	Low-level risk
	High	High-level risk	Intermediate risk	Low-level risk

Confidence levels in risk rating are assigned based on the level of confidence regarding the impact of a given driver on biological components [as assessed in the SROCC (IPCC, 2019)].

TABLE 2 | Summary risk assessment for ecosystem services (only those in **Supplementary Table S2a** have been assessed).

Ecosystem Service	Drivers						Overall risk rating
	Sea ice	Ocean temperature	Ocean acidification	Stratification	Glaciers, ice shelves, and ice sheets	Ocean circulation	
Provisioning							
Antarctic krill	●●	●●	●				
Toothfish		●					
Other harvested species		●					
Regulating							
Blue carbon pathway					●●		
Supporting							
Primary production (open ocean)	●●		●	●●			
Primary production (coastal)	●●		●●	●	●●		
Nutrient cycling							
Cultural							
Tourism and recreation	(●●)						

*Colour indicates the assessed level of risk (based on **Table 1**, blue/green = low-level risk, orange = intermediate risk, red = high-level risk) and black dots indicate the level of confidence (●low confidence, ●●medium confidence, ●●●high confidence, no dot indicates no assessed level of confidence available). The overall assessment assumes that the drivers are neutral to one another, such that the maximum risk for any driver is the overall risk. Light grey shaded cells indicate cases where there may be a risk to ecosystem service provision associated with a particular driver but there is currently insufficient evidence to assess that level of risk. The level of confidence regarding the effect of sea ice change on tourism and recreation is indicated in brackets (●●) to indicate that there is medium confidence for the effects on wildlife, but no assessment of the level of confidence for the effect of sea ice change on tourism and recreation overall.*

or uncertain (where the current state of knowledge is such that the strength of these links is unclear). In the context of this paper, the network representation provides a method for tracing risk pathways for particular case studies (see below) and for visualising the connections and feedbacks between different services and drivers. Direct and indirect effects can be identified, providing further context for the risk assessment (where we consider direct effects of drivers only). Biodiversity (which, in this case, also includes ecosystem structure and processes but is labelled simply as 'biodiversity' because of space constraints in the network figure) is represented as underpinning ecosystem services (Seddon et al., 2016). It should be noted that the network representation is not intended to be a precise representation of all factors detailed in our assessment and case studies, but instead as a complementary approach for viewing pathways of change.

RESULTS

From Climate to Ecosystem Services

It is evident that many climate-related drivers of change, including sea ice, ocean temperature, ocean acidification, stratification (including mixed layer depth), retreating glaciers, ice sheets and ice shelf loss, and ocean circulation, have clear connections with the delivery of key Southern Ocean ecosystem services through their influence on ecosystem structure and processes (**Supplementary Table S1**). Our stepwise consideration of the effects of climate-driven change on ecosystem services, from physical drivers (and the nature of projected change in these drivers) through to biological impacts and on to the benefits obtained by people (**Figure 1**), provides a structured approach to (i) consider the complexity of climate-driven change on ecosystem service delivery and (ii) track uncertainty from drivers to impacts. For example, changes in sea ice habitats are known to have high biological importance, with cascading effects on ecosystem structure and processes that underpin a number of ecosystem services (**Supplementary Table S1**). Despite *low confidence* in future projections of Antarctic sea ice, future declines in extent are indicated over the course of the 21st century (Meredith et al., 2019, **Supplementary Table S1**), with negative associated impacts for Antarctic krill (*Euphausia superba*) populations (*medium confidence*), mixed effects on phytoplankton (*medium confidence*) and on marine mammals and penguins (*high confidence*), and potentially positive effects on carbon uptake and storage by benthic communities (Meredith et al., 2019, **Supplementary Table S2**). These impacts will in turn affect the ecosystem's capacity to deliver provisioning (fishery products), supporting (primary production), regulating (climate regulation), and cultural services (e.g. tourism) (see also Case Studies 2 and 3 below).

Risk Assessment of the Impacts of Climate Change on the Capacity of the Ecosystem to Deliver Each Service in the Future

Our risk assessment was based on each of the stages in the stepwise approach. Our findings suggest that overall, Southern Ocean provisioning services face an *intermediate* (finfish) to *high-level* risk (Antarctic krill) from climate change, with supporting services *low-level* through to *high-level* risk, with cultural services and regulation services facing

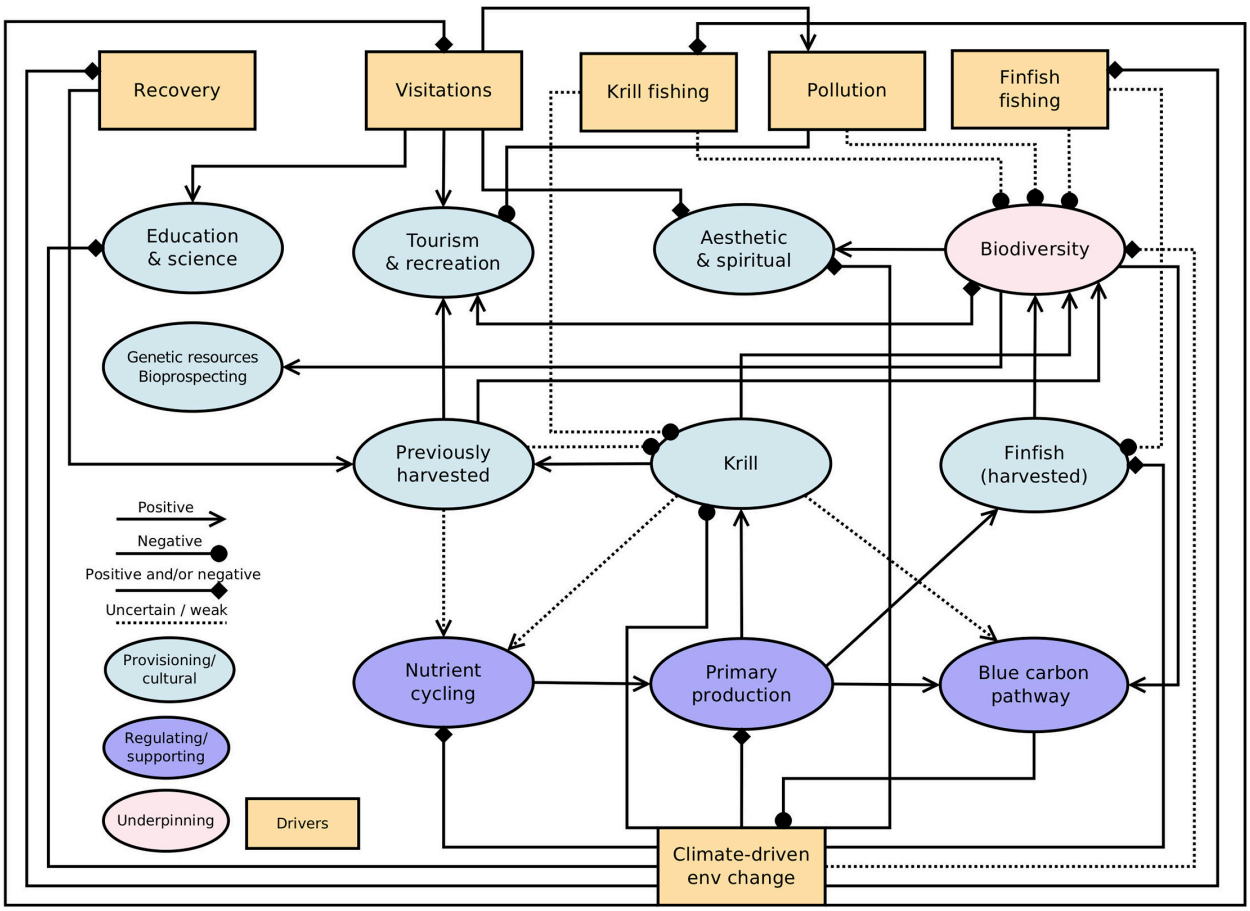

FIGURE 2 | Network representation of the links and feedbacks between ecosystem services and drivers. Connections between components indicate the direction of effects from one node to another, as indicated in the legend. Diamonds indicate cases where the direction of the effect is not known or unclear (i.e., it could be positive and/or negative), and dashed lines represent uncertain or weak linkages. The effect of fishing on associated ecosystem services (krill and finfish) is represented as weak, because we assume that current management is effective in minimising the impact of fishing on the capacity of stocks to continue to deliver ecosystem services. Services and key drivers included in the network are summarised from **Supplementary Table S2** and grouped as provisioning and cultural or regulating and supporting. Biodiversity is represented as underpinning ecosystem services (and also includes ecosystem structure and processes) but can be directly affected by drivers, with consequent effects for services. Bioprospecting refers collectively to biochemicals, medicines, and pharmaceuticals. Changes to drivers have cascading effects to ecosystem services, including feedbacks across other linked drivers.

intermediate and *low-level* risks respectively (**Table 2**). The information we used in our assessment is summarised in **Supplementary Tables S1, S2a**. For example, for the Antarctic krill fishery, the key drivers are sea ice, ocean temperature and acidification. The levels of confidence for directional change in these drivers are *low*, *medium,* and *high* respectively, all assumed to have overall negative effects on the biological components of this ecosystem service, which we assign as *intermediate*, *high-level,* and *high-level* risk respectively, as per **Table 1**, with confidence levels *medium*, *medium,* and *low* respectively. The overall risk to this ecosystem service from climate-driven change is therefore *high-level* (**Table 2**). In summary, our assessment indicates that climate change related risk is highest for the Antarctic krill fishery and for coastal primary production (supporting service), that the risk level is *intermediate* for most services, but that it is currently *low-level* for the blue carbon pathway and for nutrient cycling (**Table 2**). Confidence levels underpinning these assessments are generally *low*-to-*medium* level.

Exploring Connections – Qualitative Network Representation

The network analysis revealed a complex suite of interdependencies, including feedbacks across other linked drivers, such as fishing (**Figure 2**). Our network representation highlights that not only are there connections and feedbacks between Southern Ocean ecosystem services, but that there is also a high degree of connectivity between drivers. Indeed, climate-driven environmental change is connected to all other human drivers shown in **Figure 2** (fishing, visitations, and recovery of previously exploited species), except for pollution. These connections mean that, for example, climate-driven environmental change can affect the capacity of Southern Ocean

ecosystems to support tourism and other cultural services, both via direct effects on biodiversity, and indirectly through the effects of enhanced visitations (as areas become more accessible due to reduced sea ice; see Case Study 3 on Antarctic tourism below). **Supplementary Table S2** includes brief information on other key drivers (see also Grant et al., in preparation), future demand (see also Chown and Brooks, 2019; Rogers et al., 2020), and conservation and management measures within the ATS. We consider these factors in more detail in the case studies below.

Case Studies

Case Study 1. Blue Carbon Pathway

Brief description of the ES

The blue carbon pathway is the process of carbon capture and fixation by marine organisms, through storage in the bodies of organisms (for up to 100 years) to sequestration (which is removal of carbon from the carbon cycle for 100 + years). Southern Ocean continental shelves are seasonally highly productive through carbon capture and fixation by phytoplankton. Some of this carbon sinks to the seabed and is buried, some is stored in the bodies of consumers (zooplankton and benthos) and some is recycled by bacteria. Burial at the seabed can lead to sequestration.

Importance of the ES

The reduction of atmospheric carbon is a major societal goal (United Nations Framework Convention on Climate Change (UNFCCC) Paris Agreement[5] and with the so-called 'shadow cost of carbon' (i.e. of industrial carbon capture) reaching ∼US$38-78 tCO_2, the storage and sequestration of blue carbon is recognised as a powerful and valuable ecosystem service. Coastal marine habitats are very efficient at carbon pathways but are decreasing in area almost everywhere because of habitat destruction, land reclaim, pollution etc; the exception is the polar regions, where they are increasing due to declines in sea ice, glacier retreat and ice shelf collapse (Barnes et al., 2018; Gogarty et al., 2020). In recent years it has become apparent that biodiversity within polar oceans hold some important 'natural capital' in stored carbon. Carbon storage by marine organisms is dwarfed by physical storage in the water, however, it is important to note that biological capture and storage of carbon is increased by ocean warming (negative feedback on global warming) whereas physical storage is decreased (positive feedback), so they respond in different ways to climate change (Barnes et al., 2018).

Biological components essential to the provision of the ES

There are essentially four components to this ES. These are: (1) phytoplankton capture carbon from dissolved CO_2; (2) zooplankton and benthos consume the phytoplankton and store this carbon; (3) on death some phytoplankton and animals are buried at the seabed sequestering carbon; but (4) most carbon is recycled in the microbial loop by bacterial breakdown of phytoplankton and animals. Some species are disproportionately important to carbon storage, particularly those with high biomass (e.g., krill) and those which are longer lived (e.g., barrel sponges, corals, and baleen whales). Their impact on genuine carbon sequestration may also be higher but to date remains unclear.

Polar continental shelves have extreme light climate, sea ice (reducing light penetration), and low temperature (slow enzyme work rate). Carbon capture is predominantly in phytoplankton blooms, which differ to those in warmer water by being very brief and dominated by diatoms. These have hard silica tests that are difficult to assimilate without physically rupturing cell walls. Such blooms are limited by the low availability of micronutrients, especially iron, throughout much of the Southern Ocean (Moore and Abbott, 2000). It has been argued however that recovery of baleen whale populations could result in greater nutrient recycling in the upper water column and therefore more intense or widespread blooms (Lavery et al., 2014; Ratnarajah et al., 2015). Carbon capture rates from Antarctic primary production approximate to 200 gC m^2yr^{-1} (Ducklow et al., 2007) but vary with year and region. Phytoplankton are a crucial part of the provision of the ecosystem service, but unlike trees on land, they cannot store carbon because their lives are brief.

The long lived components of polar marine foodwebs are animals, so most carbon storage occurs in these (see Henley et al., 2020). Below regular ice scour depths, Southern Ocean animals develop and grow slowly and live long lives. Antarctica's continental shelves are deep, wide and little disturbed, all of which allows considerable accumulation of biomass and stored carbon (Arntz et al., 1994). However, the immediate fate of about half of Southern Ocean primary production is breakdown in the water or seabed microbial loop, and so it is recycled (Azam, 1998; Henley et al., 2020). Transfer of carbon to primary consumers in the foodweb is efficient; about 30% amongst pelagic and benthic suspension feeders (Hill et al., 2012; Barnes, 2017, respectively). Rate of carbon accumulation decreases offshore and with depth, seemingly due to reduced exposure to phytoplanktonic food (Barnes, 2017). Of the carbon that is stored in Southern Ocean pelagic and benthic animals, most of this too will be broken down on death through the microbial loop, but some is buried upon death.

Sequestration of blue carbon happens through various paths, the simplest being direct sinking (∼1%) of primary production to the seabed (typically < 4 gC m^2 yr^{-1}, Ducklow et al., 2007). Some is consumed by zooplankton which can potentially sequester through faecal pellets and/or carcasses raining to the seabed and (a small proportion) escaping microbial breakdown in the water column and seabed (see Barnes and Tarling, 2017). The rate of such pelagos burial below oxygenated surface sediments (below zones of bioturbation and bio-irrigation) is yet to be quantified. Most Southern Ocean species are benthic, and the primary consumers amongst them include suspension, deposit and grazing feeders, some with estimated lifespans making them amongst the oldest animals on Earth (some live for 100+ years). This is a shorter route to sequestration (no exposure to water column microbial loop) and many have organic carbon sandwiched within thick, external skeletons (e.g., some corals, bryozoans, and sponges).

[5]http://unfccc.int/resource/docs/2015/cop21/eng/l09r01.pdf, accessed September 2020.

In terms of carbon storage and cycling, the contribution of biology in the polar oceans is relatively small, e.g., with respect to forests and low latitude coastal habitats. However, the wide, deep and mainly undisturbed polar continental shelves may be very efficient at burial and thus sequestration (at which forests are poor). Most importantly polar continental shelf carbon capture and storage increases with marine ice losses and mild warming, so acts as a negative feedback on climate change.

How is the ES expected to change?

Threats to the ecosystem service are complex, poorly understood and difficult to evaluate, but have some alignment with general threats to Southern Ocean biodiversity (e.g., see Gutt et al., 2015; Morley et al., 2019). These include climate-driven change, disruption by non-indigenous species establishments, pollution, harvesting (e.g., longline bycatch), and habitat destruction from increased ice scour. The quantification of the status of carbon capture, storage, and sequestration by polar organisms is in its infancy. However, it has been shown that biological stores of carbon on the seabed increase with declines in sea ice extent (Barnes, 2015) and vice versa (Pineda-Metz et al., 2020), due to links between sea ice and phytoplankton timing, duration and bloom size (Arrigo et al., 2008). The uncertainty in sea ice projections (IPCC, 2014, 2019; Cavanagh et al., 2017; Turner and Comiso, 2017) means that future predictions for biological carbon pathways to sequestration also have considerably uncertainty (Rogers et al., 2020). Such uncertainty is further bolstered by the possibility that seabed biological carbon may not be linked to sea ice extent in the Arctic (at least in the Barents Sea, see Souster et al., 2020).

Whilst forests, mangroves, salt marshes and other non-polar carbon sinks are shrinking, polar blue carbon is increasing considerably, at least around West Antarctica. Polar carbon sinks are rare examples of negative feedbacks on climate change (Barnes et al., 2018; Pineda-Metz et al., 2020). Phytoplankton blooms have increased (Arrigo et al., 2008) and zoobenthic blue carbon storage has doubled around West Antarctica (Barnes, 2015) in response to sea ice losses over the last 25 years. Giant icebergs formed from ice shelf collapses also generate considerable increases in onshore capture (Peck et al., 2010) and offshore capture (DuPrat et al., 2016). Primary consumers convert this to storage of blue carbon, to the order of about a million tonnes per giant iceberg (Barnes et al., 2018). Furthermore small (∼1°C) temperature rises may further increase zoobenthic growth and carbon storage (Ashton et al., 2017). This powerful negative feedback is not without its complexities though, with changing species composition of phytoplankton and zooplankton (Rogers et al., 2020).

Sea ice around the Antarctic had been increasing in extent since the 1970s, but more recently it decreased to record low levels, with the greatest decline in the Weddell Sea (Turner and Comiso, 2017; Turner et al., 2020). There is considerable regional variability, but if such reductions continue there could be major gains in biologically stored carbon, measurable within a decade, although gauging the extent to which this is converted to sequestered carbon may take longer. This will lead to redistribution of hotspots of blue carbon. Areas that were gaining sea ice and losing blue carbon (Pineda-Metz et al., 2020) may now start gaining blue carbon in response to new sea ice losses (Turner and Comiso, 2017; Barnes et al., 2018).

Overall, the responses of this ecosystem service to climate forcing may be parabolic; blue carbon increases with phytoplankton availability, which in turn increases with sea ice, glacier and ice shelf losses (Barnes et al., 2018) and independently also increase with moderate warming (Ashton et al., 2017). However sea ice, glacier, and ice shelf losses are finite and losses of sea ice during winter darkness will yield little enhancement to phytoplankton. Furthermore temperature increases beyond 1°C might start to threaten temperature survival envelopes of species (Ashton et al., 2017; Peck, 2018). End of century onwards decreases may be increasingly driven by strengthening ocean acidification making storage slower and sequestration more difficult (IPCC, 2019). **Figure 3** provides a network representation of connections and feedbacks between the blue carbon pathway and other Southern Ocean ecosystem services, together with some key drivers of change.

What might these changes mean for humans who depend on/benefit from the ES?

The increasingly urgent need to meet climate and carbon agreements means that increased efforts to protect coastal habitat, and the ecosystem services conferred therein, are likely to be sustained. However, the level of most Antarctic biological carbon storage is unmeasured in the majority of areas, so large scale change is currently unquantified. Even without directly-comparable metrics it is clear that, relative to absorbtion into oceans or rainforests, the stored carbon budget is small, and when considered alongside mangroves or seagrasses the efficiency of sequestration is poor.

Current management/existing policy for the ES

There is currently no specific management or policy for this ecosystem service in the Southern Ocean. However, there are policies and active management on fishing, pollution and prevention of non-indigenous species transport, as well as those to protect or reduce impact on benthic habitats and Vulnerable Marine Ecosystems (VMEs) (see **Supplementary Table S2**). All these actions have the potential to influence biological carbon storage and its likelihood of sequestration, despite not being specifically designed to meet this objective.

Adequacy of current management/policy with respect to change

Current management policies within the ATS have little impact on the global origin of threats to the ecosystem service, such as climate change and pollution. Recent fishing impacts have been mostly minimised by CCAMLR regulations and practices (e.g., Trathan et al., 2014), and there has been progress on limiting ballast water exchange but none on hull fouling by non-indigenous marine species (Hughes et al., 2020). However, current management and policy is not sufficiently agile to respond to sea ice losses (e.g. by implementing protection for newly-opened areas), so uncertainty remains in relation to safeguarding important recent gains in biological carbon stores (Gogarty et al., 2020).

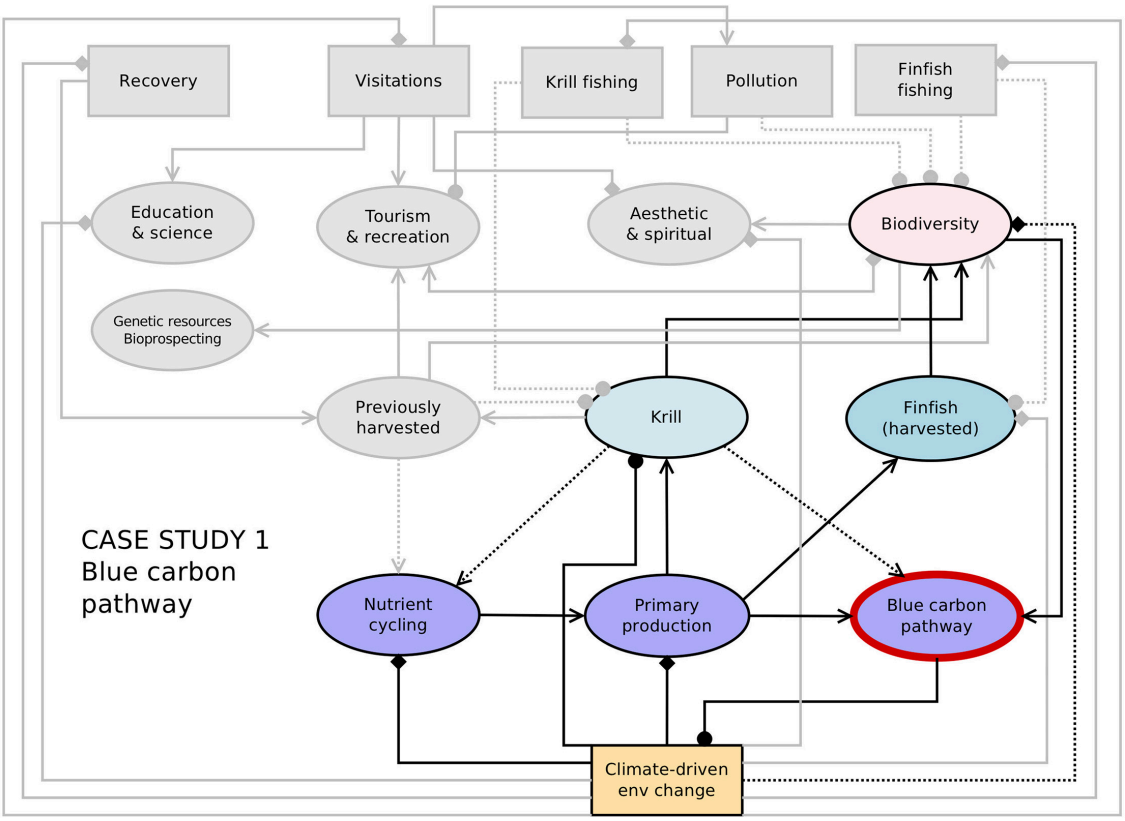

FIGURE 3 | Network representation of the links and feedbacks between ecosystem services and drivers (from **Figure 2**) with key elements for the blue carbon pathway highlighted. Connections between components indicate the direction of effects from one node to another, as indicated in the legend. Diamonds indicate cases where the direction of the effect is not known or unclear (i.e., it could be positive and/or negative), and dashed lines represent uncertain or weak linkages.

Recommendations/what is needed?

The carbon pathway in terrestrial ecosystems forms part of the consideration and merit of protected area status elsewhere in the world. An important area of progress could be to similarly consider the blue carbon pathway as part of the decision-making process on the establishment of marine protected area systems. Intuitively it is hard to envisage a more cost-effective pathway to maintain carbon sequestration than protection of large areas of remote continental shelf that are currently little utilised, especially when they are a rare ecosystem service which works as a negative feedback on climate change. However, measurement of this ecosystem service has not been possible by Earth observation remote sensing, and thus is expensive and time-consuming, requiring multidisciplinary scientists on research vessels working far from research stations, and over limited areas. Development of new approaches for larger-scale analyses would therefore be beneficial in further quantifying and mapping areas that are important for the blue carbon pathway.

Case Study 2. Antarctic Krill Fishery

Brief description of the ES

Antarctic krill (*Euphausia superba*) is a characteristic pelagic invertebrate of the Southern Ocean, which is noted for its relatively large size (maximum length c. 60 mm), high biomass, and highly aggregated spatial distribution (Atkinson et al., 2008, 2009; Siegel and Watkins, 2016; Tarling et al., 2016, 2018). These characteristics underpin its importance to various ecosystem services, including as a key food source for an array of vertebrate predators (Trathan and Hill, 2016) that attract tourism and as a contributor to biogeochemical cycles (Belcher et al., 2019; Cavan et al., 2019). They also make it an attractive resource for the fishing industry, which currently operates in the Scotia Sea region, specifically the waters of the North Antarctic Peninsula and around the islands of the Scotia Arc (Grant et al., 2013a; Kawaguchi and Nicol, 2020).

Importance of the ES

In the 2017/18 fishing season, 11 vessels from five nations participated in the fishery, catching 312,989 tonnes ([6]CCAMLR Krill Fishery Report 2018). This accounts for 95% of the annual catch in the Southern Ocean but <0.5% of the global annual marine fisheries catch (GAMFC). The main products are fishmeal, which is used as aquaculture feed, and omega 3 rich oils sold as premium priced diet supplements, while very little of the catch is used as a direct food source for people (Hill, 2013b; Nicol and Foster, 2016). Nonetheless, the fishery

[6]https://www.ccamlr.org/en/system/files/00%20KRI48%202018.pdf, accessed September 2020.

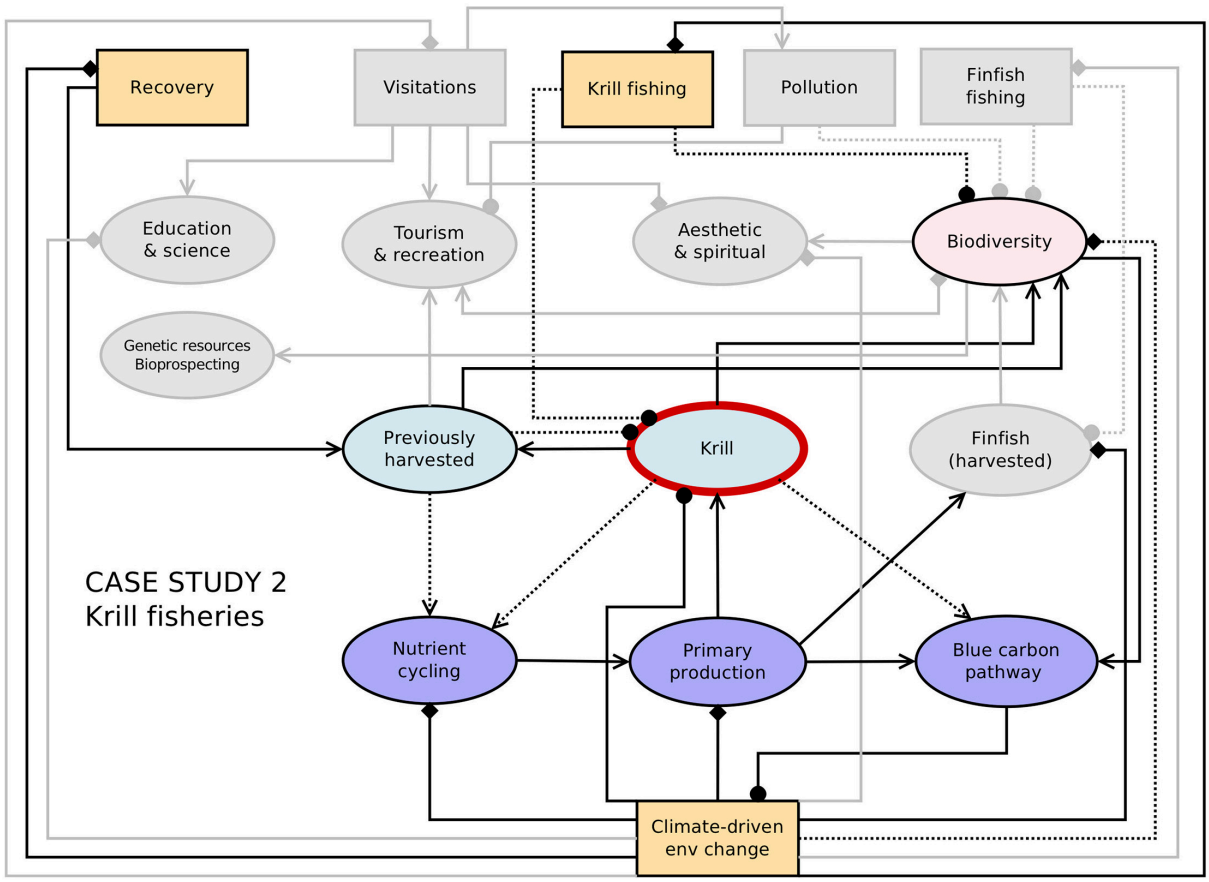

FIGURE 4 | Network representation of the links and feedbacks between ecosystem services and drivers (from **Figure 2**) with key elements for the Antarctic krill fishery highlighted. Connections between components indicate the direction of effects from one node to another, as indicated in the legend. Diamonds indicate cases where the direction of the effect is not known or unclear (i.e., it could be positive and/or negative), and dashed lines represent uncertain or weak linkages.

is one of a handful that are theoretically capable of supporting significantly higher catches and may therefore become important future food resources (Garcia and Grainger, 2005). Catch limits established by CCAMLR suggest that the ecosystem could sustain krill catches of >8 million t yr^{-1}, equivalent to >10% of GAMFC (Nicol and Foster, 2016) and enough to supply 1.5% of the human population with 1 g day^{-1} of omega 3 (Hill, 2013b). The financial value of krill catches is unclear and depends on the relative production of meal and higher value krill oil. Using the oil:meal ratio of a major krill oil producer, Grant et al. (2013b) estimated that the catch value for 2011 (181,000 tonnes) could be up to $241 million, whereas a study on behalf of CCAMLR found that value at the point of landing averaged $69 million yr^{-1} in the period 2011–2015 when catches averaged 216,000 tonne $year^{-1}$ (CCAMLR Commission Report 2016). These lower values probably reflect a much lower oil:meal ratio than that (18:82) assumed by Grant et al. (2013b). However, this ratio is likely to change over time as the krill oil market grows.

Biological components essential to the provision of the ES

The productivity of the krill stock is the main factor affecting the ecosystem's capacity to support the fishery. No stock-recruit relationship has been identified for Antarctic krill but it is likely that low population levels would impact productivity (Siegel and Nicol, 2000; Hill, 2013a). Productivity also relies on the availability of food and appropriate habitats for processes such as spawning, hatching, larval overwintering and growth (Atkinson et al., 2006, 2008; Murphy et al., 2017; Perry et al., 2019). Each of these habitat types is patchily distributed, so connectivity between them is also important (Hofmann and Murphy, 2004; Piñones et al., 2013; Perry et al., 2019; Thorpe and Tarling, 2019). The distribution of fishing effort is highly aggregated at the circumpolar and regional scales (Grant et al., 2013a; Nicol and Foster, 2016; Kawaguchi and Nicol, 2020). In the Scotia Sea region, all catches have been concentrated in less than a quarter of the sea area open to fishing (Grant et al., 2013a; Kawaguchi and Nicol, 2020). The fishery relies on exploitable concentrations of krill in operationally suitable areas, which are generally close to land (Hill et al., 2009) and in the upper few hundred metres of the water column which is accessible to fishing gear. The majority of Antarctic krill biomass is not located in these fishing grounds but in the open ocean, and in lower concentrations that might not be possible for the fishery to efficiently exploit (Atkinson et al., 2008; Hill et al., 2009). Furthermore the animals are capable

of occupying a variety of habitats including the bathypelagic zone (Schmidt et al., 2011). Thus, the current provision of the service relies on the specific behaviour of a fraction of the krill population.

How is the ES expected to change?

The projected effects of climate change are expected to cause contraction of krill habitat and reductions in productivity as a result of direct physiological effects on krill, loss of critical habitat and changes in the community of primary producers (Flores et al., 2012; Hill et al., 2013; Kawaguchi et al., 2013; Constable et al., 2014; Piñones and Fedorov, 2016; Klein et al., 2018; Meredith et al., 2019; Tulloch et al., 2019; Veytia et al., 2020). Key potential drivers include warming and loss of sea ice. Krill are adapted to a narrow range of temperatures with those > 3°C impeding both embroyonic development and adult growth (Atkinson et al., 2006; Perry et al., 2020). Sea ice is an important overwintering habitat for larval krill and reductions in its extent and duration could negatively impact recruitment to the adult population (Meyer et al., 2017; Schaafsma et al., 2017). Laboratory experiments have confirmed that low pHs impact embryonic development (Kawaguchi et al., 2013) although the effects in the field are not well understood. Changes in the timing of events such as ice break out and phytoplankton blooms might also have negative impacts as the krill life cycle is tightly synchronised to the current seasonal cycle (Quetin et al., 2007; Veytia et al., 2020). As the Southern Annular Mode (SAM; the leading extratropical mode of climate variability in the Southern Hemisphere, and a first-order indicator of circumpolar wind strength) is one of the strongest correlates of past changes in krill productivity in the Scotia Sea region (Atkinson et al., 2019), any future changes in advection and eddy activity could also affect krill distribution and abundance. Projections suggest that changes to the distribution and abundance of both krill and its predators are likely to be apparent by the end of the current century (Hill et al., 2013; Piñones and Fedorov, 2016; Klein et al., 2018; Tulloch et al., 2019; Veytia et al., 2020). While there is some debate over the magnitude of recent changes in krill numerical density in the Scotia Sea region (Atkinson et al., 2004, 2019; Cox et al., 2018; Cox et al., 2019; Hill et al., 2019), evidence of climate-driven changes in productivity and distribution (Huang et al., 2011; Forcada and Hoffman, 2014; Atkinson et al., 2019; McMahon et al., 2019; Yang et al., 2020), suggest that change has already occurred.

Some studies suggest that climate change may bring limited benefits to some life stages. For example modelling studies suggest that habitat availability for some larval krill stages might increase as sea ice becomes less stable (Melbourne-Thomas et al., 2016) and that adult growth rates might increase in some areas (Veytia et al., 2020). The productivity of the krill stock might also be affected by factors such as the recovery of depleted whale populations and the extent to which the krill stocks are impacted by exploitation.

The prognosis is that climate change will reduce the extent of productive krill habitat and the productivity of the krill stock, at least in the Scotia Sea region. In projection studies, the severity of these impacts increases with the severity of climate change (i.e., the RCP scenario). Paradoxically, demand for krill products could increase as the krill stock declines, especially if ecosystem degradation diminishes the capacity of ecosystems elsewhere to supply the food needs of a growing human population (Garcia and Grainger, 2005). Equally, demand could be fuelled by increasing demand for omega 3 (Hill, 2013b). Parts of the fishing industry have invested heavily in krill fishing over the last two decades, suggesting that demand for krill products is stable or increasing. However, the industry has not indicated any desire to increase catches beyond current limits (Cavanagh et al., 2016b). Simulation studies suggest that fishing at currently permitted levels could exacerbate climate-driven population declines in some krill predators in areas open to fishing (Klein et al., 2018). Thus one of the main factors that will affect the supply of krill products into the future is how CCAMLR's management of the fishery responds to change. **Figure 4** provides a network representation of connections and feedbacks between the krill fishery and other Southern Ocean ecosystem services, together with some key drivers of change.

What might these changes mean for humans who depend on/benefit from the ES?

Current management allows the fishing industry to increase catches and to adapt to changes in the krill population by relocating to more productive fishing grounds either within the Scotia Sea region or at the circumpolar scale. Reduced winter sea ice around the Antarctic Peninsula has allowed the fishery to become more concentrated in winter and move southwards in the last two decades (Kawaguchi and Nicol, 2020; Meyer et al., 2020). While climate change might open up new fishing grounds as ice retreats, it could also disrupt fishing if wave intensity increases (Collins et al., 2019) or the number and size of icebergs increase with ice shelf collapse. Parts of the Southern Ocean other than the Scotia Sea region may become increasingly attractive to the industry as markets and supply chains change.

Antarctic krill contributes <1% of global production of fishmeal and omega 3, and it is not currently an important human food source. The companies responsible for most of the krill catch are relative newcomers to the fishery (joining in the last 15 years) and their business plans might already account for the risks and opportunities associated with climate change. Thus the key implications of future change degrading the ecosystem's capacity to support the krill fishery are a reduction in the availability of a potential but currently minor food source, and the potential for the combined effects of climate change and fishing to impact the other ecosystem services that krill has a role in supporting, including climate regulation and tourism.

Current management/existing policy for the ES

Current management of the krill fishery is based on a series of interim measures pending the development of an approach that appropriately protects the wider ecosystem including krill predators (Hill et al., 2016, 2020; Nicol and Foster, 2016). The fishery is managed through the application of fixed catch limits applied to large spatial units (>0.6 million km^2) without reference to the current status of the stock in these units (Hill et al., 2020).

Adequacy of current management/policy with respect to change

The krill fishery is characterised by extremely low exploitation rates (catch per unit biomass) relative to other similar fisheries, and industry compliance with regulations (Cullis-Suzuki and Pauly, 2010; Hill et al., 2016, 2020; Nicol and Foster, 2016). In addition current circumpolar catches remain below 70% of the combined catch limit for the Scotia Sea region (Meyer et al., 2020). However, a recent study concludes that this is not sufficient to protect krill predators from the combined effects of fishing and climate change (Watters et al., 2020). Krill fishery management lags behind that of other similar fisheries in that catch limits do not respond to changes in stock size (Hill et al., 2020). Nor can fixed catch limits respond to changes in distribution. Without finer-scale management CCAMLR will be unable to prevent the localised impacts on krill and its predators that might result from the combined effects of fishing and climate change, or from changes in fishing patterns (Klein et al., 2018; Watters et al., 2020; Meyer et al., 2020). While CCAMLR's scientific working groups have been working for three decades to improve krill fishery management, their focus has been on the Scotia Sea regions which means that CCAMLR is less well equipped to manage the fishery if it expands into other regions.

One of CCAMLR's current regulations identifies potential mechanisms "to further improve future management of krill" and recognises that "advances are urgently needed." CCAMLR also has a resolution on climate change which "urges increased consideration of climate change impacts in the Southern Ocean to better inform CCAMLR management decisions" (CCAMLR Resolution 30/XXVIII). However in the decade since passing that resolution, CCAMLR has not altered the catch limits for krill or clarified how consideration of climate change impacts will inform future decisions. Thus the challenge for CCAMLR is to progress from aspiration to implementation. A test of its ability to do so will come in 2021 with the expiry of a key current regulation which has successfully limited catches in the North Antarctic Peninsula seas to 155,000 tonne yr^{-1}.

Recommendations/what is needed

Management of the krill fishery in a changing climate requires an agility that has eluded CCAMLR to date. The single advance that would most help to manage the fishery through future change is to make regular monitoring of krill stock size at an appropriate scale for management a precondition for any catch limit. Such monitoring is necessary to ensure that exploitation rates do not exceed safe limits (Hill and Cannon, 2013; Hill et al., 2016, 2020). Given CCAMLR's obligations to protect the wider ecosystem, there is a need for mechanisms that minimise the risk of localised impacts on critical krill life stages and on krill predators (Meyer et al., 2020; Watters et al., 2020). Better prognostic information would also be useful, including forecasts of future demand for krill products and of impacts on the krill stock from climate change and from predator populations recovering from past overexploitation. The former may already exist within the krill fishing industry while the latter requires a coordinated and properly resourced effort by the scientific community. Arguably the unresolved debate about past change in krill populations is an impediment to progress which could be resolved through a more complete articulation of uncertainties (Hill et al., 2019; Meyer et al., 2020).

Case Study 3. Antarctic Tourism

Brief description of the ES

Antarctica provides cultural ecosystem services through tourism and recreation. Benefits include visitor enjoyment of nature and spectacular landscapes of high wilderness and aesthetic value, as well as the provision of income opportunities for nature tourism service providers.

Most Antarctic tourists (>95%) visit the Antarctica Peninsula on cruise vessels, with many calling at coastal sites for brief shore-based activities. Around 50 yachts travel to Antarctica each year, with either independent travellers or fee-paying passengers (United Kingdom et al., 2019). Land-based tourism provides opportunities to visit 'deep field' sites that are to some extent driven by recreational adventure tourism centred on mountaineering (for example Mount Vinson or Ulvetanna).

Importance of the ES

Antarctic tourism is one of the most significant human activities undertaken in the region, beginning in the 1950s followed by a long period of expansion dating from the late 1980s. The duration of the Antarctic tourism season has expanded to >150 days (November to April). During the 2019/20 season, 74,401 tourists visited Antarctica, including cruise-only visitors. Assuming a ship-based visit to Antarctica to cost around US$8000, the Antarctic tourism industry may have had a turnover of >US$600 million in 2019/20. COVID-19 may greatly reduce tourist visitor numbers, at least in the short term, as demand drops, nations with gateway ports limit visitor access and Antarctic Treaty governments take steps to prevent the virus reaching Antarctica (Hughes and Convey, 2020).

Biological components essential to the provision of the ES

Many of the activities, such as birdwatching (including penguin colony visits), whale watching, diving, use of submersibles and photography, are dependent on the local marine wildlife and habitats (Burger and Gochfeld, 2007).

How is the ES expected to change?

Given the expansion of the tourism industry during the past 30 years, the predicted increase in global demand for Antarctic visits, and increasing diversity of activities, the ecosystems attracting Antarctic tourism may be vulnerable to over exploitation (Eijgelaar et al., 2010; Liggett et al., 2017; Pertierra et al., 2017).

Ecosystem impacts caused by increasing visitation and the potential establishment of permanent infrastructure (noting that these are not exclusive to tourism) could include (a) a loss of wilderness and aesthetic values (Summerson and Tin, 2018), (b) increased risk of non-native species introduction (Chown et al., 2012), (c) increased risk of pollution events at both small (e.g., dropping of litter) and large scale (e.g., fuel spill from a ship; Aronson et al., 2011) resulting in impacts on biota, (d) trampling of vegetation or disturbance of wildlife (Burger and Gochfeld, 2007; Tejedo et al., 2016), (e) increased atmospheric

emissions from vessels, aircrafts, and land vehicles (Amelung and Lamers, 2007; Eijgelaar et al., 2010) and (f) increasing cumulative impacts at ice-free locations, including where scientific, logistic and tourism activities coincide (e.g., Deception Island).

The Antarctic Peninsula region has exhibited the greatest levels of climate change in the continent in the past 60 years, as well as being the area most visited by tourists (between 95 and 99% of tourists visit the Peninsula compared to the rest of Antarctica). Climate models predict substantial climate change across the whole continent in the coming century, resulting in increases in ice-free ground through glacier and ice sheet retreat, reductions in sea ice extent, shifts in the distribution range of wildlife and increases in distribution and spatial coverage of terrestrial species (both native and non-native) (Chown et al., 2012; Turner et al., 2014; Lee et al., 2017; Siegert et al., 2019). Climate change impacts may increase tourism industry interactions with Antarctic ecosystems and wildlife by potentially facilitating access to new locations, but may also affect the biota present at established landing sites. **Figure 5** provides a network representation of connections and feedbacks between Antarctic tourism and other Southern Ocean ecosystem services, together with some key drivers of change.

What might these changes mean for humans who depend on/benefit from the ES?

While visual tourism impacts appear to be minimal, the recent dramatic rise (and predicted longer-term increase) in tourist visitation could result in rapid change being detectable in the near future.

The industry imposes strict control of vessel movement between landing sites to maintain an impression of remoteness for visitors; as such, an increase in vessel traffic may degrade this experience for the visitor. Consequently, as some sites reach their carrying capacity, there may be increasing pressure to access previously little visited locations, with associated anthropogenic impact upon resident biota.

Positive benefits from increased tourism may include increased revenue receipt and an increase in individuals with greater appreciation of the beauty and fragility of Antarctic environments (often termed 'Antarctic Ambassadors' by the industry's member organisation, the International Association of

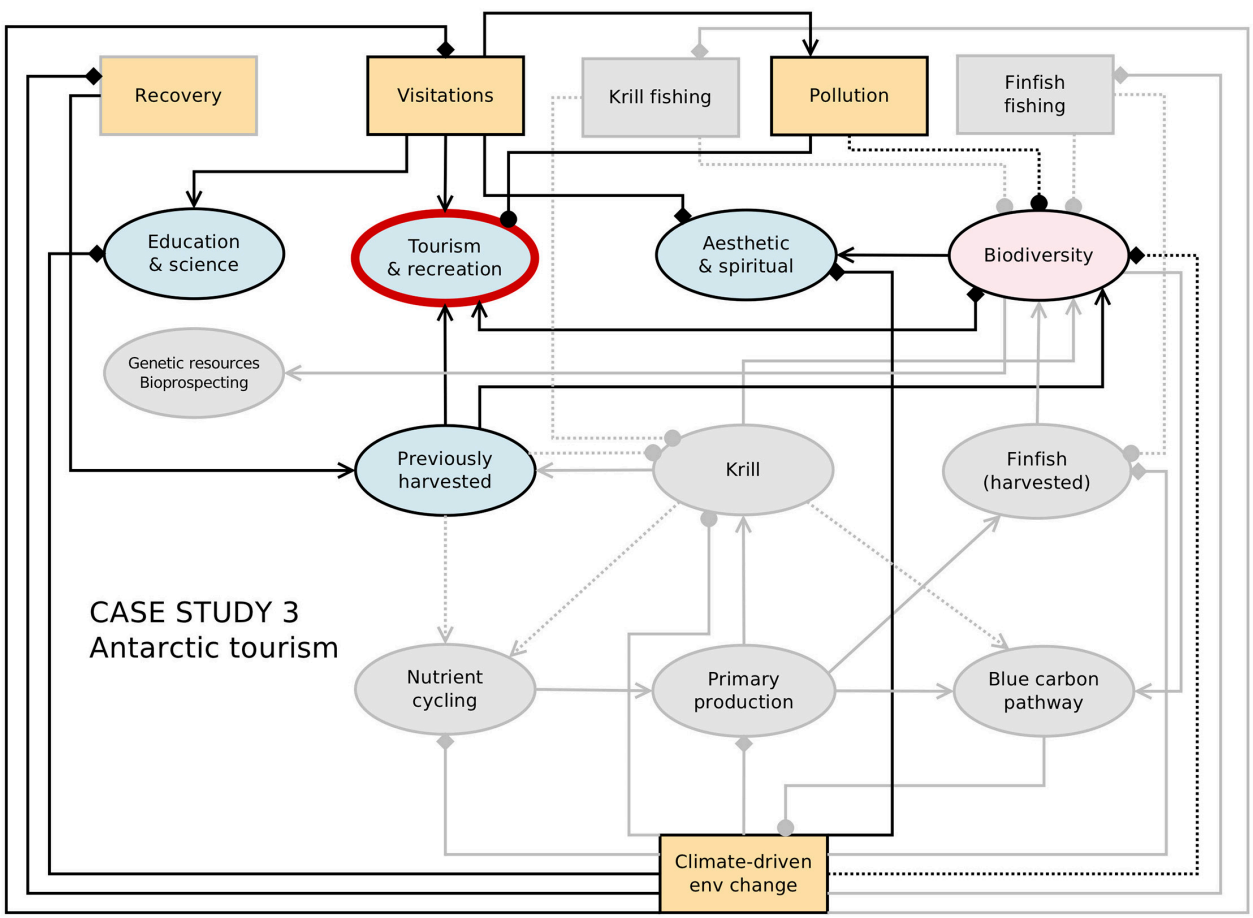

FIGURE 5 | Network representation of the links and feedbacks between ecosystem services and drivers (from **Figure 2**) with key elements for Antarctic tourism highlighted. Connections between components indicate the direction of effects from one node to another, as indicated in the legend. Diamonds indicate cases where the direction of the effect is not known or unclear (i.e., it could be positive and/or negative), and dashed lines represent uncertain or weak linkages.

Antarctica Tour Operators, IAATO), who may be prepared to promote Antarctic conservation messages in their home nations (Eijgelaar et al., 2010; Lamers et al., 2011).

The non-linear relationship between environmental degradation and attraction to tourism should also be considered. Meredith et al. (2019) cite the increase of 'last chance tourism' whereby tourists explicitly seek to experience vanishing landscapes or seascapes, endangered wildlife, and natural and social heritage, before they disappear (Lemelin et al., 2010; Lamers et al., 2013; Meredith et al., 2019).

Current management/existing policy for the ES

The Antarctic Treaty Consultative Meeting (ATCM) has responsibility for managing tourism activities in Antarctica, in accordance with the objectives of the ATS, and has put in place international agreements to regulate Antarctic tourism (Liggett et al., 2011; Bastmeijer, 2013; Jabour, 2014). All tourism operators undertaking activities under the jurisdiction of nations that are signatories to the Protocol on Environmental Protection to the Antarctic Treaty must also comply with the Protocol. Since the Protocol entered into force in 1998, two Measures and several non-binding Resolutions have been adopted, including the 'General Principles of Antarctic Tourism' [Resolution 7 (2009)]. The ATCM has established Visitor Site Guidelines, currently for 42 locations, to direct tourist and national governmental operator activity in order to minimise human impact.

Tourist operators originating in nations that are not signatories to the Antarctic Treaty may not be bound by its agreements, including on tourism activities.

IAATO co-ordinates most tourism activities in Antarctica and represents the industry at the ATCM.

Adequacy of current management/policy with respect to change

Antarctic Treaty Parties have expressed concerns regarding the environmental impacts of tourism, impacts on wilderness values, difficulties in regulation and monitoring of the industry and effective sharing of tourism expertise and co-operation by Parties. However, little comprehensive ecological assessment and monitoring of tourist visitor locations has occurred, resulting in little evidence to support policy decision-making. Furthermore, Treaty Parties have been reluctant to agree more general limits on levels of tourism visitations.

Recommendations/what is needed?

Antarctic Treaty Parties have noted that to date, 'regulation of Antarctic tourism via the ATS has been largely reactive and that a more proactive, strategic vision for Antarctic tourism development and regulation is warranted' (Netherland and New Zealand., 2019).

The future of tourism expansion and regulation remains in doubt (Bastmeijer et al., 2008; Liggett et al., 2017) but development of a strategic vision that can be practically implemented will be necessary to limit potential impacts on Antarctica.

On the sub-Antarctic island of South Georgia (located just to the north of the Antarctic Treaty area), tourists pay a substantial landing fee for access to the island, with the income going to the Government of South Georgia and the South Sandwich Islands and used to fund environmental protection and management. A system whereby the tourism industry pays for access to Antarctic ecosystem services, as successfully used in many other parts of the world, previously did not gain agreement (see [7]ATCMXXXIX Final Report, para 245, Secretariat of the Antarctic Treaty, 2016), but reconsideration of this suggestion may be timely (Verbitsky, 2018).

DISCUSSION

The absence of a permanent human population, together with the remote and hostile nature of the Southern Ocean, constrains direct use of its ecosystem services (Grant et al., 2013b). Nevertheless, these services are of increasing global importance to remote beneficiaries, as is clear from the three case studies described above: the blue carbon pathway, the Antarctic krill fishery, and Antarctic tourism. That climate change has the potential to affect these important services is highlighted by Rogers et al. (2020) who concluded that "ecosystem services in the Southern Ocean will likely increase" by 2100. Our findings suggest that climate change will decrease the overall capacity of the Southern Ocean to supply ecosystem services even if there is an increase in the capacity to supply some services. We expect this reduction in provision to be accompanied by an increase in demand for most services.

We assert that in order to fully understand the consequences of climate change on the delivery of ecosystem services, it is necessary to factor in each stage of the risk pathway from climate to people, illustrated in **Figure 1**. Our stepwise approach tracks the effects of climate change from observed and projected habitat change (with associated uncertainty) through to impacts on ecosystem structure and processes, and the consequences for the capacity of ecosystems to support ecosystem service delivery. For example, the seasonal presence and extent of Antarctic sea ice will affect and be affected by future ocean heating. Disruptions to this important habitat for Southern Ocean biota will have multiple direct and indirect effects on ecosystem structure (e.g., distribution and connectivity) and processes (e.g., productivity), affecting a range of services, from supporting (e.g., primary production) and regulating (e.g., blue carbon pathway) to provisioning (e.g., Antarctic krill fishery) and cultural (e.g., Antarctic tourism). These services might also be impacted by other effects of ocean heating (e.g., degradation of habitat quality at lower latitudes) and those of other climate-related drivers. Increased ocean temperatures may be detrimental to krill and to Antarctic toothfish, but could also create the potential to target new species due to poleward range shifts (as is being observed in the Arctic; Frainer et al., 2017; also see Pinsky et al., 2018).

By combining information on the drivers of change and how they might affect the biological components that underpin each service, our assessment indicates that for the majority of Southern Ocean ecosystem services (with the exception of

[7]https://documents.ats.aq/ATCM39/fr/ATCM39_fr001_e.pdf, accessed September 2020.

BOX 1 | Research gaps and priorities.

A key priority is to conduct a comprehensive, spatially-resolved ecosystem services assessment of the Southern Ocean (Grant et al., 2013b; Hill and Grant, 2013) to provide a baseline against which projected changes can be evaluated. Fundamental to this is improved understanding of the mechanisms that link physical variables to ecological processes, their interactive effects, and connections to ecosystem services. We recommend that this work is undertaken within a framework that facilitates consideration of environmental, economic and social factors, enabling the wider implications of decisions to be evaluated (United Nations et al., 2014; Cavanagh et al., 2016a; IPBES, 2019; Bateman and Mace, 2020).

Our analysis identified key knowledge gaps which currently limit assessment of the future potential of Southern Ocean ecosystems to support ecosystem services. These relate primarily to (i) uncertainties in model projections of key habitat variables (particularly sea ice), and (ii) understanding of the interactive effects of projected changes in multiple habitat variables and how these will affect ecosystem services. Projections of Antarctic sea ice in CMIP6 (Coupled Model Intercomparison Project) models that are informing the IPCC's sixth assessment report are considered to be significantly improved compared with the previous set (CMIP5), but there is still a large intermodel spread. In particular, these updated models project sea ice loss over the 21st century in all scenarios, but confidence in the rate of loss is limited (Roach et al., 2020). There is a mismatch between the temporal scale of climate projections and those of ecological processes and policy responses. On the decadal timescales required for ecosystem-based management, future change will be dominated by natural variability of the climate system which is difficult to predict with current climate models (Cavanagh et al., 2017). However, given that directional ecosystem change is already being observed and that there are inherent lags in the capacity of management to respond to these changes, there is a need to consider and implement adaptive management responses now or in the near future. Our risk assessment approach should help in this regard, although future refinement will be useful to consider different scenarios at finer spatial and temporal scales.

Ecosystem models provide a tool to consider how changing habitat variables and multiple drivers might interact to affect particular species or networks of interacting species (e.g., Klein et al., 2018; Tulloch et al., 2019), and over what timeframes. But these models are yet to be directly applied in a systematic way to assess and project change in ecosystem service delivery. Ecosystem models might also assist in addressing uncertainty about how ecosystem structure and function respond to change, such as shifts in dominance of energy pathways, tipping points and emergence of new stable states. Significant changes in the configuration of ecological networks in Southern Ocean systems have the potential to cause non-linear changes in the capacity of these systems to support ecosystem services.

Improved forecasts of future demand for services are required. As indicated in the main text, changes in both the demand for and provision of ecosystem services vary between different regions of the Southern Ocean, with some, such as the south west Atlantic under particular pressure from tourism and fishing, and also experiencing rapid rates of climate-driven environmental change. The network models developed here could be used to directly simulate the effects of interacting drivers on the direction of change in ecosystem service provision at regional scales (e.g. at the scale of the MEASO assessment sectors; Constable et al., in preparation).

A further challenge for end-to-end ecosystem modelling (and bioeconomic modelling) with respect to assessment and prediction of provisioning ecosystem services (particularly fisheries) is to resolve whether the emergence of new target species due to climate-driven poleward range shifts or even targeting mesopelagic fish (as indicated in Rogers et al., 2020) might have the capacity to bolster resilience of Southern Ocean fisheries and support delivery of provisioning ecosystem services into the future. This uncertainty does not obviate the need to factor climate change into management of current target species, given the key ecological roles of both krill and toothfish.

the blue carbon pathway and nutrient cycling) the risk from climate change ranges from *intermediate* to *high-level*. Although detailed quantitative and region-specific information is currently lacking on, for example, the magnitude of change in the different drivers and their impact on ecosystem structure and processes, we suggest that conveying climate change impacts in terms of overall risk to ecosystem services is useful for decision-makers. The information on the components contributing to the risk assessment (including levels of confidence) (**Tables 1**, **2**), can be used to inform decisions and to highlight gaps in knowledge, uncertainty and priorities for future work to further our understanding of change (see **Box 1**). The inclusion of the case studies has allowed us to explore the risk pathways of three of the services in more detail.

The blue carbon pathway case study reflects our assessment of *low-level* risk for this ecosystem service through the detail it provides on the positive effects of aspects of climate-driven change, and how they influence biological components crucial to the functioning of the pathway. These positive effects arise primarily from moderate warming and the loss of ice (sea ice, glaciers, and ice shelves). However, the case study cautions that if climate-driven changes continue to increase, some benefits may be lost. Temperature increases beyond 1°C might start to threaten the survival of important species, and increasing ocean acidification may mean that carbon storage is slower and sequestration more difficult. In addition, negative effects such as benthic habitat destruction from increased ice scour need to be factored in, albeit on more localised scales. In the case of the Antarctic krill fishery we assess the risk to be *high-level* based on the predominantly negative impacts of changes to sea ice, ocean warming and ocean acidification. The case study discusses the complexity of such changes on the biological components that support the fishery, with further contraction of krill habitat and declines in productivity of the krill stock expected. The uncertainty regarding the effects of acidification on krill highlights the need to carefully consider the information underlying the risk assessment, although the overall risk of climate change to the fishery would still be considered *high-level* with or without this driver. The importance of ocean circulation is also discussed in that changes in mean flow and eddy variability have the potential to affect krill distribution, thus highlighting the need for further consideration of the "grey areas" (**Table 2**) in the risk assessment. Moreover, climate change may bring limited benefits to some krill life stages.

The case studies also demonstrate that the effects of climate change need to be considered alongside other factors that may affect ecosystem services, and that regional-scale differences in the impacts of change, as well as in the demand and use of services, must be taken into account. It is noteworthy that the strongest effects of climate change occur in the main region in

which the krill fishery operates. As described in the tourism case study, the Antarctic Peninsula region has not only experienced dramatic climate-driven changes, it is also the area most visited by tourists. Climate change impacts such as loss of sea ice may increase tourist interactions with Antarctic ecosystems and wildlife by potentially facilitating access to new locations and affecting the range of wildlife present at established landing sites. The demand for, and global importance of, Southern Ocean ecosystem services seems set to increase during the 21st century (Chown and Brooks, 2019; Rogers et al., 2020). This may increase the use of some services (e.g. fisheries and tourism), depending on how demand is managed. Indeed, as discussed in Case Study 2, demand for krill products could increase as the krill stock declines, especially if ecosystem degradation diminishes the capacity of ecosystems elsewhere to supply the food needs of a growing human population. Case Study 3 mentions the emergence of 'last chance tourism' whereby tourists seek to experience vanishing landscapes or threatened wildlife species.

The combined effects of increased demand and climate change impacts on supply poses a significant challenge for the conservation of Southern Ocean ecosystems and management of activities that affect them. These activities, including fishing and visitation (tourism, education, and research), are part of a group of potential drivers of ecosystem change that also includes the recovery of previously harvested species such as whales (see Morley et al., 2020 and Grant et al., in preparation) (**Figure 2**). The majority of these drivers are influenced by global issues external to the region, including socio-economic drivers (Murphy et al., in preparation). The case studies discuss some of these, including non-indigenous species establishments and pollution in the context of the blue carbon pathway. In addition to climate change, the productivity of the krill stock might also be affected by factors such as the recovery of depleted whale populations and the extent to which the krill stocks are impacted by fishing. Our representation of the network of connections between ecosystem services, ecosystem structure and processes, climate change, and other important drivers provides a basis for understanding the complexity of interactions. For instance, krill fishing has the potential to impact every other service in the network through its interaction with the krill population (**Figure 2**), e.g., increased krill fishing could impact the blue carbon pathway through disrupting carbon flux to deep water via krill faecal pellets or moulted exoskeletons (Cavan et al., 2019; Manno et al., 2020). Furthermore, the effects of climate change on supporting services, such as the projected overall increase in primary production, will also have implications for provisioning services. Policy interventions that target critical interactions might be necessary to maximise resilience. A next step is to develop models based on our network representation to identify critical interactions and pathways (**Box 1**).

While demand for Southern Ocean ecosystem services may be increasing, our assessment of their future state assumes the maintenance of existing measures within the ATS to manage the impacts of human activities now and into the future. For example, we assume maintenance of CCAMLR's current operational fisheries management approach and no significant increase in fishing effort. At present the area under CCAMLR management constitutes 10% of the Earth's sea areas but has the lowest annual fisheries catch of any ocean; equivalent to c. 0.5% of global marine capture fishery production. Existing conservation and management actions through the ATS regulate fishing, tourism, scientific research and other human activities, with the overarching aim of minimising impacts on Antarctic ecosystems, and thus the services they provide (although the maintenance of ecosystem services is not stated as an explicit aim). Management actions may in some cases help to protect several ecosystem services simultaneously. For example the prohibition of all bottom trawling activities in the CCAMLR Convention Area reduces impacts on benthic ecosystems and thus contributes to the protection of demersal fish stocks and the blue carbon pathway. Large scale conservation actions, such as the 1.55 million km^2 no-take zone of the Ross Sea region Marine Protected Area, may also help to protect multiple ecosystem services at the regional scale. However, management is often limited to local scales, for example, limits on krill fishing in nearshore areas, protection of VMEs, or restrictions on numbers of tourists at landing sites. At all scales, management actions implemented under the instruments of the ATS may help to limit the potential effects of other human activities that might otherwise exacerbate the impacts of climate change. Ecosystems that are protected from these additive effects might be more resilient than those that are not. The recommendations from the case studies in this paper provide a compelling case to explicitly consider a wider range of ecosystem services within the ATS, the key being to ensure that precautionary measures are in place to minimise impacts on them. However, none of these measures alone can prevent climate-driven changes to Southern Ocean ecosystems. Given the risks presented by climate-driven change, the provision of Southern Ocean ecosystem services into the future is therefore heavily reliant on global policy and action on climate change, particularly the UNFCCC Paris Agreement, which must be implemented in addition to local and regional management measures in order to protect ecosystem health in the longer term.

Despite their global importance, there is limited recognition of the wide range of benefits people receive from polar ecosystems (Meredith et al., 2019; Pertierra and Hughes, 2019). Beyond the more obvious direct-use benefits there is an array of non-use values, such as bequest (knowledge of benefits being used by future generations) and existence (knowledge that species and ecosystems continue to exist) values (Grant et al., 2013b). These present some persuasive reasons for conservation (Chan et al., 2012). Indeed CCAMLR's precautionary approach to management encompasses non-use values such as conserving resources for future use and the avoidance of irreversible decisions (**Supplementary Table S2**); see Roberts et al. (in preparation) and Solomonsz et al. (in preparation) for more detailed consideration of cultural values and connections. Conducting a comprehensive ecosystem services assessment of the Southern

Ocean, including consideration of the relative value of each service, as recommended by Hill and Grant (2013), remains a key priority. In the meantime, our assessment of potential change should be regarded as relative to an uncertain baseline. An important challenge in evaluating potential change to Southern Ocean ecosystem services is that the current capacity of the ecosystem to support these services is poorly understood. Our structured approach and risk assessment provides an important step toward comprehensive, spatially-resolved assessments of Southern Ocean ecosystem services, and highlights the potential benefits of this approach in conservation and management decision-making, particularly in terms of considering risk and trade-offs. Increased consideration of the linkages and feedbacks between these services may assist in developing robust management responses into the future.

SUMMARY STATEMENTS

(1) The demand for, and global importance of, Southern Ocean ecosystem services is set to increase over the 21st century.
(2) Climate change effects on Southern Ocean habitats, foodwebs and ecosystems will affect the provision of Southern Ocean ecosystem services.
(3) In general, climate change poses an *intermediate* to *high-level* risk for Southern Ocean ecosystem services, but there are some cases where climate change might increase the capacity of Southern Ocean ecosystems to support ecosystem services, at least in the medium-term.
(4) Increased consideration of the linkages and feedbacks between these services may assist in developing robust management responses into the future.

KEY MESSAGES FOR POLICY MAKERS

(1) Southern Ocean ecosystem services are globally important. Examples include the three case studies in this paper (blue carbon pathway; Antarctic krill fishery; Antarctic tourism).
(2) These ecosystem services are generally at *intermediate* to *high-level* risk due to climate change drivers.
(3) Existing management actions within the Antarctic region are focused on the regulation of fishing, tourism, and other human activities.
(4) There are trade-offs between the extent to which the benefits of different ecosystem services can be realised, due to the complexity of interactions between different services and the drivers that affect them.
(5) Despite their global importance, understanding of Southern Ocean ecosystem services lags behind the understanding of ecosystem services in the rest of the world.
(6) A spatially-resolved baseline assessment is therefore lacking and urgently needed.

DATA AVAILABILITY STATEMENT

The data analysed in this study is the information compiled in the IPCC Special Report on the Ocean and Cryosphere in a Changing Climate (IPCC, 2019) which can be found here: https://www.ipcc.ch/srocc/.

AUTHOR CONTRIBUTIONS

RC, SG, and SHi conceived the study. RC led the study and writing of the manuscript. JM-T, SHi, and SG contributed substantially to developing the manuscript. DB, SHi, and KH led the writing of the case studies. SHa, MM, EM, and RT contributed to writing the manuscript. SHi, RC, JM-T, and SG designed **Figure 1** with assistance from the MEASO Support Group. JM-T produced **Figures 2–5**.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.615214/full#supplementary-material

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REVIEW
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A Review and Meta-Analysis of Potential Impacts of Ocean Acidification on Marine Calcifiers From the Southern Ocean

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Understanding the vulnerability of marine calcifiers to ocean acidification is a critical issue, especially in the Southern Ocean (SO), which is likely to be the one of the first, and most severely affected regions. Since the industrial revolution, ∼30% of anthropogenic CO_2 has been absorbed by the global oceans. Average surface seawater pH levels have already decreased by 0.1 and are projected to decline by ∼0.3 by the year 2100. This process, known as ocean acidification (OA), is shallowing the saturation horizon, which is the depth below which calcium carbonate ($CaCO_3$) dissolves, likely increasing the vulnerability of many resident marine calcifiers to dissolution. The negative impact of OA may be seen first in species depositing more soluble $CaCO_3$ mineral phases such as aragonite and high-Mg calcite (HMC). Ocean warming could further exacerbate the effects of OA in these particular species. Here we combine a review and a quantitative meta-analysis to provide an overview of the current state of knowledge about skeletal mineralogy of major taxonomic groups of SO marine calcifiers and to make projections about how OA might affect a broad range of SO taxa. We consider a species' geographic range, skeletal mineralogy, biological traits, and potential strategies to overcome OA. The meta-analysis of studies investigating the effects of the OA on a range of biological responses such as shell state, development and growth rate illustrates that the response variation is largely dependent on mineralogical composition. Species-specific responses due to mineralogical composition indicate that taxa with calcitic, aragonitic, and HMC skeletons, could be at greater risk to expected future carbonate chemistry alterations, and low-Mg calcite (LMC) species could be mostly resilient to these changes. Environmental and biological control on the calcification process and/or Mg content in calcite, biological traits, and physiological processes are also expected to influence species-specific responses.

Keywords: carbonate mineralogy, magnesium, aragonite, climate change, vulnerability, Antarctica, saturation horizon

INTRODUCTION

Since the industrial revolution, the concentration of carbon dioxide (CO_2) released to the atmosphere has increased from 280 to above 400 μatm due to human activities such as burning of fossil fuels and deforestation. Approximately 30% of this has been absorbed by the oceans (Feely et al., 2004). This results in changes in seawater CO_2 chemistry [e.g., oceanic partial pressure of CO_2 (pCO_2), pH, bicarbonate concentrations ($[HCO_3^-]$), calcium carbonate ($CaCO_3$) saturation state (Ω)], a process known as ocean acidification (OA) (**Figure 1**). In particular, OA induces an increase in pCO_2 and $[HCO_3^-]$ and a decrease in pH and Ω, which is a function of $[CO_3^{2-}]$ and calcium ion concentrations ($[Ca^{2+}]$) expressed as

$$\Omega = [Ca^{2+}][CO_3^{2-}]/K_{sp}$$

where K_{sp} is the solubility product, which depends on the specific $CaCO_3$ mineral phase, temperature, salinity, and pressure (Zeebe, 2012).

Surface waters are naturally supersaturated with respect to carbonate ($\Omega > 1$), where the highest $[CO_3^{2-}]$ is found as a result of surface photosynthesis. The $[CO_3^{2-}]$ decreases, and the solubility of $CaCO_3$ minerals (such as aragonite) increases, with depth due to the increased pressure and lower temperature. Thus, Ω is greater in shallow, warm waters than in cold waters and at depth (Feely et al., 2004). Current aragonite saturation in Southern Ocean (SO) surface waters ranges from Ω_{Ar} of 1.22 to 2.42, compared with values of 3.5 to 4 in the tropics (Jiang et al., 2015), and varies spatially, e.g., across ocean basins and with depth, and seasonally. However, OA is both decreasing saturation levels and shallowing the carbonate saturation horizon, which is the depth below which $CaCO_3$ can dissolve ($\Omega < 1$). This is likely to increase the vulnerability of $CaCO_3$ sediments and many marine calcifiers ($CaCO_3$ shell/skeleton-building organisms) to dissolution (Haese et al., 2014). As $CaCO_3$ sediments have important roles in global biogeochemical cycling and provide suitable habitat for many marine calcifying species, undersaturated seawater conditions will lead to unprecedented challenges and alterations to the function, structure, and distribution of carbonate ecosystems exposed to these conditions (Andersson et al., 2008).

The processes underlying organisms' vulnerabilities to OA have been much discussed between biologists and chemists (e.g., Waldbusser et al., 2015, 2016; Cyronak et al., 2016a,b). While some studies highlight how the energetic cost of calcification increases with decreasing Ω (Waldbusser et al., 2016), other studies indicate that Ω *per se* may not always be a good indicator, and that it is important to consider other components of carbonate chemistry, and the biocalcification process (Roleda et al., 2012; Fassbender et al., 2016). For instance, some studies illustrate that the reduction in seawater pH is the main driver of changes in calcification rates (the production and deposition of $CaCO_3$), rather than the reduction in $[CO_3^{2-}]$ (Roleda et al., 2012; Cyronak et al., 2016b), with a projected drop in calcification rates by 30 to 40% by mid-century due to OA (Kleypas et al., 1999). Future studies should attempt to tease apart the influence of Ω and pH on calcification, which are not mutually exclusive, to improve our predictions of OA long-term effects in marine calcifiers.

A number of marine calcifiers, particularly benthic populations from the tropics and deep waters, are already exposed to undersaturated conditions with respect to their species-specific mineralogies (Lebrato et al., 2016). This suggests these organisms have evolved compensatory physiological mechanisms to maintain their calcified structures (Lebrato et al., 2016). This does not mean that all taxa can adapt to rapid decreases in the Ω, rather it illustrates the complexity of taxon-level responses. For instance, SO marine calcifiers may be particularly sensitive to these changes since the SO is characterized by a much lower natural variability in surface ocean $[CO_3^{2-}]$ (Conrad and Lovenduski, 2015) relative to the rate of projected change (Turley et al., 2006). For species with some biological control over calcification and other physiological processes, we can expect variation in responses depending on local adaptation. Species inhabiting coastal areas, which naturally experience rapid fluctuations in environmental conditions, compared to the open ocean (e.g., from ice melting, phytoplankton blooms, corrosive upwelling events), may have a greater level of resilience and/or adaptation to changes in CO_2 exposures (Fassbender et al., 2016; Vargas et al., 2017).

Seawater pH levels have already decreased by 0.1 since ∼1850, and are predicted to decline by ∼0.3 (851–1,370 μatm) by the year 2100 (IPCC, 2014, 2019). The long-term persistence of calcifying taxa is dependent upon calcification exceeding the loss of $CaCO_3$ that occurs through breakdown, export, and dissolution processes (Andersson and Gledhill, 2013). Therefore, even though species-specific responses to OA are expected, a tendency toward reduction in overall $CaCO_3$ production at the local or community level is anticipated (Andersson and Gledhill, 2013) with potentially adverse implications across SO ecosystems.

Southern Ocean Acidification

The SO, which covers about 34.8 million km^2, is widely anticipated to be the one of the first, and most severely affected region from OA due to naturally low levels of $CaCO_3$, the increased solubility of CO_2 at low temperatures, and a lower buffering capacity (Orr et al., 2005; Fabry et al., 2009). Thus, understanding the vulnerability of Antarctic marine calcifiers to OA is a critical issue, particularly in Antarctic Peninsula, which is also one of the fastest warming areas on Earth (Vaughan and Marshall, 2003). To establish the potential threat of OA to SO marine calcifiers, it is crucial to consider different factors that may influence the vulnerability of their skeletons to OA. These include interacting factors (e.g., warming), the local seasonal and spatial variability in seawater carbon dioxide chemistry, the distribution of sedimentary $CaCO_3$ (which provides suitable habitat for many benthic calcifiers), and a range of different phyla and species with diverse geographic range, skeletal mineralogies, biological traits, physiological processes, and strategies to compensate for pH changes.

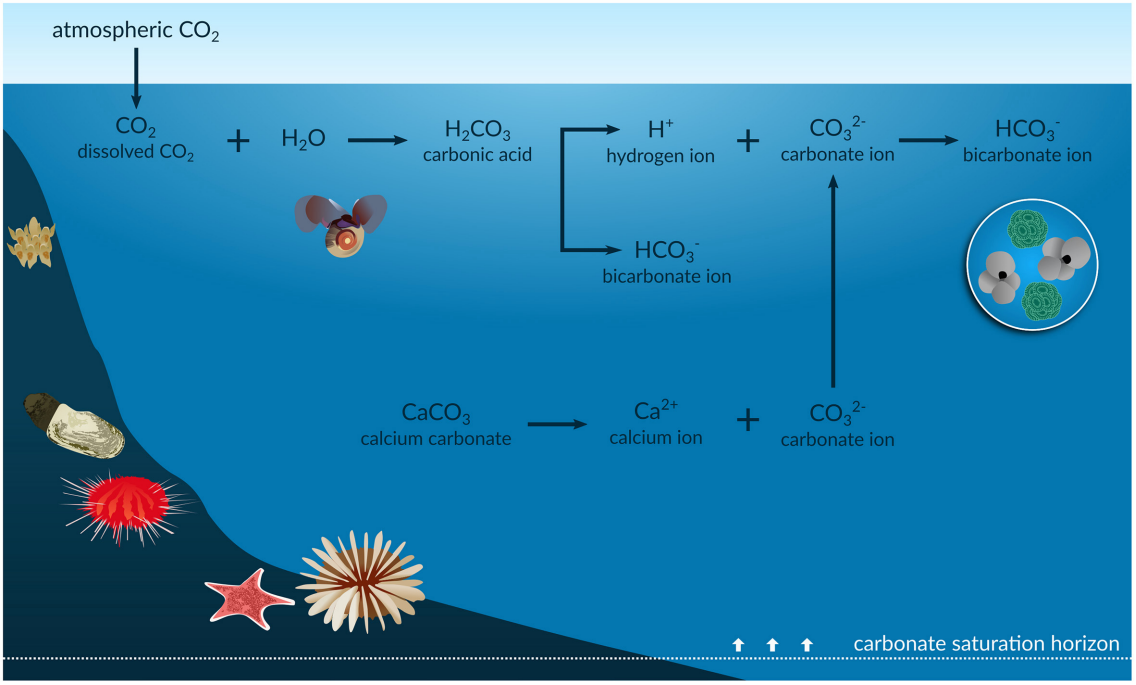

FIGURE 1 | Infographic of the ocean acidification process. The anthropogenic CO_2 absorbed by the oceans results in an increase in the concentration of hydrogen ions (H^+) and in bicarbonate ions (HCO_3^-) and a decrease in carbonate ions (CO_3^{2-}). The reduction in CO_3^{2-} is shallowing the carbonate saturation horizons, with potential impacts on shells and skeletons of marine calcifiers such as foraminifera, corals, echinoderms, molluscs, and bryozoans.

Local Seasonal and Spatial Variability in Seawater Carbon Dioxide Chemistry

Differences in solar irradiance and temperature, which can lead to changes in the duration of primary production, modify seawater CO_2 chemistry seasonally, and latitudinally (Takahashi et al., 2002; Racault et al., 2012; Kapsenberg and Cyronak, 2019). For instance, seawater pH and Ω_{Ar} increase during phytoplankton blooms in Austral summer (McNeil et al., 2011; Kapsenberg et al., 2015). While SO areas with higher primary productivity could act as spatial refugia, studies are needed to test whether seasonally high pH may benefit marine calcifiers (Kapsenberg and Cyronak, 2019).

The depth of the present-day SO Aragonite Saturation Horizon (ASH) exceeds 1,000 m across most of the basin, while naturally shallower saturation horizons (~400 m) occur in the core of the Antarctic Circumpolar Current due to upwelling of CO_2-rich deep water (Negrete-García et al., 2019). The Calcite Saturation Horizon (CSH) is much deeper (>2,000 m in some parts of the SO) than the ASH, since aragonite is more soluble than calcite (Feely et al., 2004; Barnes and Peck, 2008). It is thus projected that the ASH will reach surface waters earlier than the CSH (McNeil and Matear, 2008). In particular, it is anticipated that aragonite in some SO regions (south of 60°S) will be undersaturated by 2050 (Orr et al., 2005; McNeil and Matear, 2008) and that 70% of the SO could be undersaturated by 2100 (Hauri et al., 2016). OA will drive even the least soluble form of calcium carbonate, calcite, to undersaturation by 2095 in some SO waters (McNeil and Matear, 2008). However, the depth and year of emergence of a shallow ASH still vary spatially due to natural variation in the present-day saturation horizon depth and in the physical circulation of the SO (Negrete-García et al., 2019).

Aragonite undersaturation in surface waters is projected initially during the austral winter (Conrad and Lovenduski, 2015; Negrete-García et al., 2019) as the $[CO_3^{2-}]$ of surface waters decrease south of the Polar Front due to the strong persistent winter winds that promote the upwelling of carbonate-depleted deep waters (Orr et al., 2005). In addition, lower temperatures enhance uptake of atmospheric CO_2 (Orr et al., 2005). Specifically, several studies (McNeil and Matear, 2008; McNeil et al., 2010; Mattsdotter Björk et al., 2014) have projected that wintertime aragonite undersaturation will occur by 2030 in the latitudinal band between 65 and 70°S where deep-water upwelling occurs. Recently, Negrete-García et al. (2019) considered that the rate of change, and therefore the onset of aragonite undersaturation, was occurring more rapidly than previously projected. These forecasted changes imply there will be a sudden decline in the availability of suitable habitat for diverse SO taxa such as pteropods, foraminifera, cold-water corals, and coralline algae in the near-future (Negrete-García et al., 2019).

Distribution of Carbonate Sediments

The distribution of sedimentary $CaCO_3$ on the Antarctic shelves displays distinct regional and depth patterns (Hauck et al., 2012). This is evident from the deposition and preservation of carbonates in the surface sediments. These are driven by

the flux of organic matter to the ocean floor (related to primary production) and its respiration and remineralization in the sediments, transport of carbonate material by currents, and Ω of the water mass above the sediment (Hauck et al., 2012). In particular, an enhanced flux of organic matter to the seafloor increases respiration in sediments and alters carbonate chemistry. $CaCO_3$ content of shelf surface sediments is usually low, however high values (>15%) of $CaCO_3$ occur at shallow water depths (150–200 m) on the narrow shelves of the eastern Weddell Sea and at a depth range of 600–900 m on the broader and deeper shelves of the Amundsen, Bellingshausen, and western Weddell Seas (Hauck et al., 2012).

Regions with high levels of primary production, such as the Ross Sea and the western Antarctic Peninsula, generally have low $CaCO_3$ contents in the surface sediments as carbonate produced by benthic organisms is subsequently dissolved and thus not preserved. Conversely, carbonate contents of sediments in areas of low levels of primary productivity reflect the concentration of planktonic foraminifera that are especially abundant in sea ice (Hauck et al., 2012). As carbonate-rich sediments on the continental shelf can rapidly react to the decreasing Ω with respect to carbonate minerals (Haese et al., 2014), OA will potentially have critical implications to their distribution and, consequently, the habitats of benthic organisms.

Carbonate Mineral Composition of Shells and Skeletons

Ocean acidification will not only impact carbonate mineral composition in surface sediments of coastal and continental shelf environments but also on diverse shelf assemblages of marine calcifiers. Globally, most scleractinian cold-water corals (>70%) will be exposed to undersaturated conditions by 2100 when the ASH is expected to reach surface waters (Guinotte et al., 2006; Turley et al., 2007). Many SO organisms are expected to be unable to adapt to projected rapid changes, as this region is characterized by low interannual variability in surface ocean $[CO_3^{2-}]$ (Orr et al., 2005; Conrad and Lovenduski, 2015). OA may consequently impact biomineralization of their skeletons and promote their dissolution (Andersson et al., 2008; Fabry, 2008). Currently, studies of OA impact on organisms are few, and therefore, further studies are required to better understand the influence of carbonate chemistry on marine calcifiers, as mentioned above.

While there is great uncertainty in the predictions of "winners" and "losers" under forecasted global-change, the $CaCO_3$ form of shells and skeletons, when combined with other biological traits, could be a key factor in determining their response to change. Carbonate shells and skeletons may be composed of three different phases: aragonite, calcite and Mg-calcite. Calcite and aragonite are polymorphs (different mineral structure) of $CaCO_3$. Mg-calcite has the same mineral structure as calcite but some Ca^{2+} ions have been replaced by Mg^{2+} ions. These $CaCO_3$ minerals have different physical and chemical properties. The structure of aragonite is known to be less stable, and thus more soluble, than that of calcite. A high percentage of marine calcifiers incorporate significant amounts of Mg into their skeletons, which additionally reduces mineral stability. Their shells and skeletons are categorized as low-Mg calcite (LMC; 0–4 wt% $MgCO_3$), intermediate-Mg calcite (IMC; 4–8 wt% $MgCO_3$), and high-Mg calcite (HMC; >8 wt% $MgCO_3$) (Rucker and Carver, 1969). Thus, HMC shells or skeletons are also more soluble than those comprised of LMC and pure calcite and even, in some situations, aragonite; consequently, they may be most susceptible to OA impacts (Andersson et al., 2008; Fabry, 2008).

Energetic cost associated with acid-base regulation in response to OA is another important issue to consider OA impacts, which may even have more influence on the species sensitivity to OA than the $CaCO_3$ composition of their shell or skeleton (Collard et al., 2015; Duquette et al., 2018). The increase in energetic investment into acid-base regulation may lead to a decrease allocation to other functions such as reproduction, growth or calcification.

Ocean warming could further exacerbate the effects of OA in species with Mg-calcite shells/skeletons, as Mg content in calcite generally increases with seawater temperature and thereby further accelerates skeletal solubility. Ocean warming, in combination with OA, is thus forecasted to increase the vulnerability of some marine calcifiers, particularly taxa depositing more soluble $CaCO_3$ mineral phases (aragonite or HMC) (Andersson et al., 2008). However, the IMC or LMC cold-water species are potentially less soluble than those from warmer waters, and could also be at increased risk to near-future OA, as Antarctica is acidifying at a faster rate than much of the rest of the global ocean (Fabry et al., 2009). In addition, species with known limited thermotolerance and/or mobility (e.g., some cold-water species) are of particular concern, as they may not be able to shift their distribution to higher latitudes and/or deeper waters, to respond to these changing conditions.

Information on skeletal mineralogy of Antarctic marine calcifiers is currently limited and biased to only a small number of taxa, and to specific geographic and bathymetric ranges (Borisenko and Gontar, 1991; Taylor et al., 2009; McClintock et al., 2011; Figuerola et al., 2015; Krzeminska et al., 2016; IPCC, 2019). For instance, little attention has been paid to Antarctic benthic communities from the deep-sea and important areas such as the Vulnerable Marine Ecosystem (VME) in East Antarctica (Post et al., 2010). These communities are characterized by high levels of species richness in marine calcifiers, in particular habitat-forming bryozoans and hydrocorals (Stylasteridae) (Beaman and Harris, 2005; Post et al., 2010; Bax and Cairns, 2014).

Many studies have focused on the impacts of OA without considering its interactions with other environmental (e.g., warming, food quality, or salinity) and biological (e.g., skeletal growth rate) factors which are involved in mediating the susceptibility of marine calcifiers to OA, for example, through controlling the incorporation of Mg into the skeletal calcite (Chave, 1954; Andersson et al., 2008; Hermans et al., 2010; Sewell and Hofmann, 2011; Swezey et al., 2017). Here we review, and for the first time, provide a quantitative meta-analysis to give an overview of the current state of knowledge about skeletal mineralogy of major taxonomic groups of SO marine calcifiers; and utilize these findings to project future implications of OA impacts on different groups of organisms.

METHODS

In order to project how OA could impact SO marine calcifiers, environmental, and biological data for a broad range of organisms were compiled. These included species geographic range, skeletal mineralogy, the calcification responses, and strategies to overcome OA. Their $CaCO_3$ composition was reported as aragonite and/or calcite. Calcite composition was further classified as LMC, IMC and HMC (Rucker and Carver, 1969). Data previously reported as mol% $MgCO_3$ were converted to weight% (wt%) $MgCO_3$ for comparisons. Individual SO maps with species distributions were then produced for two groups (echinoderms and bryozoans) with Mg-calcite skeletons for which there is relatively good data and for benthic species identified here as particularly vulnerable to OA.

With the aim of performing a meta-analysis, a thorough database search was conducted to compile all peer-reviewed journal articles and literature reviews that investigated the effect of altered seawater carbonate chemistry on SO marine calcifiers. We conducted searches using three databases (ISI Web of Science, Scopus and Aquatic Sciences, and Fisheries Abstracts). Keywords used are provided in **Supplementary Table 1** (database searches completed May 2020). Articles were screened to include studies that manipulated the carbonate chemistry to investigate the effects of OA on specifically SO marine calcifiers. The CO_2 treatment levels were separated into two categories for the meta-analysis: ambient treatment and elevated CO_2/lowered pH treatment. The ambient treatment used from each study was the ambient treatment defined by the individual studies with obvious variation between these based on what is ambient at the particular study site/time of year (all ambient treatments were below 500 µatm). Due to the limited number of studies, all elevated CO_2/lowered pH treatments were combined for the meta-analysis. If a study had multiple elevated CO_2/lowered pH treatments, the highest value of treatment of these was included, and no treatments above 1,500 µatm CO_2 were included. After manual screening, 20 studies remained for inclusion in the meta-analysis (**Supplementary Figure 1**). Data included bivalves (Mollusca; Bivalvia), brachiopods (Brachiopoda), limpets (Mollusca; Gastropoda; Patellogastropoda), pteropods (Mollusca; Gastropoda; Pteropoda), sea snails (Mollusca; Gastropoda; Trochida), sea stars (Echinodermata; Asteroidea), sea urchins (Echinodermata; Echinoidea), and coccolithophores (Haptophyta; Coccolithophyceae). The effects of OA on the following biological responses were investigated: development (bivalves, sea stars, and sea urchins; fertilization rate or normal development), growth rate (brachiopods, pteropods and coccolithophores), shell state (bivalves, limpets, pteropods, and sea snails; adult calcification or dissolution rate), coccolith volume (coccolithophores), and survival (sea urchins). We analyzed the data following previous methods (Kroeker et al., 2010, 2013; Hancock et al., 2020). For each study the ln-transformed response ratio to OA was calculated using the formula

$$\mathrm{LnRR} = \ln(R) = \ln(\overline{X}_E) - \ln(\overline{X}_C)$$

where $\overline{X}_E$ and $\overline{X}_C$ are the mean value for the biological responses in the CO_2 experimental treatment and the ambient treatment, respectively (Hedges et al., 1999). We used the log response ratio (LnRR) due to its robustness to small sample sizes and its ability to detect true effects (Lajeunesse and Forbes, 2003). For all response ratios, a positive ratio is a positive response to OA, a negative response ratio is a negative response to OA, and a response ratio of zero indicates there is no effect of OA. These response ratios (LnRR) were then weighted by the variance (v), calculated by their associated standard error and sample size using

$$\upsilon = \frac{(S_E)^2}{n_E \overline{X}_E^2} + \frac{(S_C)^2}{n_C \overline{X}_C^2}$$

where S_E and S_C are the standard error for the experimental treatment mean and ambient (control treatment mean, respectively, and n_E and n_C are the sample size for the experimental mean and ambient (control) mean, respectively (Hedges and Olkin, 1985). Studies with a lower standard error and higher sample size were weighted more heavily than those with a higher standard error and lower sample size (Hedges and Olkin, 1985). Meta-analyses were conducted with all studies combined and separated based on the mineralogical composition of the study organism (as outline above) using the R package metafor (Viechtbauer, 2010) in R version 3.5.0 (R Core Team, 2018). We used a random-effects model to estimate a summary response ratio for each biological response in each CO_2 category, weighted by the inverse-variance weights (v). This model accounts for both random sampling variation in each study and the variation among studies in estimating the effect size. The true variation in effect size is calculated by the between-study variance (using the ln-transformed response ratios, LnRR), with each study weighted by the inverse sum of the individual study variance (v). We used restricted maximum-likelihood estimator (REML) to estimate the amount of (residual) heterogeneity (Q), which tests whether the variability in the effect size is larger than would be expected based on sampling variance alone (Brown and Kempton, 1994). Statistical significance of the mean response ratio was based on the 95% confidence interval on the estimated summary response ratio (Viechtbauer, 2010).

RESULTS

For the Mg calcite-producing species, the calcite composition was classified in a total of 123 species belonging to 89 bryozoan and 34 echinoderm species (**Supplementary Tables 2, 3**). Individual SO maps showed a general pattern of increase of Mg content in calcite toward lower latitudes in bryozoans and echinoderms (**Figure 2**).

Twenty studies on the effect of altered carbonate chemistry on marine calcifiers south of 60°S were included in the meta-analysis (**Supplementary Figure 1** and **Supplementary Table 4**). A total of 25 response ratios (two for bivalves, two for brachiopods, two for sea stars, nine for sea urchins, two for pteropods, one for a sea snail, one for patellogastropoda, and six for coccolithophores) were calculated from the 20 studies (some

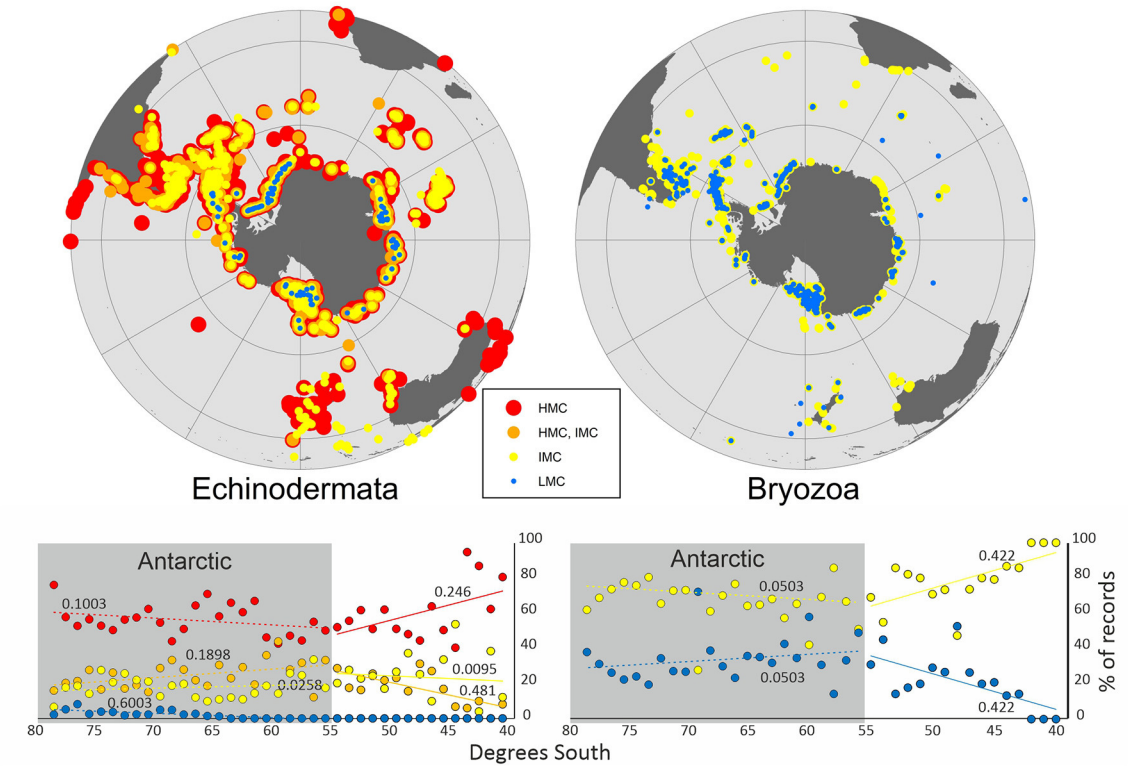

FIGURE 2 | General distribution patterns for Echinodermata (24 HMC, 3 HMC/IMC, 6 IMC, and 1 LMC species) and Bryozoa (59 IMC and 30 LMC species) based on Mg-calcite distribution in the Southern Ocean.

studies reported more than one experiment and/or species response). With all response ratios combined, there was a negative response to OA in marine calcifiers (**Figure 3**). However, significant heterogeneity was found ($Q = 48{,}669.264$, $df = 24$, $p < 0.001$; **Supplementary Table 3**), indicating that the variability between the studies is greater than expected by chance alone. The response varied depending on the mineralogical composition of the organism (**Figure 3**). Whilst there was a negative response to OA in calcitic, aragonitic, and HMC species, LMC species were mostly unaffected [noting there was limited data for this group with only three response ratios calculated from *Liothyrella uva* (Broderip, 1833)]. Significant heterogeneity was observed for aragonite, calcite and HMC ($p < 0.001$) but not for LMC ($Q = 0.6085$, $df = 1$, $p = 0.4354$; **Supplementary Table 3**). The echinoderms, *Sterechinus neumayeri* (Meissner, 1900) and *Odontaster validus* (Koehler, 1906), were sensitive to increased CO_2 above current levels (>500 μatm), with a negative effect on their development. The shell state and growth of the pteropod *Limacina helicina* (Phipps, 1774) and the shell state of the sea snail *Margarella antarctica* (Lamy, 1906) were negatively affected at moderate CO_2 levels (>800 μatm). The response was also negative in CO_2 treatments exceeding 1,000 μatm in the brachiopod *Liothyrella uva* (growth), the bivalve *Laternula elliptica* (P. P. King, 1832) (development and shell state), the coccolithophore *Emiliania huxleyi* (Lohmann) W.W. Hay & H. P. Mohler, 1967 (growth), and the sea urchin *S. neumayeri* (survival) (see **Supplementary Figure 1** for details).

Information on the vulnerability of a range of different common Antarctic phyla was assessed based on their mineralogy-related sensitivity and their strategies to overcome OA (**Table 1**).

EFFECTS OF OCEAN ACIDIFICATION ON SOUTHERN OCEAN CALCIFYING TAXA

It is predicted that marine calcifiers living in SO regions will be exposed to undersaturated seawater conditions with respect to aragonite by 2050 (Orr et al., 2005; McNeil and Matear, 2008) and with respect to calcite by 2095 (McNeil and Matear, 2008). The situation of some regions south of the Polar Front may be aggravated during austral winters (Orr et al., 2005), when wintertime aragonite undersaturation may occur as early as 2030 in the latitudinal band between 65 and 70°S (McNeil and Matear, 2008; McNeil et al., 2010; Mattsdotter Björk et al., 2014), and during the seasonal decline in primary production, when there is less biological drawdown of CO_2.

As the saturation horizon shoals, deep water calcifying species that currently live just above the saturation horizon may be amongst the earliest to be affected by OA (Turley et al., 2007). Many benthic organisms could potentially be affected

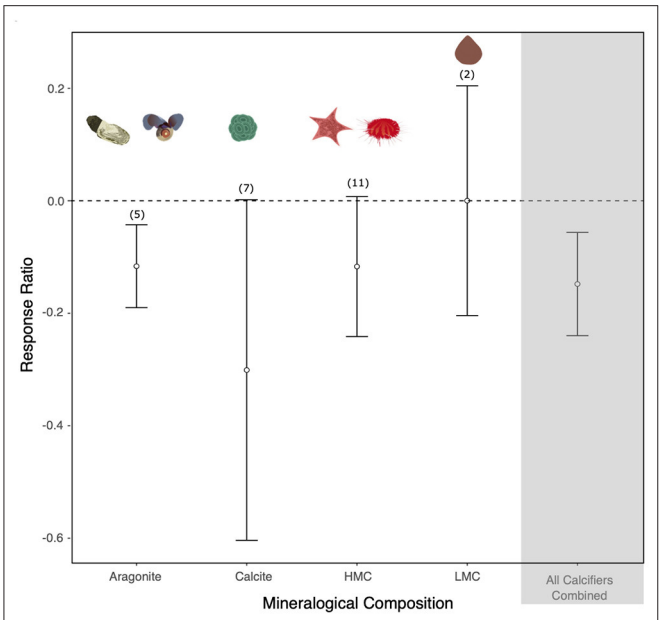

FIGURE 3 | The effect of ocean acidification on aragonitic, calcitic, high-Mg calcite (HMC), and low-Mg calcite (LMC) species. Mean response ratios and 95% confidence intervals are shown, with the number of data points in each category given in brackets. A mean response ratio of zero (hashed line) indicates no effect. Background shading indicates response ratios of all the phyla.

by reductions of their habitat, particularly those on the narrow shallow water shelves of the eastern Weddell Sea and deeper shelves of the Amundsen, Bellingshausen, and western Weddell Seas, which currently have higher levels of $CaCO_3$ in their sediments. As organic matter alters carbonate chemistry of sediments, species inhabiting regions where the flux of organic matter to the seafloor is expected to increase (e.g., new ice-free areas) could also be at risk. Although taxa characterized by broad bathymetric ranges and/or circumpolar distributions [e.g., *Laternula elliptica*, *Glabraster antarctica* (E. A. Smith, 1876), and *Sterechinus neumayeri*; **Figure 4**] may find temporary refuge in shallower waters, and/or in some SO areas where undersaturation may occur later (e.g., far from latitudinal band between 65 and 70°S), distribution shifts are also likely to be influenced by other environmental factors such as warming. However, further molecular studies are needed to determine if broad circumpolar and/or eurybathic ranges are actually separate cryptic species (Baird et al., 2011; Allcock and Strugnell, 2012).

Calcified invertebrates and plants perform important roles in Antarctic ecosystem functioning including: as important food sources (e.g., pteropods) for higher trophic levels such as carnivorous zooplankton, fishes and other predators; creating habitats used as spawning, nursery and feeding areas of higher trophic levels (e.g., corals, spirorbid polychaetes); as grazers or predators influencing the structure of benthic communities (e.g., echinoderms) (Dayton et al., 1974; Prather et al., 2013; Wright and Gribben, 2017); and/or contributing to marine carbon cycling and storage (e.g., foraminifera, coccolithophores, molluscs) (Lebrato et al., 2010). Some Antarctic calcifying species with circumpolar distributions and broad bathymetric ranges could be potential indicators or sentinel species of chemical changes in the SO if they show sensitivity to environmental changes (Dayton et al., 1974; Brandt et al., 2007; Barnes and Kuklinski, 2010; Figuerola et al., 2012). A number of factors determine the influence of OA on a species including its mineralogy, biological traits (including physiology), and environmental constraints (such as variation).

Mineralogy-Related Sensitivity to Ocean Acidification

Our meta-analysis of the known effects of the OA on a range of biological responses (development, growth rate, survival, and/or shell state) in relation to the mineralogy of SO calcifiers found that SO calcitic, aragonitic, and HMC species are likely to be more vulnerable to OA, whereas LMC species were found to be unaffected (**Supplementary Table 4**). However, the available data is currently limited and the need for further studies was reinforced. A series of earlier comprehensive global meta-analyses of responses to OA have also shown reductions in survival, calcification, growth, and development in a range of marine calcifiers in comparison to non-calcifying taxa (Kroeker et al., 2010, 2013). These meta-analyses concluded that organisms depositing high-Mg calcite could be more resilient to OA than those depositing calcite or aragonite, bringing into question the usefulness of simplified mineralogical composition in predicting organism sensitivities to OA (Kroeker et al., 2010). A subsequent constructive debate led to suggestions to improve the accuracy of predictions, such as including other biological variables as well as the mineralogical composition, and redefining the HMC category as skeletons containing >12 mol% $MgCO_3$ and excluding those with very complex mineralogy (e.g., crustaceans) (Andersson and Mackenzie, 2011; Kroeker et al., 2011). These studies also reinforced the need for more mineralogical studies to characterize a wider range of species. A more recent meta-analysis specifically investigated the effect of altered carbonate chemistry on marine organisms south of 60°S (from 60 studies) and found results consistent with the previous meta-analyses including reduced survival and shell calcification rates, increased dissolution in adult calcifying invertebrates, and a reduction in embryonic survival and larval development rates (Hancock et al., 2020). Some generalizations can be made for taxonomic groups, for example our study indicated that molluscs are one of the groups most sensitive to OA, whereas crustaceans are more resilient (**Table 2**). However, exceptions to such generalizations can be found within groups.

Recent studies have examined the relationships between variation in the mineralogical composition of Antarctic and sub-Antarctic marine calcifiers and decreasing seawater pH and greater solubility of HMC and aragonite. A hypothesized decrease of skeletal Mg-calcite along a depth gradient in four Antarctic bryozoan species was not supported (Figuerola et al., 2015), and nor was an hypothesized increase of aragonitic forms toward shallower waters in sub-Antarctic stylasterid populations

TABLE 1 | Potential vulnerability of a range of different common Antarctic phyla based on their mineralogy-related sensitivity and their strategies to overcome ocean acidification.

	Phylum	Class	Order	Taxa	Skeletal mineralogy	Impacts	Strategies to overcome OA	Vulnerability	References
Plankton	Mollusca	Gastropoda	Pteropoda	*Limacina helicina* (dominant species of pteropods)	Thin aragonitic shells	Levels of shell dissolution were observed in undersaturated conditions. Increased metabolic rates when exposed to projected pH and temperature changes. Larval development during winter pH minima	Outer organic layer (periostracum) that can protect the outer shell surface from dissolution	High	Bednaršek et al., 2012, 2014; Hoshijima et al., 2017
	Haptophyta (coccolithophores)	Prymnesiophyceae	Isochrysidales	*Emiliania huxleyi*	Delicate calcitic shells with low calcium carbonate content ("B/C" morphotype)		They produce calcified scales (coccoliths) in an intracellular compartment and secrete them to the cell surface	Medium	Müller et al., 2015
	Foraminifera	Globothalamea	Rotaliida	*Globigerina bulloides*	Calcitic shells	Reduced calcification when comparing modern shell weights with shells preserved in the underlying Holocene-aged sediments. Reduction of calcification and oxygen consumption as pH declined from 8.0 to 7.5		Medium	Moy et al., 2009; Davis et al., 2017
Benthos	Mollusca	Gastropoda	Trochida	*Margarella antarctica*	Aragonitic shells		Resilience to initial exposure to temperature and pH changes projected to occur over the next several 100 years (Ω_{Ar} and Ω_{Ca} >1.10)	Medium	Schram et al., 2016
			Patellogastropoda	*Nacella concinna*	Calcitic shells		Resilience to initial exposure to temperature and pH changes projected to occur over the next several 100 years (Ω_{Ar} and Ω_{Ca} >1.10)	Medium	(Schram et al., 2016)
		Bivalvia	Not assigned	*Laternula elliptica*	Aragonitic shells	Shell dissolution and slower development of larvae under Ω_{Ar} 0.79–0.52 (pH 7.80–7.65)	Upregulation in expression of chitin synthase. External organic layer (periostracum) may provide protection from ambient seawater	High	Cummings et al., 2011; Bylenga et al., 2017

(Continued)

TABLE 1 | Continued

Phylum	Class	Order	Taxa	Skeletal mineralogy	Impacts	Strategies to overcome OA	Vulnerability	References
Cnidaria	Anthozoa	Scleractinia	*Desmophyllum dianthus*, *Solenosmilia* sp. and *Madrepora* sp	Aragonitic skeletons	Studies using *D. dianthus* from other areas suggest that the projected combination of rising temperatures and ocean acidification may severely impact this cold-water coral species. Some species have limited larval dispersal, which will affect the potential for recovery of these species	Some species can regulate the pH of their calcifying fluid	High	Miller et al., 2011; Margolin et al., 2014; Gori et al., 2016
	Hydrozoa	Anthoathecata	Stylasterid species	Aragonitic and calcitic skeletons			Medium	(Cairns and Macintyre, 1992; Bax, 2015)
Arthropoda	Malacostraca	Decapoda	*Paralomis birsteini*	Robust, calcitic exoskeletons		High levels of mobility/activity. Crustaceans generally have exoskeletons which are enclosed within epicuticles	Low	Ries et al., 2009; Steffel et al., 2019
Rhodophyta	Florideophyceae	Corallinales		HMC skeletons (8–18 wt% $MgCO_3$)		External organic layers that provide protection from ambient seawater	High	Irving et al., 2005; Ries et al., 2009
Porifera	Calcarea			HMC spicules ($\leq$15 wt% $MgCO_3$)	Likely vulnerable as we know very little about this sponge class. More than half of calcareous sponge species are endemic to this region. There are a few deep-sea calcarea, these may not be as affected	Strategies	Not known (data deficient)	Smith et al., 2013a
Echinodermata	Most species are HMC. Sea stars and brittle stars are the most vulnerable echinoderm groups						High	Ries et al., 2009; McClintock et al., 2011
	Asteroidea	Valvatida	*Glabraster antarctica*	HMC			High	McClintock et al., 2011; Moore et al., 2018
	Echinoidea	Camarodonta	*Sterechinus neumayeri*	HMC (>6 wt% $MgCO_3$)	The growth of the calcifying larval stage was negatively correlated with decreased pH and carbonate mineral saturation state but calcification was not reduced at lowered pH ($pH_{NBS} = 7.6$, $\Omega_{Ca} = 0.66$, $\Omega_{Ar} = 0.41$)	Sea urchins have external organic layers that provide protection from ambient seawater	High	Clark et al., 2009; Ries et al., 2009; McClintock et al., 2011; Byrne et al., 2013

(Continued)

TABLE 1 | Continued

Phylum	Class	Order	Taxa	Skeletal mineralogy	Impacts	Strategies to overcome OA	Vulnerability	References
Bryozoa		Most species are classified as having IMC skeletons (global trend)					Medium	Taylor et al., 2009; Krzeminska et al., 2016
	Gymnolaemata	Cheilostomata	*Beania erecta*	HMC (>8 wt% $MgCO_3$) or IMC			High	Figuerola et al., 2019
Annelida	Polychaeta	Sabellida	Spirorbid species	Aragonite, HMC or a mixture of the two	Spirorbid polychaete tubes are impacted heavily by acidified conditions		High	Cigliano et al., 2010; Smith et al., 2013a; Peck et al., 2015; Figuerola et al., 2019
Brachiopoda	Rhynchonellata	Terebratulida	*Liothyrella uva*	LMC shells	Energetic costs to create thicker shells	Deterioration after 7 months exposure to pH 7.54	Medium	Cross et al., 2019

LMC, low-Mg calcite (0–4 wt% $MgCO_3$); IMC, intermediate-Mg calcite (4–8 wt% $MgCO_3$); HMC, high-Mg calcite (>8 wt% $MgCO_3$).

FIGURE 4 | Distribution patterns for benthic species from the Southern Ocean identified here as particularly vulnerable to ocean acidification.

(Bax and Robinson, unpublished data). These mineralogy findings do not consider other factors influencing species distributions, such as gene flow across depth gradients, which may work against selective pressures influencing mineralogy (Miller et al., 2011). Our meta-analysis highlights the detrimental impact of OA on dispersal stages which could have significant long-term consequences for isolated populations (Miller et al., 2011), or eventually lead to depth related differences in mineralogy. A further step will be to consider a broader array of species and a wider depth range to test the effect of the lower $CaCO_3$ Ω on distributions. Several common Antarctic marine calcifiers secrete more soluble $CaCO_3$ mineral phases: aragonite (e.g., scleractinian cold-water corals, infaunal bivalves, pteropods) or HMC (e.g., bryozoans and echinoderms) (Turley et al., 2007; McClintock et al., 2009, 2011; Figuerola et al., 2019).

There is a need for information on mineralogy of all major groups of calcifying invertebrates over a wider depth range to evaluate patterns related to environmental (e.g., local CSH and ASH) and biological factors (e.g., food availability), with a focus on identifying taxa or communities that may be potentially

TABLE 2 | Effects of acidification on survival, calcification, growth, development, photosynthesis in marine calcifier groups from Kroeker et al. (2013), including new data of mineralogy-related sensitivity and vulnerability.

Group	Survival	Calcification	Growth	Development	Photosynthesis	Mineralogy	Vulnerability
Corals	0	−32%	0		0	Aragonite	High
Molluscs	−34%	−40%	−17%	−25%		Aragonite	High
Echinoderms	0	0	−10%	−11%		HMC	Medium
Coccolithophores		−23%	0		0	Calcite	Low
Crustaceans	0	0	0	0		Calcite	Low
Calcified algae			0		−28%	HMC	Medium

Effects represented as mean percent (–) decrease in a given response, no effects (or too few studies) represented as 0, and untested variables by blank space. Groups are scored from low to high vulnerability to ocean acidification, considering the result of each response variable and skeletal mineralogy.

vulnerable to near-future OA, and that may make suitable indicators (sentinels) to monitor effects of OA in the SO.

Taxonomic Variation in Mineralogy

Cold-water corals form a dominant component of some SO benthic communities and have a wide range of mineralogy. The discovery of large field-like aggregations of deep-sea stylasterid coral reefs in the Antarctic benthos and their classification as a vulnerable marine ecosystem (VME) under the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) highlights their conservation importance, and recognizes the role these reefs play in the maintenance of biodiversity (Bax and Cairns, 2014). VMEs have been described throughout the Antarctic and sub-Antarctic which include: gorgonian corals (Moore et al., 2017), colonial scleractinian corals such as *Solenosmilia* and *Madrepora* (Cairns, 1982; Cairns and Polonio, 2013), and stylasterid corals (e.g., *Errina* sp.) (Bax and Cairns, 2014). These coral groups have been shown to have differential carbonate mineralogy: gorgonians: calcite/aragonite (Thresher et al., 2011); scleractinians: aragonite (Margolin et al., 2014), and stylasterids: calcite/aragonite (Cairns and Macintyre, 1992). Notably, stylasterid corals have the ability to utilize both aragonite and calcite (Cairns and Macintyre, 1992), and therefore, could have a greater capacity to acclimate to changing oceanic pH than purely aragonite calcifiers (Bax and Cairns, 2014). Therefore, it is likely that coral response to OA will be varied, however, there is very little data on Antarctic coral species beyond taxonomic descriptions (Cairns, 1982, 1983), and biogeographic studies (Bax and Cairns, 2014), leaving their calcification responses to OA largely unknown, despite their expected vulnerability (Tittensor et al., 2010). One exception is the cosmopolitan aragonite scleractinian coral *Desmophyllum dianthus* (Esper, 1794) (**Figure 4**), for which there is a reasonable literature relating to OA impacts (Miller et al., 2011; Fillinger and Richter, 2013; Jantzen et al., 2013). Most of these studies, however, are based on populations outside of Antarctica, predominantly within the Chilean fjords. The scleractinid coral species *D. dianthus*, *Solenosmilia sp.* and *Madrepora* sp., with aragonitic skeletons, could also be impacted by OA, due to their mineralogy-related sensitivity and their biological traits. *D. dianthus* has a common depth range between 200 and 2,500 m (Miller et al., 2011; Fillinger and Richter, 2013), and exhibits reduced respiration rates under a combination of rising temperatures and OA scenarios (Gori et al., 2016). Thus, it is likely that this species may be severely impacted by these two key CO_2-related stressors. Scleractinid corals comprise dominant components of VMEs on the Antarctic shelf and the effects of OA at the species level could lead to broader and potentially negative ecosystem level effects.

Aragonite Producing Species

One of the effects of OA predicted to occur in coming years is the shoaling of the ASH, resulting in undersaturation of aragonite in shallow waters. This is of a particular concern for shallow water species with aragonitic shells and/or skeletons such as benthic molluscs and zooplankton species such as pteropods. SO pteropods are the major pelagic producers of aragonite and comprise up to one-quarter of total zooplankton biomass in several Antarctic regions (the Ross Sea, Weddell Sea, and East Antarctica), with *Limacina helicina* the dominant species (McNeil and Matear, 2008). The thin aragonitic shells of these free-swimming marine gastropods are vulnerable to OA. Shell dissolution was observed when individuals of *L. helicina antarctica* were exposed to undersaturated conditions ($\Omega_A = 0.8$) (Bednaršek et al., 2012, 2014), along with increased metabolic rate when exposed to lowered pH (pH 7.7), and a high temperature (4°C). These responses are likely to be related to the increased energetic costs for shell repair (Hoshijima et al., 2017). *L. helicina* has a life cycle of 1–2 years and its veliger larva develops during winter, when the projected aragonite undersaturation will first occur. If *L. helicina* is not able to cope with anticipated OA, it will likely lead to cascading impacts through higher trophic levels (Seibel and Dierssen, 2003). Pteropods may be particularly vulnerable to the projected emergence of a shallow saturation horizon since they generally live in the upper 300 m (Hunt et al., 2008). A recent review and meta-analysis indicated that pteropods are at risk in the Ω_{Ar} range from 1.5 to 0.9, and that OA effects on survival and shell dissolution are exacerbated with warming (Bednaršek et al., 2019). Our meta-analysis shows significant effects of OA on growth (Hoshijima et al., 2017) and shell state (Bednaršek et al., 2014) in the pteropod *L. helicina* (**Supplementary Figure 1**). This species was already considered an OA sentinel due to its thin aragonitic shell, which is

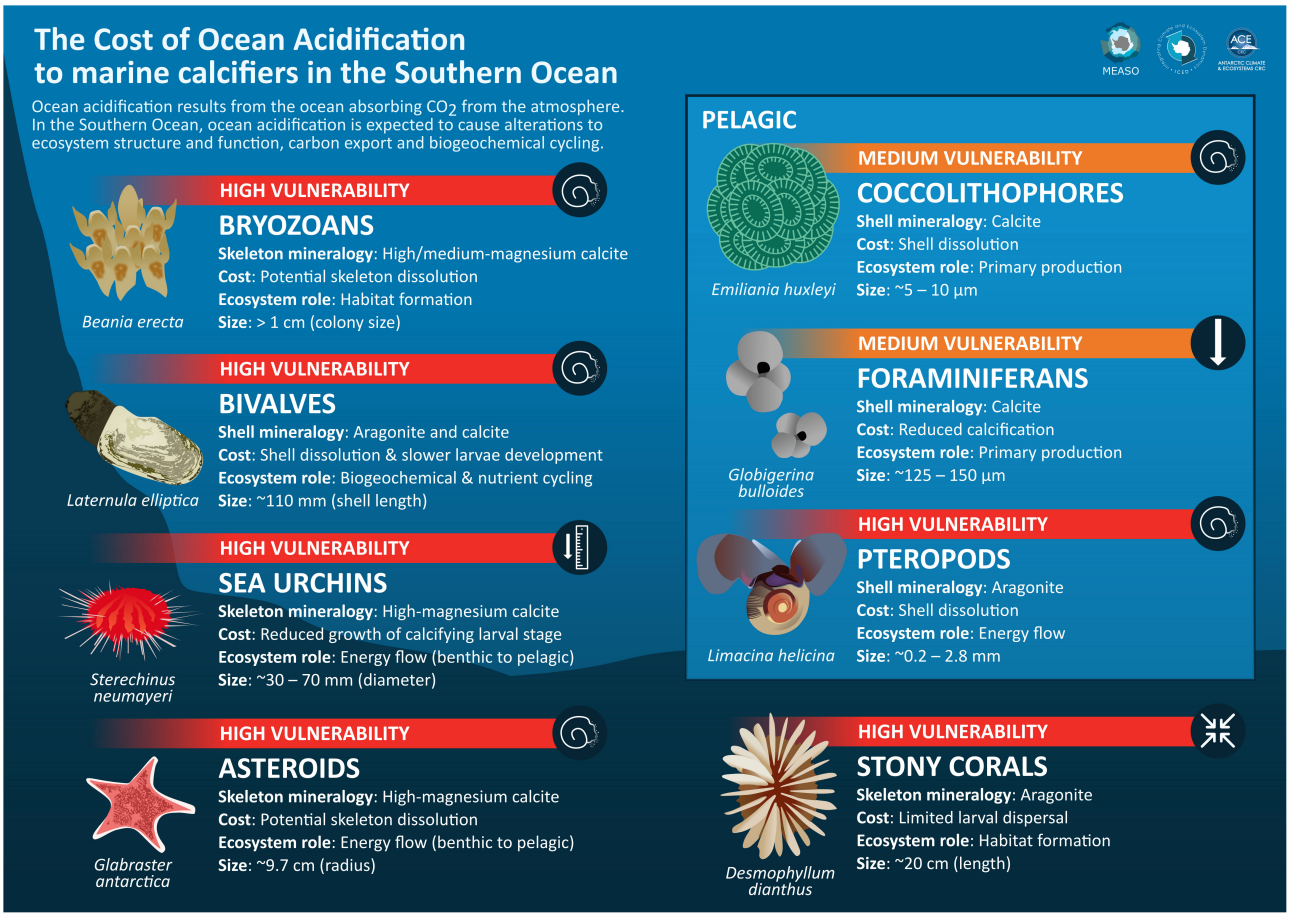

FIGURE 5 | Infographic of predictions about how ocean acidification will affect particular groups of marine calcifiers from Antarctica. Information on different mineral composition, functional, and life history traits is provided for each group.

susceptible to dissolution (**Figure 5**) (Manno et al., 2017). *L. helicina* may also not have the genetic plasticity required to adapt to projected OA changes in the SO (Johnson and Hofmann, 2017).

Similarly, the D-larval stage of the common circumpolar Antarctic bivalve *Laternula elliptica*, which possess aragonitic shells (**Figure 4**), showed shell dissolution and slower development under OA conditions (Ω_{Ar} 0.79–0.52, pH 7.80–7.65) (Bylenga et al., 2015, 2017). Empty adult shells of other SO molluscs (bivalves and limpets), including calcitic species, also show significant dissolution when exposed to reduced pH (pH = 7.4, $\Omega_{Ar} = 0.47$, $\Omega_{Ca} = 0.74$) (McClintock et al., 2009). Such species may be suitable as sentinels of OA in the SO (Bednaršek et al., 2014). In contrast, aragonitic shells of the gastropod *Margarella antarctica* were resilient to initial exposure to temperature and pH changes projected to occur over the next several 100 years (Ω_{Ar} and $\Omega_{Ca} > 1.10$) (Schram et al., 2016). The larvae of the bivalve *L. elliptica*, which have predominantly aragonite shells, also seem to be sensitive to undersaturated conditions (shell dissolution and slower development) (**Supplementary Figure 1**; Bylenga et al., 2015, 2017). Given its circumpolar distribution (**Figure 4**) and broad depth range (<10–~700 m) (Waller et al., 2017), individuals from shallower waters could avoid the initial projected occurrences of aragonite undersaturation events.

Calcite-Producing Species

Coccolithophores are a globally ubiquitous, major phytoplankton calcitic calcifier group, accounting for nearly half of global $CaCO_3$ production (Moheimani et al., 2012). These unicellular flagellate algae play a significant role in the SO carbon cycle, contributing 17% to annually integrated net primary productivity south of 30°S (Nissen et al., 2018). Coccolithophores show taxon-specific and regional variation in response to increased pCO_2 and light intensity (Donahue et al., 2019). *Emiliania huxleyi*, the most abundant species, has different morphotypes that exhibit a clear north-to-south distribution gradient, with the SO "B/C" morphotype forming delicate coccoliths with relatively low $CaCO_3$ (calcite) content compared to other more calcified morphotypes from lower latitudes (Müller et al., 2015). Three morphotypes from different latitudes reduced their rate of calcification under simulated OA scenarios; the B/C morphotype

was found to be the most sensitive, although even in the more resilient morphotype A a 3-fold reduction in calcification was observed (Müller et al., 2015, 2017).

In contrast, net calcification in the limpet *Nacella concinna* (Strebel, 1908), with calcitic shells (Mg-calcite; J.B. Schram, unpublished X-ray diffraction data), was resilient to seawater changes projected to occur over the next several 100 years (temperature and pH changes Ω_{Ar} and $\Omega_{Ca} > 1.10$) (Schram et al., 2016).

Mg Calcite-Producing Species

High latitude surface seawater is currently undersaturated with respect to Mg-calcite minerals containing >10 wt% $MgCO_3$ (Andersson et al., 2008), yet species with Mg-calcite mineralogy are common and important components of Antarctic benthic communities. Encrusting organisms like spirorbid polychaetes and bryozoans, with r-selected life-history strategies, are amongst the most remarkable early Antarctic colonizers (Stark, 2008). The skeletal Mg-calcite composition has been determined for a considerable number of species from several Antarctic groups (e.g., echinoderms and bryozoans), although there is still a significant gap in knowledge of other taxonomic groups, and their geographic variation in general.

Most genera of foraminifera have calcitic shells with varying amounts of Mg, ranging from LMC to HMC (Blackmon and Todd, 1959). Planktonic foraminifera are ubiquitous in the SO and a major component of calcifiers among marine zooplankton, with ∼25% settling on the seafloor and their calcitic shells contributing ∼32–80% to the total deep-marine calcite budget (Schiebel, 2002). It is known that reductions in pH and $[CO_3^{2-}]$ generally alter the performance of this group, together with pteropods and coccolithophores (Barker and Elderfield, 2002; Manno et al., 2012). *Globigerina bulloides* d'Orbigny, 1826, is one of the most commonly used species for environmental paleo-reconstructions at high latitudes (Anand and Elderfield, 2005). The common SO species have shown reduced calcification when comparing modern shell weights with shells preserved in the underlying Holocene-aged sediments (Moy et al., 2009). The authors linked the change to anthropogenic OA. Other lab and field studies using different species of planktonic foraminifera showed the same trend (Manno et al., 2012; Marshall et al., 2013). Consistent with these findings, a recent study showed a reduction of calcification and oxygen consumption of *G. bulloides* as pH declined from 8.0 to 7.5 (Davis et al., 2017). The lack of studies on the OA effects on foraminifera in the SO, and in general, highlights the significant gap in knowledge, and therefore the importance of further research to aid more accurate predictions.

Crustose coralline algae (CCA) is abundant and diverse worldwide and in a range of habitats on hard substrata of the continental shelves and is an important component of shallow water benthic communities and is a key substrate for benthos in some Antarctic fjords at 10–30 m (Wiencke et al., 2014), and it has been found to colonize most newly ice-free areas (Quartino et al., 2013). The distribution of CCA in Antarctica is not well known and the taxonomy is also not well-resolved (Wiencke et al., 2014). It has been found to cover up to 70–80% of the substrate under macroalgal canopies in Antarctica in shallow water (Irving et al., 2005). The tissue of CCA skeletons typically ranges from 8–18 wt% $MgCO_3$ (Chave, 1954). One Antarctic species, *Phymatolithon foecundum* L. Düwel & S. Wegeberg (Alongi et al., 2002), has been reported to depths of 70 m (Cormaci et al., 2000) in the Ross Sea, but the mineralogy of this species has not been investigated. A recent investigation of four *Phymatolithon* spp. in the north Atlantic revealed that, within a single crust, Mg content of the carbonate ranged from 8 to 20 mol% $MgCO_3$ (Nash and Adey, 2017). Furthermore, the proportions of carbonate types varied within the tissues, and also between species (Nash and Adey, 2017), making it difficult to predict OA impacts. Antarctic crustose macroalgae may be resilient to OA, with a study conducted on *Clathromorphum obtectulum* (Foslie) W. H. Adey, 1970 observing no negative impacts on $CaCO_3$ content and Mg/Ca ratio with OA (Schoenrock et al., 2016).

Sponges are often species-rich, dominant, high biomass, habitat-providers in many Antarctic seafloors, with calcareous sponges representing more than 12% of all species, which is far higher than the global average (McClintock et al., 2005; Soest et al., 2012). Calcareous sponges are also found to be highly endemic, and have two genera found only in this region (Downey et al., 2012). Species belonging to the class Calcarea generally produce $CaCO_3$ spicules with very high Mg contents (≤15 wt% $MgCO_3$), and are likely to be vulnerable to projected lowered pH (Smith et al., 2013a). Close to 90% of calcareous sponges are only found on the shelves of the Antarctic continent and sub-Antarctic islands (Janussen and Downey, 2014), and most of these species have very narrow longitudinal and latitudinal ranges, which likely increases their vulnerability to projected OA in the SO. More research is needed to ascertain the impacts of OA on SO calcareous sponges.

Recent studies have investigated the skeletal Mg contents in calcite of 29 Antarctic echinoderm species to understand how OA may affect different groups (McClintock et al., 2011; Duquette et al., 2018) (**Supplementary Table 2**). Most species were found to be HMC, although variation of skeletal Mg-calcite existed between taxonomic classes (asteroids, ophiuroids, echinoids, and crinoids), and for the same species from different locations. McClintock et al. (2011) suggested sea stars (e.g., *Glabraster antarctica*), which can be Antarctic keystone predators (Dayton et al., 1974), and brittle stars, with higher mean Mg values, will likely be the first echinoderms to be affected by OA. The fertilization and early development of the common Antarctic sea urchin *Sterechinus neumayeri* were not affected by near-future changes and its fertilization success only declined significantly when exposed to one stressor (pH) at reduced levels projected for 2300 (decreases of ∼0.7 pH units) (Ericson et al., 2010; Ho et al., 2013). However, a negative interactive effect of projected changes in seawater temperature (3°C) and pH was found in fertilization (11% reduction at pH 7.5) (Ericson et al., 2012) and on cleavage success (pH 7.6) (Foo et al., 2016), although the results may vary depending on sperm concentrations, population or experimental conditions (Sewell et al., 2014). The growth of the calcifying larval stage of this species was also found to be negatively correlated with decreased pH and Ω (Byrne et al., 2013), but calcification was not reduced at lowered pH

(pH_{NBS} = 7.6, Ω_{Ca} = 0.66, Ω_{Ar} = 0.41) (Clark et al., 2009). Additionally, its larvae had shorter arm lengths when exposed to undersaturated conditions (730 µatm, Ω = 0.82) (Yu et al., 2013). Similarly, normal development of the seastar *Odontaster validus* was reduced at low pH (7.8) (Karelitz et al., 2017), as was survival and growth of the larvae at pH_{NIST} 7.6 (Ω_{Ca} = 0.89, Ω_{Ar} = 0.57) (Gonzalez-Bernat et al., 2013), indicating that they are unable to adjust to changes in extracellular pH, even though Asteroidea are non-calcifying during their larval development. The latter study illustrates how polar organisms are affected by characteristics of OA other than direct effects on carbonate structures, which could explain their different responses and sensitivities, as well as their lack of relationship to Ω (Ries et al., 2009; Waldbusser et al., 2015). Recent results have also illustrated that Antarctic regular euechinoid and cidaroid species have acid-base regulation systems, suggesting they are not particularly at risk although more experimental studies combining different stressors (e.g., temperature) and using other species are needed (Collard et al., 2015).

Sea stars and brittle stars may also be highly vulnerable to OA due to their HMC skeletons, and the apparent lack of strategies to overcome reduced pH/carbonate conditions (**Table 2**). One example is the sea star *Glabraster antarctica*, which has higher mean Mg values (>10 wt% $MgCO_3$) than other SO species. Gonzalez-Bernat et al. (2013) found the growth of the seastar larvae *Odontaster validus*, is significantly affected when exposed to low pH levels. Prior studies indicate differential sensitivities depending on the biological responses in the common Antarctic sea urchin *Sterechinus neumayeri* (Ericson et al., 2010; Ho et al., 2013). While this species fertilization success and early development were not affected by near-future changes, the former declined significantly when only exposed to low pH levels (Ericson et al., 2010; Ho et al., 2013). In addition, other studies have revealed significant interactive effects of projected changes in seawater temperature and pH on the percentage of fertilization (Ericson et al., 2012) and on the cleavage success (Foo et al., 2016). The growth of *S. neumayeri*'s calcifying larval stage was also found to be negatively correlated with reduced pH and Ω (Byrne et al., 2013), although its calcification was not reduced in a previous study (Clark et al., 2009). This sensitivity of larvae could cause a key bottleneck in their life-cycle (Dupont et al., 2010). Both species are circumpolar and exhibit a high range of eurybathy, ranging from the shallow subtidal to 2,930 m (*O. validus*) and to 500 m depth (*S. neumayeri*) (Pierrat et al., 2012; Moore et al., 2018). The negative impact of OA on echinoderms, especially on some sea star species which are common key predators in Antarctic ecosystems, could alter the structure and biodiversity of these ecosystems, with cascading impacts on multiple trophic levels. Like other SO echinoderm taxa, the distribution of these common species may become limited to shallow waters above the ASH, therefore, they could be affected by warming.

The Mg content from individuals of 90 Antarctic bryozoan species (nearly one-quarter of all Antarctic bryozoan species), has found extreme intraspecific and interspecific variation (Borisenko and Gontar, 1991; Taylor et al., 2009; Loxton et al., 2013, 2014; Figuerola et al., 2015, 2019; Krzeminska et al., 2016) (**Supplementary Table 3**). These studies showed that most species consisted of IMC. Taylor et al. (2009) previously confirmed the absence of aragonitic bryozoan species at high latitudes (>40°S) and the rarity of bimineralic species. Figuerola et al. (2019) found that the circumpolar cheilostome *Beania erecta* Waters, 1904 (**Figure 4**) may be particularly vulnerable to global ocean surface pH reductions of 0.3–0.5 units by the year 2100 as some specimens had HMC skeletons. The Antarctic cyclostome *Fasciculipora ramosa* d'Orbigny, 1842 also appears to be influenced, to some degree by environmental factors, as shown by the significant variability in branch diameter and Mg levels among depths (Figuerola et al., 2015, 2017). *B. erecta*, like other Antarctic bryozoan species, can form dense mats that, in some cases, cover large areas of substratum. Potential decreases of some species could indirectly negatively impact other organisms which use their colonies as substrate, food and shelter (Figuerola et al., 2019).

Spirorbid polychaetes are impacted heavily by acidified conditions as their tubes are mainly composed of aragonite, HMC or a mixture of the two (Cigliano et al., 2010; Smith et al., 2013b; Peck et al., 2015). A recent study did not find any temporal variation over 6 yrs in the wt% $MgCO_3$ in calcite in Antarctic bryozoans and spirorbid polychaetes, suggesting that these particular taxa could be good indicator species for the potential effects of environmental change in coastal regions (Figuerola et al., 2019).

Brachiopods have some representatives in Antarctic waters, in particular, the rhynchonelliform brachiopods are locally important members in shallow water communities, and have LMC shells (Barnes and Peck, 1996). The circumpolar rhynchonelliform brachiopod *Liothyrella uva* showed deterioration after 7 months exposure to pH 7.54 (Ω_{Ca} = 0.5, Ω_{Ar} = 0.3; Cross et al., 2019) although the projected acidified conditions did not alter shell growth rates and the ability to shell repair (Cross et al., 2014).

The exoskeletons of several crustacean species have also been shown to contain Mg-calcite, although they often have a very complex mineralogy (a combination of calcite, Mg-calcite, calcium phosphate, and chitin), compared to skeletons of other groups, such as bryozoans (Chave, 1954; Andersson and Mackenzie, 2011). King crabs (Lithodidae), inhabiting deep water habitats of the SO that are already undersaturated in aragonite (Steffel et al., 2019), produce calcareous, even robust, exoskeletons (e.g., *Paralomis birsteini* Macpherson, 1988). As projected global warming removes thermal barriers controlling their distribution, king crabs may expand their bathymetric range to the Antarctic continental shelf, a region currently characterized by the absence of durophagous (skeleton-breaking) predators (Griffiths et al., 2013). Therefore, a range of calcifying invertebrates (e.g., echinoderms and molluscs) with thin and fragile shells and skeletons, could be at real risk of increased predation, were such predators to establish on the Antarctic shelf (Watson et al., 2017).

Changes in seawater temperature, which strongly influence growth rate and also Ω, are also thought to drive changes in skeletal Mg content, although other environmental factors such

as salinity could be influential (Chave, 1954; Mackenzie et al., 1983). There is a general trend of increasing aragonite and in Mg content in calcite, toward lower latitudes, in different marine calcifying taxa (Lowenstam, 1954; Taylor et al., 2009; McClintock et al., 2011). A similar trend was found in different life stages (e.g. juveniles and larvae vs. adults) and nine skeletal elements (e.g., spines and tooth) of echinoids (Smith et al., 2016). This general pattern was also observed in individuals of echinoderms and bryozoans with LMC skeletons only reported in Antarctica and in sub-Antarctic and Antarctic regions, respectively (**Figure 2**).

Other Biological Traits

As suggested in previous work, it is important to consider other aspects of the biology of organisms when assessing their sensitivity to OA. Some biological traits increase sensitivity to changes in pH and $CaCO_3$ Ω, whereas other traits provide either resistance or resilience to OA. Such biological traits, along with factors such as nutritional status and source population, enhance the variability of responses to OA (Kroeker et al., 2013). Furthermore, a range of indirect effects and variation arise when considering species response within multi-species assemblages (Kroeker et al., 2013).

Mechanisms likely to provide marine calcifiers with greater resilience to OA include high levels of mobility/activity and consequently higher metabolic rates (e.g., crustaceans), greater larval dispersal, capacity to regulate the pH of their calcifying fluid; and protection of shells or skeletons from the surrounding water (protective external organic layers) (Melzner et al., 2009; Ries et al., 2009). Marine calcifiers such as CCA, some sea urchin and molluscan taxa, possess skeletons/shells covered by external organic layers that may provide protection from ambient seawater, making them less vulnerable to OA (Ries et al., 2009). Crustaceans generally have exoskeletons which are enclosed within epicuticles, which are waxy protective outer layers (Ries et al., 2009). Some brachiopods and molluscs, such as the pteropod *L. helicina antarctica,* have an outer organic layer (periostracum) that can protect the outer shell surface from dissolution (Bednaršek et al., 2012, 2014). However, this periostracum can be easily damaged, exposing the underlying shell to surrounding seawater. Similarly, the level of epidermis protection in tests and spines of regular sea urchins is questionable due to its permeability and thinness, respectively (Holtmann et al., 2013; Dubois, 2014). Whilst spines usually have LMC compared to the tests, they are often damaged (Dubois, 2014). Mature spines of Cidaroids (a group well-represented in the SO), possess special outer polycrystalline layers (cortex) instead of epidermis, which appear to make them more resistant to acidification (Dery et al., 2014). Additionally, the biofilm and epibionts covering the cortex may also reduce its direct exposure to seawater. Some taxa lack a protective external organic sheet, such as spirorbid polychaetes, and may be highly vulnerable to OA due to their HMC and/or aragonitic skeletons (Cigliano et al., 2010; Smith et al., 2013b; Peck et al., 2015).

Biological traits such as adult sessile lifestyle and limited larval dispersal will act to increase the potential impacts of OA (Thatje, 2012) as the distribution of such organisms is less likely to shift to more favorable habitat. Fauna such as corals, bryozoans and spirorbid polychaetes are ecosystem engineers, creating habitat complexity and refugia for many associated macro- and micro-invertebrates. Dissolution effects could thus lead to the loss of habitat complexity with serious consequences to Antarctic ecosystems.

ACCLIMATION AND ADAPTATION

Responses and mechanisms for adaptation (permanent evolutionary modifications induced by response to repeated stressors) or acclimation (potential for an organism to adjust to changes in an environment) to the forecast changes are anticipated to be species-specific due to the phylogenetic control on biological processes such as calcification and the Mg content in calcite (Chave, 1954; Cairns and Macintyre, 1992). For example, an evolutionary study shows that calcification in the coccolithophore *Emiliania huxleyi* can be partly restored under OA conditions over ∼1 year or 500-generations (Lohbeck et al., 2012). Given the shorter turn-over time of phytoplankton compared to higher-level organisms (Peck, 2018), the ability of coccolithophores to rapidly adapt to changing environmental conditions could help maintain their functionality within the ecosystem. The occurrence of heavily calcified morphotypes in higher latitudes/lower pH waters, though rare, highlights that some coccolithophores have already adapted to lower $CaCO_3$ conditions (Beaufort et al., 2011).

Capacity to Regulate Calcification

Biocalcification (a biologically facilitated process) is either extracellular through deposition of $CaCO_3$ on the exterior of an organism; or intracellular and controlled from within the organism (Weiner and Dove, 2003). Extracellular mineralization of $CaCO_3$ requires the Ω to be of a high level in order for calcification to occur; and for the organism to control the $[H^+]$ in the surrounding area to prevent it bonding with CO_3^{2-}, which reduces the availability of carbonate for shell building. Through the active pumping of CO_3^{2-} out of a cell, an organism increases the amount of free CO_3^{2-} for calcification. Alternatively, CO_3^{2-} can be pumped into a vesicle within a cell and then the vesicle containing the $CaCO_3$ is secreted to the outside the cell (Weiner and Dove, 2003). Molluscs and corals generally utilize extracellular calcification secreting their shells and skeletons, respectively, from a calcifying fluid (Ries, 2011). Further studies on the capacity of SO calcifiers to control their acid-base balance, are particularly needed to estimate their capacity to regulate their extracellular pH (Collard et al., 2015).

Intracellular mineralization of $CaCO_3$ is achieved within an organism and retained internally to form a skeleton or internal structure, or is secreted to the outside of the organism where it is protected by the covering cell membrane (Weiner and Dove, 2003). Examples of organisms that utilize intracellular calcification include echinoderms and coccolithophores. In particular, coccolithophores control calcification through production of calcified scales (coccoliths) in an intracellular compartment and secrete them to the cell surface (Marsh, 2003). The capacity to regulate calcification via regulation of the pH of

intracellular calcifying fluids used to secrete $CaCO_3$ may provide some resistance to OA effects and resilience to recover from periods of low pH such as in winter. Some species (e.g., some corals) can regulate the pH of their calcifying fluid and thus they could buffer OA effects (Ries et al., 2009). While there have been no studies of SO CCA and OA (either distributions, or potential responses), the Arctic CCA *Phymatolithon* spp. exhibits strong biological control over its surface chemistry, with efficient carbon concentrating mechanisms that may prevent net dissolution by elevating pH and CO_3^{2-} at their surface (Hofmann et al., 2018). In contrast, molluscs are generally not capable of regulating the pH and carbonate chemistry of their calcifying fluid (Ries, 2012; Bednaršek et al., 2014).

Energetic Costs of Acclimation to Ocean Acidification

Maintaining calcified skeletons, especially those with high Mg content, is more energetically demanding in cold waters, as the solubility of $CaCO_3$ increases with decreasing temperature (Weyl, 1959). This is supported by a clear signal of decreasing skeletal investment with latitude and decreasing temperature, although substantial flexibility in some Antarctic species exists, e.g., laternulid clams have thicker shells than lower latitude congenerics (Watson et al., 2012). Under a global warming scenario, a general increase in skeletal Mg content is expected, likely making the skeletons even more vulnerable to dissolution (Chave, 1954; Andersson et al., 2008; Hermans et al., 2010; Sewell and Hofmann, 2011). Hence, energetic costs to counteract dissolution will likely have implications for many taxa.

For example, the congeneric deep-sea species *Solenosmilia variabilis* from New Zealand (3.5°C), maintained for 12 months under reduced pH conditions (pH = 7.65, $\Omega_{Ar} = 0.69 \pm 0.01$), only showed colony tissue loss (Gammon et al., 2018). The authors hypothesized that this response could indicate a reallocation of energy, with physiological processes (e.g., growth and respiration) being maintained at the expense of coenenchyme production (the common tissue that surrounds and links the polyps in octocorals) (Gammon et al., 2018).

Plasticity in, and control over, biomineralization is a likely mechanism by which calcifiers can adapt to OA. For example, *Laternula ellipctica* has shown upregulation in expression of chitin synthase, a gene involved in the shell formation process in response to reduced pH conditions (Cummings et al., 2011). Potentially higher energetic costs of this upregulation were indicated by elevated respiration rates which, when modeled at the population level, projected significant declines in abundance (Guy et al., 2014). A study of *Mytilus* spp. from temperate to high Arctic latitudes revealed mussels producing thinner shells with a higher organic content in the polar region (Telesca et al., 2019). The periostracum was thicker, and the shells contained more calcite in their prismatic layer than aragonite, which potentially provide greater protection against dissolution (Telesca et al., 2019). The brachiopod *Liothyrella uva* also has the ability to form thicker shells as a compensatory mechanism to dissolution under acidified conditions (Cross et al., 2019). However, the energetic cost of calcification in cold waters may also lead to other compensatory responses. For example, the Antarctic king crab *Paralomis birsteini* invest more resources in building robust, predatory chelae than in protective carapaces, suggesting a greater investment in predation than in defense as its predation pressure is limited in Antarctic waters (Steffel et al., 2019).

Local Adaptation to Ocean Acidification

The potential role of local adaptation through phenotypic plasticity in the resilience of species to OA has been investigated by examining the variability in responses between populations from different areas with contrasting physical conditions (Vargas et al., 2017). Populations from areas naturally exposed to high pCO_2 levels and high levels of pCO_2 variation show resistance and resilience to OA effects, with less impact on physiological traits, for plankton and molluscs (Vargas et al., 2017). In contrast, populations from areas with lower pCO_2 and lower variability showed significant negative effects when exposed to elevated pCO_2. Similarly, in a species of coralline algae it has been demonstrated that elevated pCO_2 more strongly negatively impacted populations that experienced both lower pCO_2 and lower variability in carbonate chemistry, including effects on physiology and growth rates (Padilla-Gamiño et al., 2016). Thus, the role of natural variability in carbonate chemistry of seawater on moderating the effects of OA on species needs to be considered when assessing species-specific responses and suitability as potential biomonitors.

The effects of such local variation on responses to OA in Antarctic species has not been investigated, however considerable variation has been found to occur in carbonate chemistry of SO waters, particularly in coastal areas (Kapsenberg et al., 2015; Stark et al., 2018). Further work is required to understand how SO carbonate systems vary on regional and local scales.

FUTURE DIRECTIONS

The SO could serve as a sentinel for evaluating the impacts of OA on marine calcifiers (Fabry et al., 2009) and aid in making predictions of the future impacts at tropical and temperate lower latitudes, where OA is expected to occur later. Some SO regions are also warming faster than other global oceans, along with other stressors such as nutrient inputs. Key marine calcifiers may not be able to cope with these multiple simultaneous projected changes, which could ultimately affect food webs and have cascading impacts from low to higher trophic levels. Combined temperature and pH studies of several Antarctic taxa indicate that temperature may have a stronger impact on survival and growth, but that the effects of OA could be severe (e.g., increased rates of abnormal development, sublethal effects). Such studies of multiple stressors are essential to explore the capacity of different species to adapt to future environmental changes. However, our understanding on the potential impact of OA on Antarctic marine calcifiers, including keystone organisms, is still constrained by the limited mineralogical and biological data available for most species. Furthermore, broader understanding is also constrained by the limited geographical coverage of

studies, lack of reliable long-term monitoring, and the overall lack of multidisciplinary studies over longer times scales integrating interactions between stressors and an array of species with different mineral composition, functional, and life history traits. In particular, other environmental and biological factors, which may influence mineral susceptibility (such as organic content, protective periostracum, physiological constraints in cold waters), need further evaluation. These studies should also incorporate natural variability to better understand the limits to plasticity across organismal traits, populations and species (Vargas et al., 2017). Understanding of ecosystem effects can be improved through the use of *in-situ* OA studies over long times scales, such as by using free-ocean CO_2 enrichment (FOCE) systems (Stark et al., 2018). Being semi-open systems, these not only allow manipulation of pH, but also incorporate natural variation in physicochemical variables, such as temperature and salinity, thus creating realistic near-future OA conditions. Recently, FOCE technology has successfully been implemented in Antarctica (Stark et al., 2018) and other *in situ* OA experiments have been conducted (Barr et al., 2017; Cummings et al., 2019), opening new possibilities for OA research in polar regions. Finally, special attention should be paid to the use of standardized protocols for experimental approaches (Cornwall and Hurd, 2016), the manipulation and reporting carbonate chemistry conditions (Riebesell et al., 2010), in order to compare results from different studies, improve reproducibility in experiments (Williamson et al., 2020), and make predictions about how OA may impact different groups. Building interdisciplinary collaborations via projects such as the Census of Antarctic Marine Life (CAML) is essential (Gutt et al., 2018) to successfully perform OA research on and in remote and at risk regions like Antarctica.

AUTHOR CONTRIBUTIONS

BF conceived the initial idea for the review, organized the database and made tables for the mineralogical data, wrote the first draft of the manuscript, and edited the final version. BF and JSS organized the sections. BF, AH, and NB participated in the design advice for the figures. HG reviewed and analyzed the data available to produce species distribution maps. AH and BF screened papers and AH performed the meta-analysis and its figures. AH and BF interpreted the results. Authors reviewed the first draft with substantial contributions by section as follows: AH (2, 3, and 4: meta-analysis), NB (4.1: corals, 6), VC (4.2: algae and echinoderms, 5.2), RD (4.5: sponges), JS (1, 1.1.2: carbonate sediments), and JSS (1, 5.1, 5.3). All authors provided comments and suggestions and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.584445/full#supplementary-material

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PERSPECTIVE
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Science and Policy Interactions in Assessing and Managing Marine Ecosystems in the Southern Ocean

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Good policy can only be built and implemented using sound advice, and a clear understanding of risk. Scientific advice will often be qualified by the extent of research and knowledge, and uncertainties about the current and future state of the environment. Bodies tasked with protecting the Antarctic environment are required to make decisions based on the best available advice. To not take decisions in the absence of certainty is contrary to clear obligations to protect the Antarctic environment contained in the instruments of the Antarctic Treaty System. The risk of foreclosing future options to protect the environment by indecision is as great, if not greater, than making decisions with incomplete advice, and then actively managing that decision into the future. This "Perspective" explores the relationship between science and policy in the context of the Conference on Marine Ecosystem Assessment for the Southern Ocean held in 2018—it is a perspective from the view of a policy-maker and end user of scientific assessment and advice.

Keywords: climate change, Antarctica, CCAMLR, CEP, Antarctic Treaty

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INTRODUCTION

Understanding what policy-makers want from researchers, and translating science into policy are not straightforward tasks. Good policy requires clear objectives and well-designed pathways to implementation and outcome. Good policy also requires objective measures of success, failure and need for adjustment.

While "good policy," "clear objectives," and "sound advice" are rather general terms, from the point of view of this "Perspective" my intention is that "good policy" is policy that is well defined and understood, and that is assessed *a priori* to not deliver perverse outcomes from its implementation. These terms were deliberately used to connote generic goals of policy-makers.

Often, decisions to create and implement a particular policy are made because something needs to be "fixed"—a previous practice or governance arrangement has failed, or something unforeseen (for example COVID-19) has appeared in the physical and geopolitical environment.

Scientific research on the other hand is almost always a long-term process, often requiring detailed preparation, field work, experimentation, modeling, analysis, and testing. Scientific knowledge is also changing in that new research leads to better or different understanding about the conclusions that have been drawn from previous bodies of work.

For a policy-maker scientific advice that contains "uncertain" conclusions can create doubt about effective policy implementation or, worse, decision paralysis. For the scientist, policy insistence on clear and concise advice is often regarded as shallow and intellectually corrupt.

But the clear facts are that effective policy-making requires the best available information provided in a way that demonstrates the strength of the advice and the limits of its conclusions. It should be then up to policy-makers to design effective and timely policies based on this information. Commonly, policy-makers are required to make decisions in the absence of complete or 'perfect' information. Designing good policy requires not only an understanding of the scientific advice given, and the uncertainties inherent in it, it also requires evaluation of the implications, or costs, of implementing available policy options. In conservation, for example, a "business as usual" policy response to uncertain scientific knowledge may result in adverse consequences, such as species decline and extinction, environmental damage, or ecosystem shift and/or collapse.

In the absence of complete or "perfect" scientific information, it is incumbent on policy-makers and scientists to understand the gaps in scientific information, to set research priorities to fill these gaps, and to adapt management approaches as new information is received.

This article provides a perspective on the discussions held during the Policy Forum that was held at the Conference on Marine Ecosystem Assessment for the Southern Ocean (MEASO) in Hobart in 2018. It looks at some of the ways that science and policy can be integrated to inform policy development and decision making for the conservation of the Antarctic marine environment given the current state of scientific understanding. It is written from the perspective of a long-time end user of scientific research and information used to develop and pursue policies for the conservation of the Antarctic environment. The context of this "Perspective" is the research and decision-making structures of the Antarctic Treaty System, rather than a perspective on national or other international frameworks.

PERSPECTIVES ON ANTARCTIC ECOSYSTEMS AND THEIR MANAGEMENT

In 2018 the journal Nature published, an editorial calling for "reform" of the Antarctic Treaty System (ATS) (Anon, 2018). The Nature editorial, and other recent work, highlight the challenges faced by scientists and policy-makers in responding effectively to existing and emerging environmental management challenges, especially those that relate directly to, or are exacerbated by climate change:

> "Pressure on the Antarctic Treaty from geopolitics can only increase, as demand for the continent's stocks of fish and expected reserves of minerals rises with the depletion of resources elsewhere. . .," and
>
> "Scientists can strengthen and harness . . . support by relentlessly telling the public and policymakers about the seriousness of the threat to Antarctica and the need to protect the region" (Anon, 2018).

Rather than deal in any practical way with how science can be better used by policy-makers, or how policy and science can better interact, Nature concluded with the unrealistic proposal that the fundamental decision-making principle of the Antarctic Treaty System, consensus, be abandoned—an impossible step that would unravel the governance of the entire Antarctic region.

Nonetheless, the Nature editorial, and other recent work, highlight the challenges faced by scientists and policy-makers in responding effectively to existing and emerging environmental management challenges, especially those that relate directly to, or are exacerbated by climate change.

Chown and Brooks (2019), for example, in their broad-ranging review of the "state of Antarctic environments" concluded that,

> "Information on key species, such as Antarctic krill, seabirds, and seals, and on key ecosystems, such as those of the West Antarctic Peninsula, remains inadequate to fully understand their dynamics. Additional long-term monitoring is essential for effective management. . .
>
> "Accelerating climate change, if mitigation of greenhouse gas emissions is ineffective, will pose considerable challenges to environmental management across the region. . .
>
> "Environmental degradation elsewhere will increase pressure for use of Antarctica and the Southern Ocean's resources". [Author's emphasis].

Given the importance of Antarctic marine ecosystems, historical exploitation of its marine living resources (particularly whales, seals, and fish), and the disruption to ecosystems that climate change brings, science must play a central role in establishing policy and governance mechanisms for the protection of the Antarctic.

THE SCIENCE-POLICY INTERFACE

One of the most difficult aspects of policy development is how relevant science is sought and received. Science is a contested space by its very nature: hypotheses are developed and tested; conclusions on cause and effect are often qualified by the current extent of knowledge; and new knowledge will alter understanding of processes and outcomes. That does not mean that 'science-into-policy' is not achievable, but it does mean that policy-makers need to understand the state of scientific knowledge and the practical limits of scientific understanding. A clear understanding of these factors can then be used to make precautionary decisions—decisions that take into account uncertainty in such a way that future options are not inadvertently foreclosed by bad (or, no) decisions.

The Intergovernmental Panel on Climate Change (IPCC), for example, has well-established and coherent practices for using the best available science to provide information and advice to policy

makers[1]. The important elements relevant to this paper are that the IPCC processes involve:

- Assessment of all available relevant scientific and technical information[2];
- Expert assessment of draft IPCC reports for their accuracy, completeness and balance; and
- The distillation of scientific and technical reports into a "Summary for Policy Makers" that has agreed and transparent language about "uncertainty"[3].

The process ensures differences of view are opened for discussion and resolution, and that IPCC reports contain verifiable information and advice that clearly establishes the state of knowledge about conclusions and advice to policy-makers. This process also enables the prioritizing of scientific research: the "uncertainties" in scientific understanding of the Earth System revealed through the IPCC process have resulted in increased research in these "uncertain" areas, for example Antarctic ice sheet mass balance.

Comparable processes are being used in other global assessments, such as the Intergovernmental Panel in Biodiversity and Ecosystem Services (Díaz et al., 2019), and the First Global Assessment of the World's Oceans[4].

THE ANTARCTIC

In the Antarctic context the Committee for Environmental Protection (CEP) established under the Protocol on Environmental Protection to the Antarctic Treaty (Madrid Protocol)[5], and the Scientific Committee (SC-CAMLR) established under the Convention on the Conservation of Antarctic Marine Living Resources (CAMLR Convention)[6], are bodies tasked with taking expert advice, including scientific evaluation and advice, and making recommendations for adoption by their respective decision-making bodies. Both bodies have established processes for review and assessment of scientific and technical information, and can call on external organizations such as the Scientific Committee on Antarctic Research (SCAR) for expert advice.

In relatively data-poor regions, such as Antarctic marine ecosystems, it is important to clearly understand the limits of currently available scientific knowledge and the context and requirements of information by policy-makers. This is especially important in managing risk (that is, failure of policy resulting in adverse outcomes). The fact that scientific information may be sparse or uncertain should not inhibit decision-making. Quite the opposite, it should provide, first, the incentive for precautionary decision making that reduces environmental risk to future conservation and, thereby, sustainable use options, and, second, the context for and needs of future long- and short-term research and assessment.

THE MEASO POLICY FORUM

The Policy Forum held during the MEASO 18 Conference was designed to bring together scientists, fishers, NGOs, and marine policy-makers to develop priorities for marine biological and ecological research "over the next two to three decades." The policy forum sought to "target research that will deliver science-based advice to support stakeholders and policy-makers." Presentations to the Policy Forum were given in four themes:

1. Future of the Southern Ocean.
2. Needs and capabilities for biological research in the Southern Ocean.
3. Filling the gaps.
4. Priorities to meet the needs.

The presentations and subsequent discussions at the Policy forum were concluded with a plenary discussion that attempted to synthesize the major outcomes and conclusions of the Policy Forum. The full program for the Policy Forum is provided as **Supplementary Material**. The presentations at the Policy Forum (**Table 1**) ranged widely over science knowledge (e.g., physical, chemical, and biological changes in the Southern Ocean); critical questions for future scientific research; timescales for understanding change and conducting research; the history of, and requirements for, scientific advice to inform policy and the scientific requirements of fishers and policy-makers; technology, modeling, collaborations and relationships; and importantly desirable futures for the Southern Ocean and pathways to delivery of research into policy.

General Conclusion

It was evident from the plenary discussion held at the end of the Policy Forum that the participants saw benefit in policy-makers and researchers working together to frame research programs and translate science into policy. Acknowledging that policy decisions often needed to be made with limited available data, the Forum concluded:

- Decision making could be aided by using the best available, even if imperfect, science which includes a combination of field studies, new technologies, and modeling.

One strong theme in the discussion was the need for scientists, policy-makers and stakeholders to understand each other's requirements for research inputs and policy outcomes, and the constraints on both decision-making and research effort. The forum concluded:

[1]IPCC Procedures. At https://www.ipcc.ch/documentation/procedures/; in particular the IPCC "Principles' at https://www.ipcc.ch/site/assets/uploads/2018/09/ipcc-principles.pdf. As accessed 21 May 2020

[2]IPCC Procedures. While preference is given to peer reviewed literature, other kinds of technical reports are assessed for review, but subject to scrutiny for veracity and relevance.

[3]The IPCC has developed defined and "calibrated" language to convey to the reader the confidence that is given to each of its assessments. See for example, Special Report on Oceans and Cryosphere, Technical Summary. At https://www.ipcc.ch/srocc/chapter/technical-summary/

[4]Summary of the first global integrated marine assessment (2015) United Nations, at https://undocs.org/A/70/112; and the ongoing oceans assessments at https://www.un.org/Depts/los/global_reporting/WOA_RegProcess.htm

[5]Protocol on Environmental Protection to the Antarctic Treaty, Madrid, 1991.

[6]Convention on the Conservation of Antarctic Marine Living Resources, Canberra, 1980.

TABLE 1 | Sections and topics presented and discussion at the Policy Forum in the conference Marine Ecosystem Assessment for the Southern Ocean, held in Hobart Australia on 11 April 2018.

Topic	Speaker
1. Future of Southern Ocean ecosystems	
Changing ecosystem forces on Southern Ocean biota	Jess Melbourne-Thomas and Nathan Bindoff (AAD, IMAS, CSIRO, ACE CRC)
Impacts of global geopolitics, economics and policies impacting on the Southern Ocean	Ray Arnaudo (United States)
Desirable futures for Southern Ocean ecosystems	Tony Press (ACE CRC) Discussion
2. Needs and capabilities for biological research in the Southern Ocean	
Critical questions for understanding Southern Ocean ecosystems: how to 'do the science' and timescales for research	Eileen Hofmann (Past Chair, IMBeR SSC)
What do policy-makers need from science?	Gill Slocum (Australian Commissioner to CCAMLR)
Fisheries needs from science	Martin Exel (Austral Fisheries)
Conservation needs from science	Andrea Kavanagh (Pew Charitable Trusts)
3. Filling the gaps	
Technology for future priority research	Oscar Schofield (recent Co-Chair, SCAR/SCOR Southern Ocean Observing System)
Models and modeling	Eugene Murphy (Chair, SCAR/IMBER program—Integrating Climate and Ecosystem Dynamics Program)
Partnerships	Katherine Woodthorpe (Chair, ACE CRC)
Public participation	Chris Johnson (WWF Australia)
4. Science priorities to meet the needs	
Global perspectives on the importance of science in the Southern Ocean	Anthony Bergin (National Security College, ANU; Australian Strategic Policy Institute)
The future of research capabilities—a global perspective	Tim Moltmann (Director, IMOS, Australia; Chair, Australian National Marine Science Committee)

- Policy makers rely on scientists to provide concise, compelling explanations of their research to inform policy. Scientists need clear guidance to respond to policy needs.
- Strengthening the link between science and policy priorities will require conversations among scientists, policy makers, industry, and diverse stakeholders.

Access to, and limitations on, data availability for the Southern Ocean were seen as a major constraint to both research and decision-making. The Forum concluded that:

- Making Antarctic and Southern Ocean data easily and publicly accessible will aid the advancement of science and the development of science-informed policy.
- A MEASO could help the scientific community communicate policy relevant findings in a collective voice that is accessible and understandable to policy makers.

Scientists and policy-makers should frequently explore how their interactions can be more productive, and how science can be used to better achieve the goals of conserving and protecting the Antarctic environment. In this context it is not only important to be clear on the modes of interaction between scientists and policy-makers, but also whether the goals sought are being achieved[7].

DISCUSSION

In essence, the conclusions from the Policy Forum could be applicable to many environments and decision-making bodies. But the context of Antarctica and the Southern Ocean makes the Forum's discussion both unique and compelling. After all, the context is 10% of the planet; Antarctica's role in the global climate system; the impending consequences of global warming; and the responsibilities of the Antarctic Treaty System (ATS)[8].

The Antarctic Treaty System has developed into a regional management system responsible for the environmental protection of the Antarctic region and the surrounding Southern Ocean since the negotiation of the Treaty itself in the late 1950s. Many of the significant developments in the ATS, for example the Agreed Measures for the Protection of Flora and Fauna (1964), the negotiation of the of the CAMLR Convention, and subsequently the Madrid Protocol, grew from concerns about the Antarctic environment, human pressure, and the need to base management decision-making on best available science.

The Need for Science

Antarctic research over the past three decades has shown that the Antarctic marine environment is changing: the ocean and atmosphere are warming with significant regional impacts; atmospheric and oceanographic changes are occurring, affecting sea-ice, ice sheet stability, and impacting the global overturning circulation of the ocean; and the chemistry of the ocean is changing with increased acidity and changes in oxygen saturation.

Biological changes are also occurring with shifts in predator distributions, pelagic species ranges, and potential changes to food-chains and ecosystems. While some marine species will be resilient to physical and chemical changes in the Southern Ocean, there is great potential for ecological disruption, and consequences for productivity. Southward shifts in global

[7]See, for example, Cvitanovic et al. (2015); Lacey et al. (2018), and Norström et al. (2020).

[8]The Antarctic Treaty System is the combination of international agreements, bodies established under these agreements, and the corpus of decisions made under them, since and including the 1959 Antarctic Treaty.

fisheries productivity as a result of climate change are also projected[9]. Understanding these changes and their impacts is critical information for policy development, management, and decision-making.

The IPCC's 2019 Special Report on Oceans and Cryosphere in a Changing Climate (SROCC) report highlighted the importance of understanding spatial and temporal scale in responding to climate change, acknowledging that established governance arrangements are often unsuited to dealing with changes over large geographical regions and long timeframes[10]. The report also emphasized the importance of precautionary and science-based management in the context of climate change.

Given that both precaution and science-based policy-making are embedded in the Antarctic Treaty System, it is imperative that clear pathways for the delivery of science into policy, and research responses to policy needs, are identified and strengthened.

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) established under the CAMLR Convention, is often cited as a "best practice" regional marine management body. It has been praised for its precautionary approach to setting catch limits for exploited fish stocks; its exemplary measures to reduce Illegal, Unreported and Unregulated (IUU) fishing; and its success in almost eliminating the by-catch of sea birds, particularly albatrosses and petrels. It is worth noting here, that the precautionary approach should be both incremental and iterative. Precautionary decisions, based on the best available science, should minimize the risk of failure and maximize chances for recovery from potential failure. CCAMLR's decision rules for krill and toothfish catch, and for exploratory fisheries are such examples.

In recent years, CCAMLR has been subject to criticism for failing to agree, through consensus, to the expansion of marine protected areas in Antarctica.

The CAMLR Convention, includes the mandate to conserve Antarctic marine living resources, including:

> "maintenance of the ecological relationships between harvested, dependent and related populations of Antarctic marine living resources and the restoration of depleted populations. . .; and
>
> "prevention of changes or minimisation of the risk of changes in the marine ecosystem which are not potentially reversible over two or three decades, taking into account the state of available knowledge of the direct and indirect impact of harvesting, the effect of the introduction of alien species, the effects of associated activities on the marine ecosystem and of the effects of environmental changes, with the aim of making possible the sustained conservation of Antarctic marine living resources"[11]. [Author's emphasis].

It follows that in order to achieve the goals of the CAMLR Convention, there must be a strong link between science and policy-making. While the absence of 'complete' scientific information is not an inhibition on developing law and Measures[12] by CCAMLR (see the extract from the Convention above) there is a need to gather scientific information that allows CCAMLR to fulfill its obligations under international law. These obligations span not only the setting of catch limits and regulation of fisheries, but they preferentially extend to the protection of the Antarctic ecosystem[13], species conservation, the management of human impacts such as fishing, and responding to the impacts of climate change.

The duty to protect the Antarctic environment contained in Antarctic law[14] requires a dynamic relationship between science and policy. Policy-makers cannot wait for perfect scientific information—to do so would foreclose options for future decision making, and restrict the ability to effectively manage environmental change. Scientific "evidence" will never be perfect, therefore effective decision making requires assessment of available knowledge, risk, and the consequences of non-action.

The Antarctic region is undergoing change, both human and climate-related, and "waiting", in the opinion of this author, is not rational. Both policy-makers and scientists should recognize that the future will be shaped by today's decisions (or non-decisions). Change is far more likely to produce more obstacles to protecting the Antarctic environment, than it will opportunities.

Given this, it follows that policy-makers require a range of scientific information for both short and long term decisions: information, for example, to establish precautionary catch limits; evaluations such as the status of species or the impacts of fishing or other environmental disturbances; and the status and trends of climate change impacts on the marine environment. Much of this information is directly relevant to the work of the CEP and decision-making in the Antarctic Treaty Consultative Meeting.

It is important to note in this context that effective science-policy dialogue requires an iterative approach that involves assessments now of trends and risks, clear articulation of policy needs, and the modes and ability of scientists and policy-makers to set tasks and programs of research.

The effective management of risk, of course, requires a willingness to make decisions.

CONCLUSION

Antarctic science is expensive, logistically difficult, requires detailed planning, and often takes considerable time to complete. Science that is directed to the conservation and management of the Antarctic environment will benefit from open and ongoing dialogue between policy-makers and scientists. Understanding

[9]IPCC (2019) Special Report on the Ocean and Cryosphere in a Changing Climate, Summary for Policy Makers, Figure SP3 pp 23–24, at https://www.ipcc.ch/site/assets/uploads/sites/3/2019/11/03_SROCC_SPM_FINAL.pdf

[10]IPCC, "Challenges" C.1.2., p29.

[11]Convention on the Conservation of Antarctic Marine Living Resources, Canberra. 1980, Article 2.

[12]Conservation Measures are legally binding decisions made under the CAMLR Convention by the Commission for the Conservation of Antarctic Marine Living Resources.

[13]Article 1 of the CAMLR Convention, including "The Antarctic marine ecosystem means the complex of relationships of Antarctic marine living resources with each other and with their physical environment."

[14]The requirements from the Antarctic Treaty and the ATCMs; the CAMLR Convention; and the Madrid Protocol.

what policy-makers need in order to make decisions, and policy-makers understanding the context and limits of the scientific endeavor, will lead to better outcomes for both "sides" of the dialogue. Planning both short term and long term scientific research programs to inform decision making should be integrated in policy development, research planning and the workplans of Antarctic organizations.

This process must incorporate dialogue that understands risk. Decision-rules, for example, can use metrics derived from science or expert advice that is provided to inform policy in order to keep risks to a satisfactory level (for example precautionary catch limits). The dialogue should involve scientists, stakeholders and policy makers in discussion of desired outcomes and risk, and the limits of policy. The desired outcome in this context is the conservation of the Antarctic marine environment, and the tolerance of the risk that decisions leading to adverse consequences will be very low.

The 2017 CCAMLR Performance review addressed these issued directly[15]. Among its recommendations were that:

> "The Scientific Committee evaluate options for ecosystem-based management of all CCAMLR fisheries, taking into account ecosystem and climate change and the types of data that can be reliably obtained. . .
>
> "CCAMLR implements practical mechanisms to coordinate and deliver research activities among Members to deliver the long-term research required by the Commission to achieve its objective, including better targeted fish stock research to ascertain productivity and yield of stocks across their ranges, and analyses of status and trends of those stocks and Antarctic marine living resources more generally. . . and,
>
> "A management-science forum across the Commission and the Scientific Committee be established to facilitate open communication and dialogue between scientists and policy makers involved in CCAMLR on key topics and issues and their respective expectations for science and policy."

These recommendations are hardly controversial. On the contrary, their implementation broadly would considerably enhance the protection of the Antarctic environment.

Policy making and scientific endeavor are two different pursuits, but the delivery of the goal of protecting the Antarctic environment requires both. While the politicization of science should be fought vigorously, dialogue between the "politicians" and the scientists is vital to Antarctica's future.

[15] See https://www.ccamlr.org/en/system/files/e-cc-xxxvi-01-w-cp.pdf, accessed 21 May 2020.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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Phenology and Environmental Control of Phytoplankton Blooms in the Kong Håkon VII Hav in the Southern Ocean

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Knowing the magnitude and timing of pelagic primary production is important for ecosystem and carbon sequestration studies, in addition to providing basic understanding of phytoplankton functioning. In this study we use data from an ecosystem cruise to Kong Håkon VII Hav, in the Atlantic sector of the Southern Ocean, in March 2019 and more than two decades of satellite-derived ocean color to study phytoplankton bloom phenology. During the cruise we observed phytoplankton blooms in different bloom phases. By correlating bloom phenology indices (i.e., bloom initiation and end) based on satellite remote sensing to the timing of changes in environmental conditions (i.e., sea ice, light, and mixed layer depth) we studied the environmental factors that seemingly drive phytoplankton blooms in the area. Our results show that blooms mainly take place in January and February, consistent with previous studies that include the area. Sea ice retreat controls the bloom initiation in particular along the coast and the western part of the study area, whereas bloom end is not primarily connected to sea ice advance. Light availability in general is not appearing to control the bloom termination, neither is nutrient availability based on the autumn cruise where we observed non-depleted macronutrient reservoirs in the surface. Instead, we surmise that zooplankton grazing plays a potentially large role to end the bloom, and thus controls its duration. The spatial correlation of the highest bloom magnitude with marked topographic features indicate that the interaction of ocean currents with sea floor topography enhances primary productivity in this area, probably by natural fertilization. Based on the bloom timing and magnitude patterns, we identified five different bloom regimes in the area. A more detailed understanding of the region will help to highlight areas with the highest relevance for the carbon cycle, the marine ecosystem and spatial management. With this gained understanding of bloom phenology, it will also be possible to study potential shifts in bloom timing and associated trophic mismatch caused by environmental changes.

Keywords: phytoplankton, Southern Ocean, phenology, bloom, sea ice zone

HIGHLIGHTS

- Five different phytoplankton bloom regimes are observed in the study area, Kong Håkon VII Hav.
- The evolution of sea ice extent plays a role for bloom initiation in large parts of the area, but not for bloom end.
- The bloom magnitude is controlled by currents interaction with ridges and other topographic features.

INTRODUCTION

Phytoplankton in the high latitudes are known to form blooms, that is, relatively short periods (<10 weeks) of intense growth and rapid increase in biomass (Racault et al., 2012; Sallée et al., 2015; Ardyna et al., 2017). A bloom can occur when algal growth is larger than the losses due to, e.g., grazing and sinking (for concepts, see Behrenfeld and Boss, 2018). Growth is primarily controlled by access to sunlight and nutrients, which typically coincide in the spring-summer part of the year. In polar areas, light availability is heavily restricted by sea ice cover as snow and ice have high albedo relative to seawater (Brandt et al., 2005; Nicolaus et al., 2010; Perovich and Polashenski, 2012), whereas the upper water column stratification regulates both light and nutrients availability. A shallow surface mixed layer both enables the algal cells to remain in the sunlit surface layer but also restricts nutrient replenishment from the reservoir below the mixed layer.

In the Southern Ocean, iron availability is particularly limiting to phytoplankton growth, partly because of the absence of atmospheric iron deposition (Tagliabue et al., 2017). Iron input from marine sources, such as sediments and deep water masses is thus essential for surface production. The mechanisms causing vertical mixing and surface nutrient supply are, e.g., ice-shelf meltwater driven circulation, dynamic instabilities and storms, and ocean currents interacting with bottom topography or land masses (e.g., Sokolov and Rintoul, 2007; Nicholson et al., 2016; Dinniman et al., 2020). Important current patterns in the region of interest include the Antarctic Slope Current flowing westward along the continental shelf break in the southern part of the study area (Le Paih et al., 2020) and the eastern inflow of the Weddell Gyre with southward and westward currents in the deep ocean further north in the study area (Vernet et al., 2019). In addition, observations and models reveal hot-spots of enhanced vertical mixing along the Antarctic continental shelf break due to interactions of tides with the sloping topography (Pereira et al., 2002; Fer et al., 2016). Strong topographic waves occur around ridges along the coast of Dronning Maud Land (Sun et al., 2019) with Gunnerus Ridge showing some of the highest energy densities for bottom trapped internal tides around Antarctica (Falahat and Nycander, 2015). These processes are expected to locally enhance cross-slope exchange (Skarðhamar et al., 2015) and mixing that can supply nutrients toward the surface layer (Dong et al., 2016).

Whereas nutrient availability controls primarily the magnitude of the blooms, light availability is important for the timing of the blooms. Phytoplankton blooms following the retreating sea ice edge in spring is a known phenomenon from both polar areas and illustrate the effect of the various controlling factors. Ice edge blooms have been observed in, e.g., the Weddell Sea (Lancelot et al., 1993), though not everywhere in the Southern Ocean (Constable et al., 2003). They are thought to be linked to increased light availability due to sea ice disappearance as well as increased water column stabilization due to increased warming and sea ice melt that adds fresh water to the surface layer. Modeling results of the Southern Ocean confirm these processes as major controlling factors of ice edge phytoplankton blooms (Taylor et al., 2013). In addition, melting sea ice releases iron to surface waters and thereby enhances growth (Lannuzel et al., 2016). On the contrary, the onset of the spring bloom in the North Atlantic and Antarctic Circumpolar Current (ACC) part of the Southern Ocean, when considering vertically integrated biomass, has been in recent studies observed to occur in winter while the mixed layer depth (MLD) was at its maximum or still deepening (Behrenfeld, 2010; Sallée et al., 2015). Therefore, it was concluded that mixed layer deepening, which causes a dilution effect and decreases encounters with zooplankton grazers and loss rates, allowed for bloom onset (defined as growth rate exceeding the loss rates for the vertically integrated bloom over the MLD), rather than the mixed layer shoaling and the associated better light conditions (Behrenfeld, 2010). In a modeling study for Southern Ocean it was concluded, however, that if mixing was too deep, the dilution effect would be counteracted by light limitation, and bloom development would be delayed (Llort et al., 2015).

The importance of understanding these high latitudes blooms lies in the high primary productivity (for the Southern Ocean see Arrigo et al., 2008), in some cases the very high vertical export affecting the benthos and CO_2 sequestration (Legendre, 1990; Smetacek et al., 2012) and that the reproduction of grazers may coincide with blooms (Søreide et al., 2010; Atkinson et al., 2012; Svensen et al., 2019). Regarding phenology (timing of the blooms), the initiation of the bloom, the timing of the maximum concentration and the termination of the bloom are key parameters to study. Studies of bloom phenology and regimes in the Southern Ocean are mainly based on satellite remote sensing data and focus on delineating different bloom regimes and the environmental control of bloom timing and interannual variability. According to these studies, oceanic fronts, iron supply sources and the sea ice extent largely define the geographical boundaries of various bloom regimes, such as the Antarctic Circumpolar Current region or the Marginal Ice Zone (Thomalla et al., 2011; Sallée et al., 2015; Soppa et al., 2016; Ardyna et al., 2017). Bloom timing is mainly controlled by the seasonal cycle in light, MLD dynamics, and sea ice phenology (Thomalla et al., 2011; Llort et al., 2015; Sallée et al., 2015; Ardyna et al., 2017).

This study was conducted in the Southern Ocean and is partly based on a research cruise that took place in early autumn (February–April 2019) in the Kong Håkon VII Hav, the areas east of the prime meridian and outside of Dronning Maud Land. During the cruise we observed phytoplankton blooms in different bloom phases, from traces of a bloom to a bloom that was still present in the surface waters. To understand the bloom patterns, we used the satellite remote sensing records of surface chlorophyll (Chl) *a* concentration to

study the bloom phenology and compared the bloom timing to temporal patterns in environmental controlling factors. Most of the above-mentioned studies have the whole Southern Ocean as a focus area, with some focusing on regions further north than our study area. In addition, the remote sensing dataset we utilized (23 years, 1997–2020) is considerably longer than what was available for many of these studies. Furthermore, there are inherent limitations to satellite remote sensing data, such as the limited depth of the observations or array of variables provided, that can only be overcome by combining other data sources to the analysis, such as the *in situ* data described here. Therefore our study can contribute to new understanding, with the specific aim to characterize this area which has seldom received detailed attention besides the Maud Rise area (e.g., von Berg et al., 2020). The objectives of this paper are to describe the phytoplankton bloom phase, timing, and magnitude as observed during the autumn cruise and from the long-term ocean color remote sensing records; to explain the observed bloom patterns based on the environmental controlling factors of the bloom development, namely sea ice cover, light and MLD, and tidally induced mixing; and to delineate regional bloom regimes.

MATERIALS AND METHODS

Cruise Observations

Cruise Area, Water Sampling and Laboratory Methods

In February to April 2019 we conducted a research cruise to the Kong Håkon VII Hav, a sea in the Atlantic sector of the Southern Ocean, onboard the research icebreaker Kronprins Haakon (**Figure 1**). The main objective of the research cruise was to study the oceanography and ecosystem dynamics of this poorly studied area.

To characterize the phytoplankton blooms, water sampling was conducted between 12 and 31 March at 37 stations with station numbers counting upward from 53 (due to continuation of the numbering after a previous cruise). The stations were located between 64.8–69.5° S and 2.3–13.5° E, and the cruise area includes topographic features such as the Maud Rise at circa 3° E and Astrid Ridge at circa 12° E (**Figure 1**). The main sampling efforts were targeted to Astrid Ridge, a north-south transect at 6° E, and Maud Rise. Water samples were collected with a 24-bottle or 12-bottle SBE 32 carousel water sampler from a multitude of depths.

In addition, during longer transits, water samples were collected every 4 h from the ship's scientific seawater intake at 4 m depth. Chl *a* samples were used to calibrate the underway fluorometer (WETStar, Sea-Bird Scientific, with a measurement frequency once per minute) with the equation $y = 0.09x + 0.06$ ($R^2 = 0.85$). Dividing the dataset between day and night time values resulted in very similar equations ($y = 0.10x + 0.07$ and $y = 0.09x + 0.04$, respectively).

Chl *a* samples were filtered (typically 1 L) through 0.7 μm GF/F filters (GE Healthcare, Little Chalfont, United Kingdom) under low vacuum pressure (approximately −30 kPa). Extraction was done with 100% methanol at 5°C in the dark for 24 h (Holm-Hansen and Riemann, 1978). The pigment concentration, including phaeopigments, was measured with a Turner 10-AU Fluorometer (Turner Designs, San Jose, CA, United States) that had been calibrated prior to the cruise.

The abundance of bacteria was determined using an Attune™ NxT Acoustic Focusing Cytometer (Invitrogen™, Thermo Fisher Scientific Inc., United States) equipped with a 50 mW 488 nm (blue) laser. Samples (4.5 mL) were fixed with glutaraldehyde (0.5% final concentration) and stored frozen at −80°C until analysis within 6 months. The samples were thawed and diluted x10 with 0.2 μm filtered TE buffer (Tris 10 mM, EDTA 1 mM, pH 8), stained with SYBR Green I (Molecular Probes, Eugene, OR, United States) at a final concentration of 1:10,000 of the commercial stock solution and then incubated for 10 min in darkness at room temperature (protocol based on Marie et al., 1999). Bacteria were discriminated and counted using biparametric plot based on side scatter and green fluorescence.

Nutrient samples for the analysis of nitrate (NO_3^-), phosphate (PO_4^{3-}), and silicic acid ($Si(OH)_4$) were collected into 20 mL vials, fixed with 250 μL of chloroform and stored in fridge until standard analysis at Institute of Marine Research, Bergen, Norway using Autoanalyzer (Skalar) and the spectrophotometric method described in detail in Grasshoff et al. (2009). The detection limits are 0.5 μmol L^{-1}, 0.06 μmol L^{-1}, and 0.7 μmol L^{-1} for nitrate, phosphate, and silicic acid, respectively.

Chlorophyll *a* Fluorescence Profiles From CTD Casts

Chl *a* fluorescence in the water column (*in situ*) was measured with a WETLabs ECO fluorometer in connection with CTD (conductivity-temperature-depth) casts (SBE911 + system) and water sampling. Data were bin-averaged in 1 m bins. The factory calibration dark count value was corrected to a value chosen by taking the mode of values below 500 m. Sensor sensitivity was adjusted mid-way through the cruise and the data before and after were processed separately. Certain stations (61, 62, and 77 to 86 – corresponding to 12 out of 65 profiles) experienced baseline shifts [the deep value (dark counts) of the fluorescence profiles was lower than in other profiles and compared to the overall mode value]. These were baseline corrected before the calibration and any further analysis by adding the difference between the mode value of the profile in question and the overall mode value. The shift in baseline was, however, minimal and corresponded to 0.03 mg Chl *a* m^{-3}.

The baseline-corrected fluorescence profiles were calibrated with the concurrent Chl *a* water samples. A linear fit was calculated with the help of the dark value defined above and the median of upcast values in a 2 m window around the water sample depth (water samples were taken during the upcast) to obtain a calibration equation ($y = 3.05x - 0.05$ and $y = 0.44x - 0.03$ for before and after the sensitivity setting change, respectively). R^2 was 0.74 and 0.67, respectively. The equation was used to calibrate the downcast values, which are assumed to be most representative of the undisturbed water column and are being used for further analysis. However, the upper 15 m of the water column was thereafter discarded in the analysis of vertical structures due to possible disturbances from the ship.

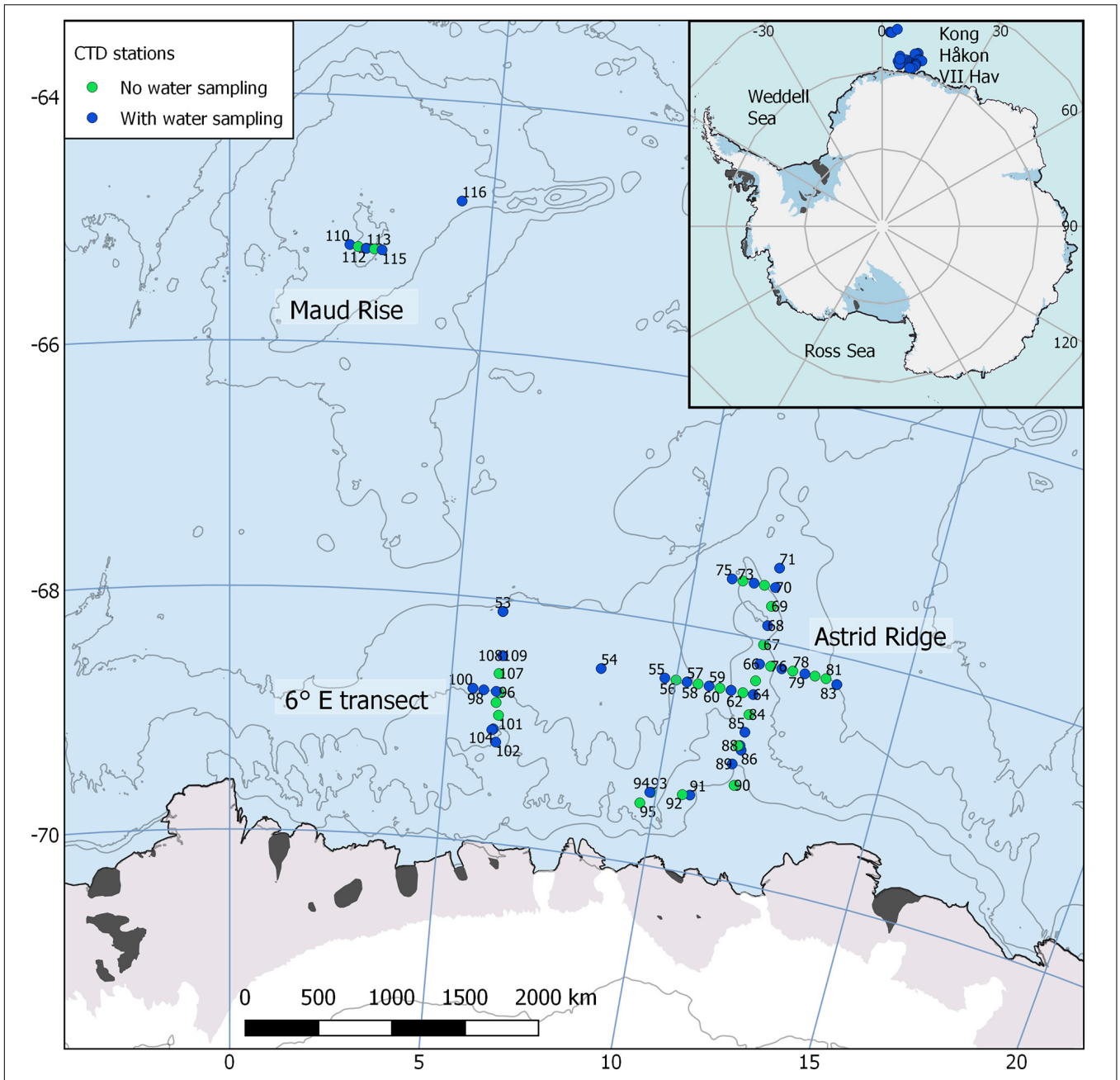

FIGURE 1 | Map of the cruise area, located east of prime meridian in the Kong Håkon VII Hav, showing the sampling stations. Water sampling was conducted at approximately every second station and was focused on the Astrid Ridge, a transect at 6° E and Maud Rise. Map created with the help of Quantarctica (Norwegian Polar Institute, 2018).

In high light intensities, the fluorescence signal is affected by algal non-photochemical quenching (cellular processes such as pigment alterations) lowering the proportion of absorbed light that is emitted as fluorescence (Brunet et al., 2011). In the absence of coinciding light backscattering profiles we have corrected for non-photochemical quenching in daytime profiles (based on local sunrise and sunset) by extrapolating the maximum fluorescence value within the MLD to the surface, a method used previously in the Southern Ocean (Xing et al., 2012).

Mixed Layer Depth

Mixed layer depth was defined as the extent of the currently active surface mixed layer, taken as the depth where the salinity (which is determining for density in our environment) increases by 0.01 between two pressure binned values (1 m bin size) after filtering the profile with a 7 pt running median filter to remove spikes. The upper 15 m of the profiles have been disregarded because of spikes in the data and possible disturbances by the ship on the vertical structure of that part of the water column. This criterion

essentially uses a density gradient threshold (Holte and Talley, 2009) to identify the surface ocean slab where physical properties such as density, salinity, or temperature are well mixed, i.e., nearly homogeneous with depth (Pellichero et al., 2017).

Zooplankton Sampling and Acoustics

Mesozooplankton was sampled by vertical hauls from 200 m to the surface using a double WP2 (bongo) plankton net (0.25 m^2, 180 μm mesh size, hauling speed 0.5 m sec^{-1}). Each sample was split in two halves with a Motoda splitter device. One half of the sample was preserved in 4% borax-buffered formaldehyde-seawater solution, and the other half in 97% ethanol. The abundance and taxonomic composition of zooplankton in the formalin fixed samples were determined using FlowCam (Yokogawa Fluid Imaging Technologies, Inc., Japan) (Sieracki et al., 1998). The samples were washed and diluted with 2750 ml of fresh-water, kept suspended using an overhead stirrer and imaged using a FlowCam macro (0.5 × objective, 10 mm × 5 mm flow-cell, and a flow rate of 375 ml min^{-1}). We applied the automatic image segregation and feature extraction procedure described by Álvarez et al. (2012) and created our training set and classifier using the r-package Zooimage (Grosjean and Denis, 2014; Vu et al., 2014). The classifier was based on a random forest machine learning algorithm and had an error rate of 12% determined by 10-fold cross validation.

Krill was studied with the help of echosounding. The acoustic equipment in use was Simrad EK80 research echosounder with six frequencies. The 38 kHz was scrutinized for this study. Scrutinization was done in LSSS (Korneliussen et al., 2016) version 2.5.0. There were two transducers on the research vessel, one on the drop-keel (3 m from hull when down) and one hull-mounted. In ice-covered areas it was not possible to have the drop-keel lowered, and the hull-mounted transducer was in use in these areas. Sea ice and the use of the hull-mounted transducer may have considerably affected registrations in depth but can be assumed to have minor effect on registrations of krill swarms, as they occur in relatively shallow waters. Krill density is given as nautical area scattering coefficient (NASC), which expresses integrated amounts of the acoustic echo that is assigned to krill and can be viewed as proportional to abundance (Maclennan et al., 2002).

Phenology Indices

Bloom Phenology

To include adjacent areas in all directions for context of the cruise area (**Figure 1**), remote sensing products are presented between 10° W and 50° E and 60° and 71° S, which also includes the Gunnerus Ridge at ca. 35° E, hereafter referred to as the study area.

Level 3 Chl *a* satellite remote sensing data from Ocean Colour Climate Change Initiative dataset (OC-CCI), version 4.2 (European Space Agency, available online at http://www.esa-oceancolour-cci.org; Sathyendranath et al., 2019, 2020) in 8-day and 4 km resolution were used for bloom phenology studies. The data span from September 1997 to March 2020 and are merged from several sensors including SeaWIFS, MODIS, MERIS, and VIIRS. To test the reliability of the OC-CCI product in such high latitude environment, we ran a similar analysis with the unmerged products from SeaWIFS and MODIS (results not shown). This yielded similar results for bloom timing indices than with the OC-CCI (the bloom amplitude was somewhat higher but in the same range). The OC-CCI product was, therefore, chosen as the main data product due to its continuity in time, higher spatial and temporal coverage, and the uncertainty estimates provided with the data.

The performance tests for OC-CCI (Sathyendranath et al., 2019) indicated that sea ice is masked effectively (99.9% of sea ice/snow pixels classified as sea ice/snow or clouds; their Table 3). However, sea ice can also affect values in nearby pixels due to the adjacency effect (reflectance from the nearby pixels containing sea ice affects the remote sensing reflectance retrieval for the pixel in question through atmospheric scattering) for up to 20 km distance (Bélanger et al., 2007). To account for this, we masked out the adjacent pixels to sea ice. Sea ice concentration (see section "Sea Ice Phenology" for details) from the beginning of each satellite week was interpolated to match the Chl *a* data coordinates and concentrations above 15% were classified as ice-containing pixels. Thereafter, five pixels (corresponding to ∼20 km) in each direction from the ice-containing pixels were excluded from the Chl *a* dataset before further analysis.

The uncertainty estimates for the OC-CCI product indicated higher uncertainty in the data along the coast (**Supplementary Figures 1A,B**). The root mean square deviation (RMSD) values are here constantly elevated and higher than the range for the different optical water classes presented in the **Figure 4** of Sathyendranath et al. (2019). In addition, an early analysis showed anomalous phenology index values in these areas (not shown). Therefore these areas were permanently excluded from the analysis (**Supplementary Figure 1C**). To do so, the long-term means of RMSD were first calculated for each satellite week. The maximum geographical appearance of out-of-range values (compared to the Figure 4 of Sathyendranath et al., 2019) in areas close to the coast (areas with less than 3000 m bottom depth south of 66°S) was masked before further analysis (that is, the maximum of the weekly means for each pixel was considered for the comparison with the **Figure 4** values). For large parts of the year, these areas are already masked because of sea ice.

A year in this context is from July to June to include the Southern hemisphere productive season (i.e., Austral summer) within 1 year. As the Austral winter months lack data for a long period, the exact choice of start date for the year is not relevant. However, phenology results are reported with satellite week numbers corresponding to the beginning of a calendar year for easier interpretation (e.g., satellite week 1 starts January 1st). We have followed the methodology of the global bloom phenology study by Racault et al. (2012). To reduce gaps in the data, a spatial median filter (3 by 3 pixels) was applied to missing pixels. Thereafter, if a pixel was still empty, an average of the week before and after (if both contained data in the original, non-interpolated matrix) was taken. To smooth spikes in the data a 3-week moving median filter was applied to the pixels that contained data (that is, empty pixels were maintained in this step and no interpolation was done). Thus, the interpolation filled gaps of maximum 1 week. The effect of the interpolation methods

TABLE 1 | Bloom phenology indices calculated for a given Austral year (i.e., July to June).

Index	Abbreviation	Definition
Used in this study		
Initiation	Bi	First time when bloom concentration exceeds the threshold for (at minimum) 2 consecutive weeks
Timing of maximum	Bt	Timing of maximum bloom concentration
Amplitude	Ba	Maximum Chl *a* concentration
Mean concentration	Bm	Mean Chl *a* concentration during the bloom
End	Be	Last time when bloom concentration exceeds the threshold for (at minimum) 2 consecutive weeks
Duration	Bd	Time between bloom initiation and bloom end
Additionally found in the literature		
Onset		When the rate of change is positive for the first time
Climax		Maximum positive rate of change
Apex		When rate of change becomes negative after bloom onset (bloom peak/timing of maximum)

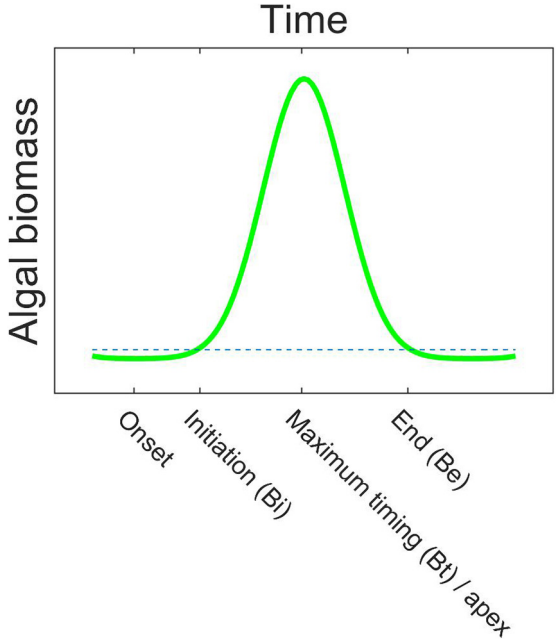

FIGURE 2 | An idealized bloom with the bloom phenology indices bloom onset, initiation (Bi), timing of maximum concentration (Bt)/apex, and end (Be) indicated. The stippled line is the 1.05 times median threshold. See **Table 1** for further index explanations.

on the phenology results is shown in **Supplementary Figure 2** and discussed in section "Methodological Challenges."

We used a relative threshold -based approach as the bloom detection method, where the threshold was set to 1.05 times the annual median, which is a commonly used method (e.g., Racault et al., 2012; and for the Southern Ocean see Thomalla et al., 2011; Soppa et al., 2016). The used bloom phenology indices are defined in the following text, summarized in **Table 1**, and a selection is shown on a bloom schematics in **Figure 2**. To determine bloom initiation (Bi), the Chl *a* concentration had to exceed the threshold for at least 2 consecutive weeks. Bloom end (Be) was determined when the concentration for the last time exceeded the threshold on at least 2 consecutive weeks. The "first" bloom initiation and the "last" bloom end were recorded – i.e., if the concentration would fall below the threshold in between, this was not considered (a single bloom is characteristic for the Southern Ocean annual phytoplankton cycle; Arrigo et al., 2008; Ardyna et al., 2017). The bloom duration (Bd) is the time between bloom initiation and bloom end. In addition, maximum concentration (bloom amplitude, Ba), its timing (Bt), and the average concentration during the bloom (Bm) were calculated. For all the indices, a mean over all the years (23) is presented, called the long-term mean hereafter. To test the sensitivity of the bloom initiation results to the choice of detection method, we further tested a method based on the rate of change in the Chl *a* concentration (bloom initiation Bi_r), as outlined in the **Supplementary Material section 2**.

Cole et al. (2012) highlighted problems in the phenology studies arising from gaps in the data. This is especially true in the Southern Ocean where the calculated bloom initiation is likely to be found later than the true bloom initiation because the absence of winter data increases artificially the annual median and, thus, the threshold (Cole et al., 2012). For our results, where the exact date is of importance (in comparison with sea ice phenology), the consequences of biases are discussed (see also section "Methodological Challenges"). Even though we have interpolated the data to reduce the gaps (see above), austral summer data still has gaps with about 42–62% of pixels missing for a given week in January–February (average over all the years; including the permanently masked areas; **Supplementary Figure 3**). However, for the long-term means of the bloom phenology indices, the geographical pattern is not altered as we apply a rule that half of the years must contain index data for the mean to be calculated for a given pixel. In this case, the phenology indices were calculated for the vast majority of pixels (73%, where the 27% contain the permanently masked coastal areas).

The phenology index maps were drawn with the Matlab package M_Map (Pawlowicz, 2020) with colormaps from Thyng et al. (2016). For the "Discussion" section, a schematics figure was created to make regions with differing phenology index characteristics visible and to function as a schematics of the regional bloom regimes. Bloom mean concentration and bloom end maps were created with a blue-red diverging color map and a composite image of the two images was thereafter created with the Matlab Image Processing Toolbox (imfuse). The color gradient thus does not have a quantitative meaning.

Sea Ice Phenology

Daily sea ice concentration data in 25 km resolution from the National Snow and Ice Data Center (Cavalieri et al., 1996; updated yearly) from the years 1997 to 2019 were used to

calculate the sea ice phenology. A year in this context was defined from 1st of February to the following 31st of January because the Austral summer sea ice extent minimum occurs in February. For sea ice phenology indices we followed the methodology used in Stammerjohn et al. (2008) for the waters west of the Antarctic Peninsula. Each year, sea-ice advance was defined for each pixel as the time when sea-ice concentration exceeded 15% for 5 consecutive days. Similarly, the sea-ice retreat was defined when sea-ice concentration was for the last time in a given year above 15% for 5 consecutive days. If the sea-ice concentration was never below 15% for a given pixel, the day of advance was set as the first day of a year, and the day of retreat as the last day of a year. The sea-ice period is the time between advance and retreat, and the sea-ice persistence is the percentage of time (days) when the sea-ice concentration is above the threshold within the sea-ice period. If the concentration was never above the threshold for 5 consecutive days, these indices (sea-ice period and sea-ice persistence) were set to 0.

To compare the timing of sea ice retreat and advance with the phytoplankton blooms, the sea-ice phenology indices were re-gridded (via interpolation) to the coordinates of the bloom phenology indices, and the temporal resolution was reduced to 8-day "weeks" (all days belonging to a given satellite week were given that week number). Difference between the sea-ice and bloom timings indicated by the long-term means is presented here. For sea ice retreat and bloom initiation, 3 satellite weeks was chosen in the figures as the cut-off value for the timing difference to indicate dependence (cf. Perrette et al., 2011). Altering the sea-ice concentration threshold between 5 and 30% did not change the overall geographical pattern in the time difference between sea ice retreat and bloom initiation (not shown) so it is a robust method.

Data Products: Euphotic Depth, Photosynthetically Available Radiation, Mixed Layer Depth, Tides and Currents

Euphotic depth (ZEu, m) and daily incident irradiance in the photosynthetically available radiation range (PAR, 400–700 nm; mol m^{-2} day^{-1}; Frouin et al., 2003) satellite remote sensing data products were obtained from merged products by GlobColour[1] in 8-day resolution in the time frame 1997–2020. ZEu is based on satellite-derived Chl *a* concentration and the 1% PAR threshold (Morel et al., 2007). Weekly means (for 8-day satellite weeks) were calculated over the time series to obtain the seasonality.

MLD for Southern Ocean were obtained from Pellichero et al. (2017). The MLD climatology is estimated with monthly and half a degree resolution based on elephant seal-derived, ship-based, and Argo float observations. The amount of data from the different data sources and for the different areas is shown in their **Figure 1**, with areas around the prime meridian and Gunnerus Ridge having the best coverage in the study area. To study the light conditions for phytoplankton and compare ZEu with the MLDs, monthly means were calculated for ZEu, and MLD was interpolated to fit the coordinates of ZEu.

[1] www.globcolour.org

To assess the role of tidally induced mixing for bloom magnitude, maps of tidal kinetic energy were derived from a regional configuration of the ice shelf-augmented version of the Finite Volume Community Ocean Model (FVCOM; Zhou and Hattermann, 2020), which covers a zonal and meridional extent of about 4000 km × 4000 km of the wider Weddell Gyre circulation in the Atlantic sector of the Southern Ocean, while at the same time resolving the Kong Håkon VII Hav and Dronning Maud Land continental shelf break regions at mesh resolution of down to 1.5 km. The model is initialized and forced along the open boundary with results from the circumpolar metROMS solution of Naughten et al. (2018) and time series of tidal elevation from the TPXO global inverse barotropic tidal solution (Egbert and Erofeeva, 2002). Patterns of tidal elevation and current amplitudes from this model resemble the results from the Antarctic inverse barotropic tidal CATS2008b, an update to the model described by Padman et al. (2002, 2008), albeit showing a more detailed spatial structure in our study region and explicitly resolving the interaction of the tides with the background stratification that has been highlighted to be important along the Antarctic continental shelf break (Flexas et al., 2015; Stewart et al., 2019).

To assess the general ocean current patterns in the area, maps of L4 monthly means of mean kinetic energy (MKE) and surface current velocities were retrieved from Copernicus Marine Services (global ocean reanalysis product available at https://resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=GLOBAL_ANALYSIS_FORECAST_PHY_001_024). Data were available from January 2016 to December 2019 in 1/12° resolution.

RESULTS

Cruise Observations

The highest Chl *a* concentrations in the vertical *in situ* fluorescence profiles were observed at the open-ocean CTD station 53 at 68.1° S and 6.0° E and at Maud Rise (**Figure 3**). In the former, Chl *a* was concentrated in the upper 50 m with a deep maximum of 0.84 mg Chl *a* m^{-3} (at 42 m), whereas at Maud Rise, the highest Chl *a* concentrations were found below 50 m, with a maximum of 0.70 mg Chl *a* m^{-3}. Astrid Ridge and the 6°E transect CTD stations were characterized by low Chl *a* concentration, with maxima of 0.25 and 0.16 mg Chl *a* m^{-3}, respectively. The underway fluorometer measured somewhat higher values, up to 1.1 mg m^{-3}, in the area west of the station 53.

Bacterial abundance was highest in the east and south of the cruise area, i.e., at Astrid Ridge and the 6° E transect CTD stations, as well as at a station at 68.5° S and 8.3° E (CTD station 54), with maximum concentration of 3.8×10^5, 3.9×10^5, and 3.9×10^5 cells mL^{-1}, respectively (**Figure 4A**). The maximum concentration at Maud Rise and CTD station 53 was 2.3×10^5 and 2.6×10^5 cells mL^{-1}, respectively. Surface values were typically higher than deeper samples at the east and south stations while the abundance was more uniform at the west and north stations.

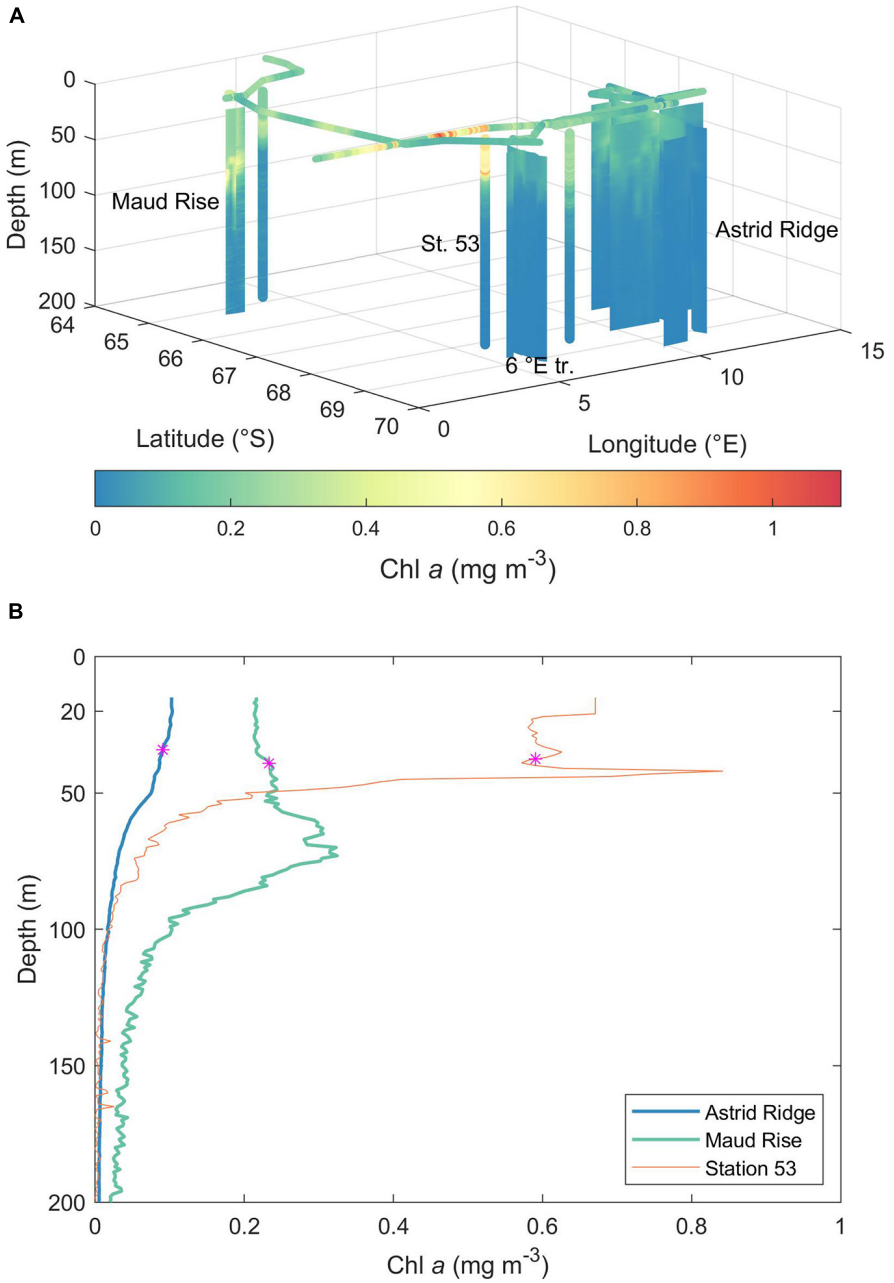

FIGURE 3 | (A) Chl *a* concentration during the cruise, as obtained from calibrated *in situ* fluorescence profiles and underway fluorescence measurements. See map (**Figure 1**) for 2D orientation of the sampling locations. St. 53, station 53; 6°E tr., 6°E transect. **(B)** Mean Chl *a* profiles of Astrid Ridge and Maud Rise stations and the profile from station 53. The magenta star shows the MLD (mean for Astrid Ridge and Maud Rise).

Macro-nutrient concentrations are shown for the upper 200 m (**Figures 4B–D**). The main features are differences between upper water column and deep values, and differences between the areas, especially regarding Maud Rise compared to the other sampling areas. The concentrations were in general lowest near the surface. For the CTD stations (upper 200 m), silicic acid ranged between 43.5 and 93.8 μM, nitrate ranged between 20.7 and 32.9 μM, and phosphate ranged between 1.5 and 2.3 μM. When including the underway samples, the lowest concentration for silicic acid was 33.0 μM and for phosphate 1.4 μM. The lowest values were observed at Maud rise except for the CTD station-based silicic acid minimum, which was at the 6° E transect. However, in general Maud Rise appears to have the smallest surface reservoirs, followed by the station 53. Regarding nitrate values at Astrid Ridge, the south-east had the lowest values.

Acoustic observations of euphausiids showed highly heterogeneous distributions across the study area (**Figure 5A**). The largest patches of krill swarms (*Euphausia superba*) occurred

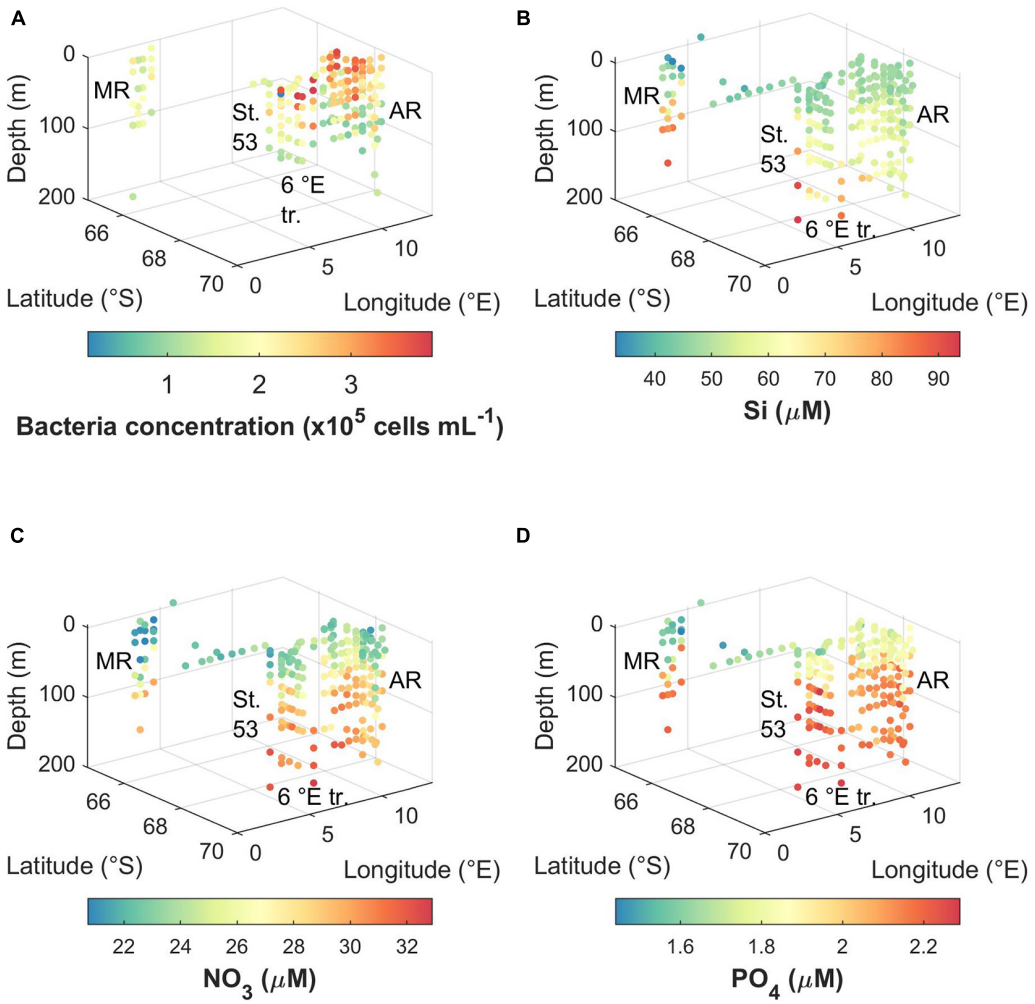

FIGURE 4 | Concentration of **(A)** bacteria, **(B)** silicic acid, **(C)** nitrate, and **(D)** phosphate during the cruise. MR, Maud Rise; St. 53, station 53; 6°E tr., 6°E transect; AR, Astrid Ridge.

in the northernmost part of the 6° E transect (yellow – red colors in the figure). Patches of euphausiids were also found at Astrid Ridge (green colors), but hardly at Maud Rise. Euphausiid larvae were also observed in net tows mainly outside of Maud Rise. Mesozooplankton abundances in upper 200 m were, on contrary, highest at Maud Rise, both in terms of numbers (960–2300 N m^{-3}; **Figure 5B**) and biomass (0.06–0.14 g m^{-3}). Abundances at Astrid Ridge and 6° E transect stations were generally lower, ranging from 330 to 1100 N m^{-3} (0.08–0.02 g m^{-3}). The zooplankton community was characterized by a large proportion of small sized copepods (180–1000 μm), nauplii and protists.

MLDs in the different sampling areas were on average (±standard deviation) 38, 34 (±14), 33 (±8), and 39 (±13) m for station 53, Astrid Ridge, 6° E transect and Maud Rise, respectively (**Figure 3B**). Average MLD of all stations was 36 (±13) m.

Bloom Phenology

In this section, results based on the long-term means of the phenology indices are presented. Blooms initiate during January in the majority of the study area (satellite weeks 1–4, January 1st to February 1st; **Figure 6A**). A band around Astrid Ridge initiates in late January – early February. Bloom initiation is in general earlier in the north than in the south, with especially the western area showing a distinction between near-slope and off-slope, open-ocean areas. The bloom initiation results based on the rate of change method are outlined in **Supplementary Material section 2** and are largely similar in that blooms initiate mainly in January, but with a somewhat different geographical pattern.

The timing of the maximum Chl *a* concentration during the bloom follows a similar geographical pattern to that of the bloom initiation, with the latest occurrences on and around Astrid Ridge and in the north-east corner of the study area (**Figure 6B**). The latter corresponds to the areas indicated as the southern boundary of the ACC and the southern ACC Front (Orsi et al., 1995), hereafter referred to as southern ACC.

The maximum Chl *a* concentration, i.e., bloom amplitude, is highest on a band starting west of Gunnerus Ridge and extending west past Astrid Ridge, and in general on the western side of the

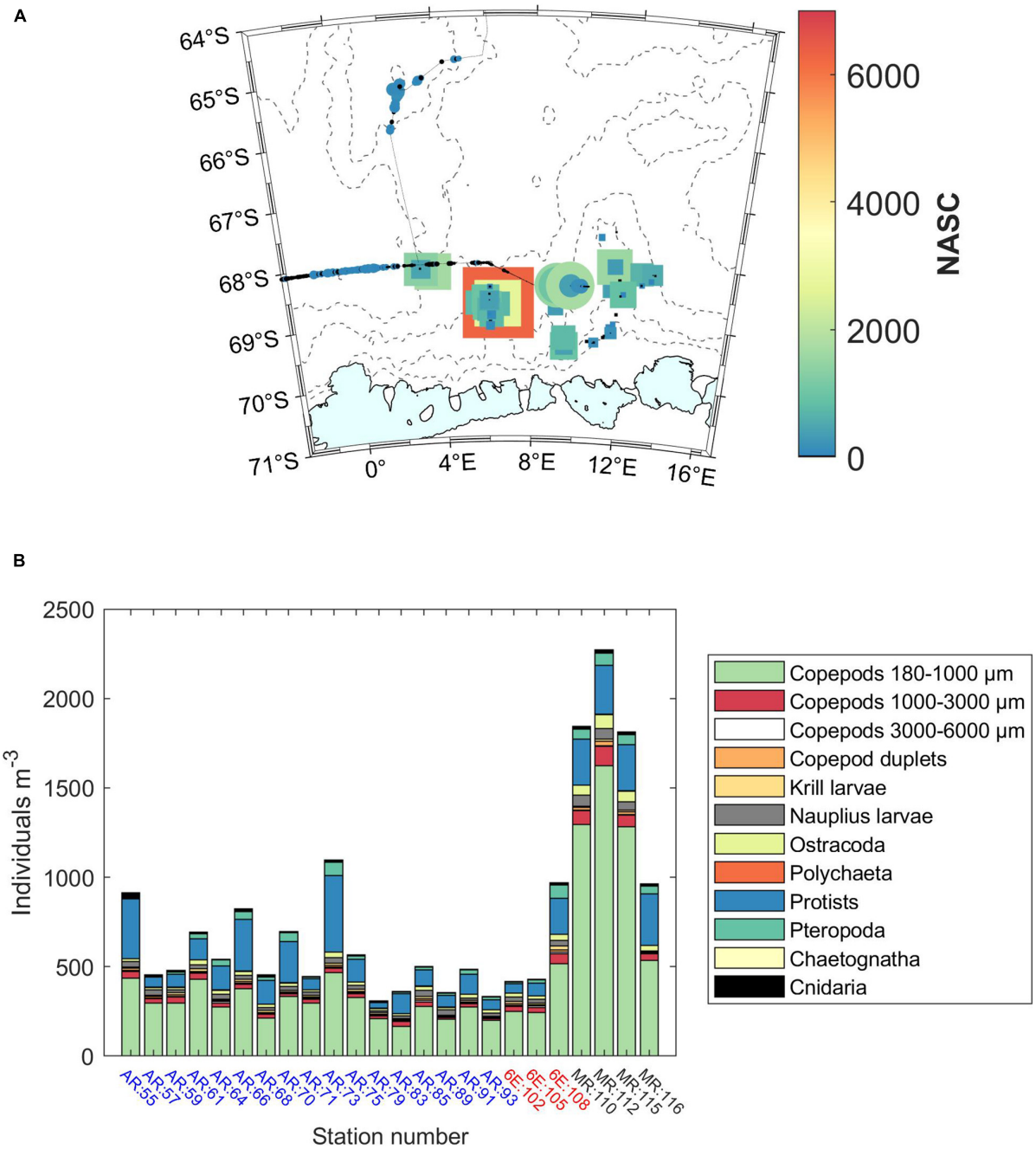

FIGURE 5 | (A) Acoustic observations of krill. Each marker represents the nautical area scattering coefficient (NASC) values integrated over 500 m distance, with size proportional to the value and color expressing the exact values (see color scale bar for values). Round symbols are used when data were retrieved with the drop-keel transducer, while square symbols are used when data were retrieved with the hull-mounted transducer. The hull-mounted transducer was used in ice-covered/ice-edge areas. **(B)** Abundances of different mesozooplankton groups obtained with the FlowCam. Astrid Ridge (AR) stations are numbers 55 to 93 and marked with blue; 6°E transect (6E) stations are numbers 102 to 108 marked with red, and Maud Rise (MR) stations are numbers 110 to 116 marked with black. Copepod duplets are images where two copepods are overlapping and can thus not be taxonomically classified.

study area, with values in the order of 0.5–2 mg m^{-3}, (**Figure 6C**). The blooms terminate in the end of January or during February (before satellite week 8, starting February 26th; **Figure 7A**). A band around Astrid Ridge, and the southern ACC have the latest bloom end in February. Bloom duration is thus 2–4 satellite weeks in the majority of the study area (**Figure 7B**), but longer in southern ACC lasting between 4 and 7 satellite weeks.

Regarding the variability of the long-term means, standard deviations (**Supplementary Figure 4**) are below 4 satellite weeks for the timing indices (bloom initiation, end and

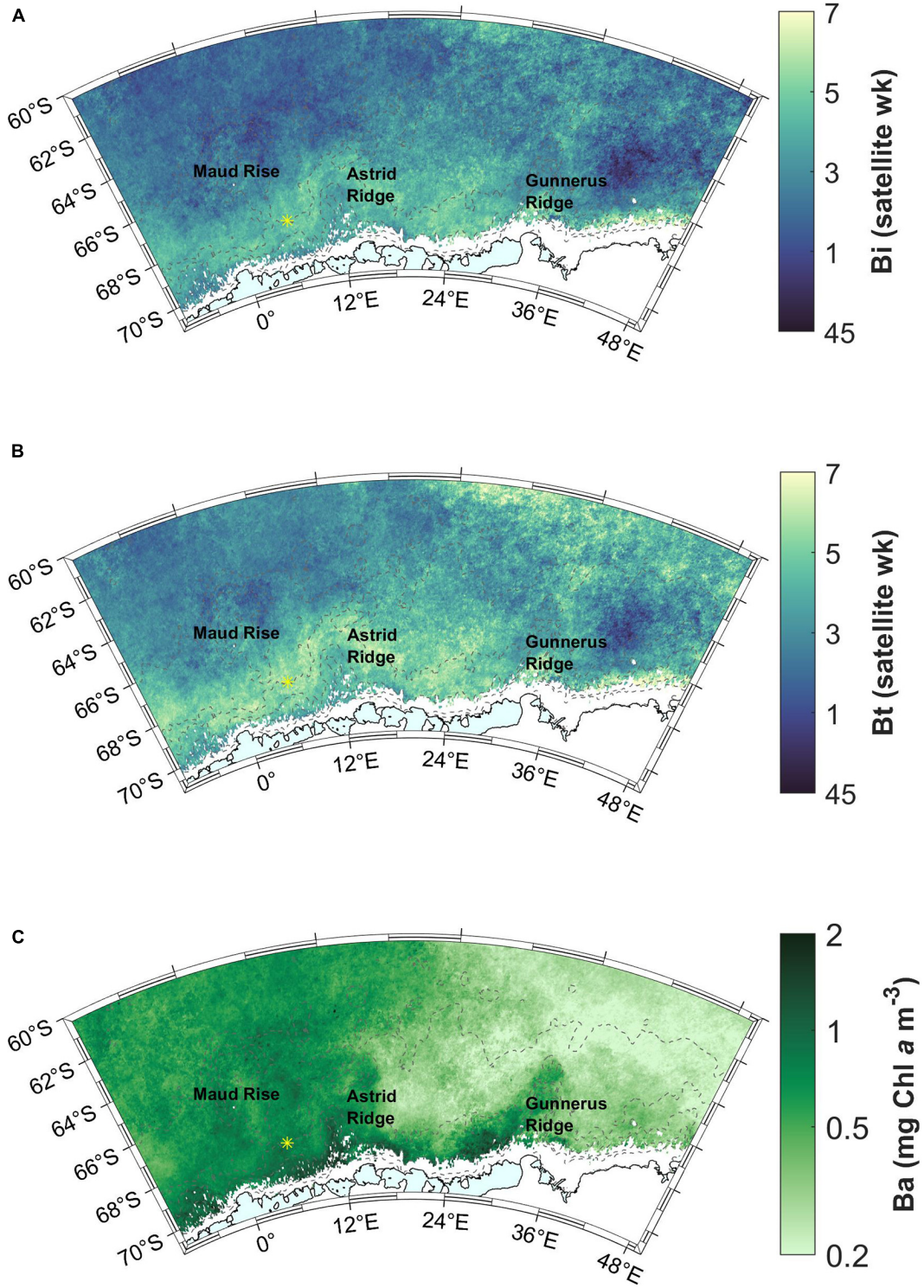

FIGURE 6 | (A) Bloom initiation (Bi) across the study area. **(B)** Timing of the bloom maximum concentration (Bt). Satellite week 1 starts on January 1st (there are 46 8-day "satellite weeks" in a year). Satellite week 5 starts on February 2nd. **(C)** Bloom amplitude (Ba). Station 53 is shown with a yellow asterisk.

maximum timing) in the majority of the study area, with southern ACC having the highest variability, whereas they are lower for the bloom duration (predominantly below 2 satellite weeks, except for the southern ACC). As such, although blooms may thus occur at somewhat different times in different years, they will have a similar bloom

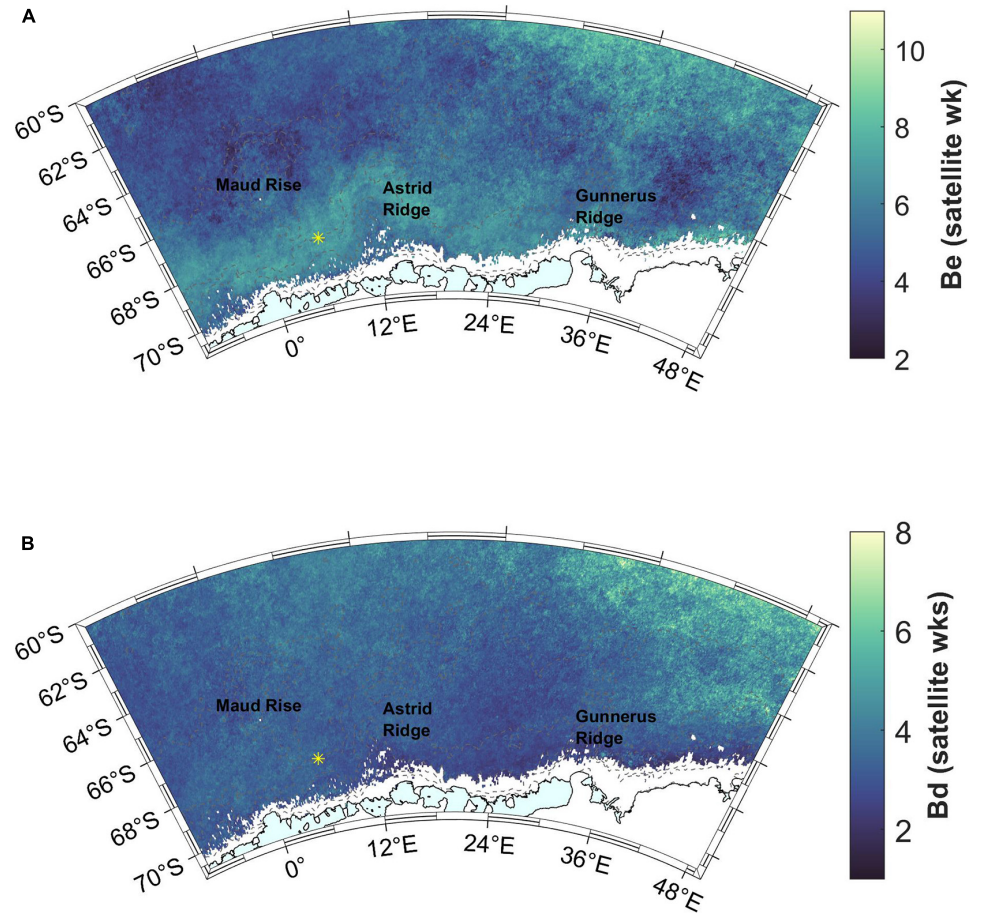

FIGURE 7 | (A) Bloom end (Be). Satellite week 5 starts on February 2nd and satellite week 8 on February 26th. **(B)** Bloom duration (Bd). Station 53 is shown with a yellow asterisk.

duration. Regarding bloom magnitude, standard deviations are highest (slightly above 1 mg Chl *a* mg^{-3}) in the areas where the highest Chl *a* concentrations are found, which indicates that the productive areas may have weak blooms in some years.

Sea Ice Phenology and Relation to Bloom Phenology

The whole study area is seasonally ice-covered with high (>90%) sea ice persistence (**Figure 8A**). Sea ice retreat is in December (between days 335 and 365) in large parts of the study area, with an earlier retreat at the southern ACC and a later retreat along the coast (**Figure 8B**). Maud Rise shows an earlier sea ice retreat than the surrounding areas. Sea ice advance is before March (before day 60) very close to the coast, and is gradually later further north (**Figure 8C**). The areas around and between Astrid and Gunnerus Ridges and the majority of Maud Rise have sea ice advance before June (before day 150), whereas the northern parts have even later sea ice advance. Standard deviations of the long-term means are shown in **Supplementary Figure 5** and are fairly low and uniform across the study area except for sea ice advance that has higher variability along the coast (standard deviation more than 30 days).

The blooms follow the sea ice retreat by less than 3 satellite weeks (24 days) in areas close to the coast (red areas in **Figure 9A**). Some other, smaller areas, especially west of Maud Rise, also fall within this time limit, whereas in large parts of the study area a longer time period elapses between sea ice retreat and bloom initiation. Especially the southern ACC shows a long time gap between sea ice retreat and bloom initiation, 6–8 satellite weeks, i.e., about 2 months. According to the rate of change method, a larger area in the west of the study area (around Maud Rise) falls within the time limit of 3 satellite weeks (**Supplementary Material section 2**).

Blooms end well before sea ice advance (more than 2 satellite weeks, i.e., 16 days) almost everywhere in the study area (blue areas in **Figure 9B**). For areas outside of the coastal ridges, this time gap is more than 10 weeks.

Light and Mixed Layer Depth

The annual maximum ZEu (study area average 138 m) and PAR (study area average 41 mol m^{-2} day^{-1}) mainly occur before

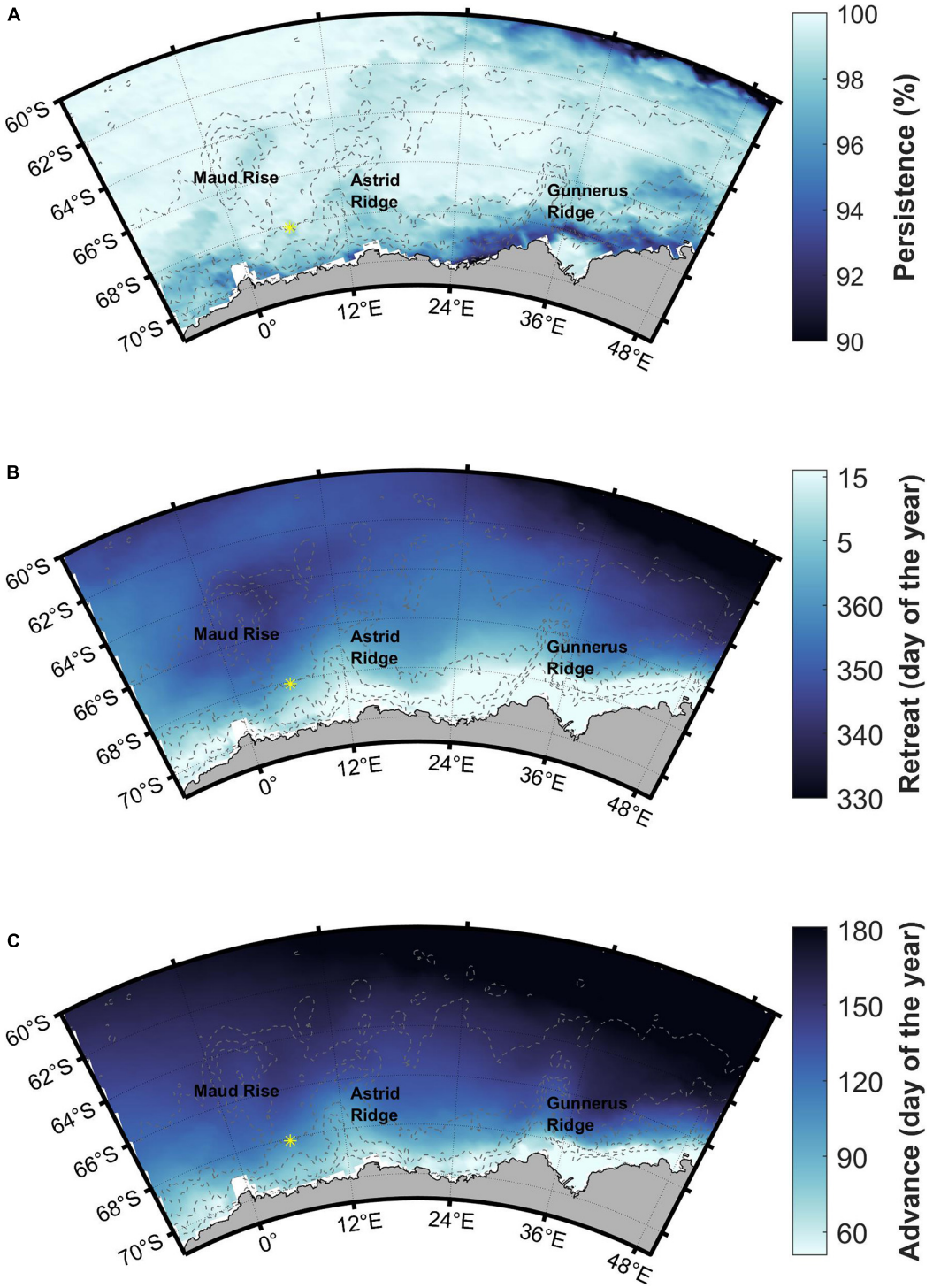

FIGURE 8 | Sea ice **(A)** persistence, **(B)** retreat, and **(C)** advance. Station 53 is shown with a yellow asterisk.

January, i.e., before the blooms; whereas ZEu is shallowest (study area average 60 m) mainly after that, i.e., during the blooms (not shown). For comparison with the MLD data, monthly means of ZEu were calculated. ZEu averaged for the entire study area for November, December, January, February, and March is 108 (±19), 78 (±13), 68 (±12), 72 (±10), and 80 (±8) m, respectively. The day length at the end of February in the study area is above 14 h (as calculated from the NOAA Solar Calculator)[2].

[2]https://www.esrl.noaa.gov/gmd/grad/solcalc/

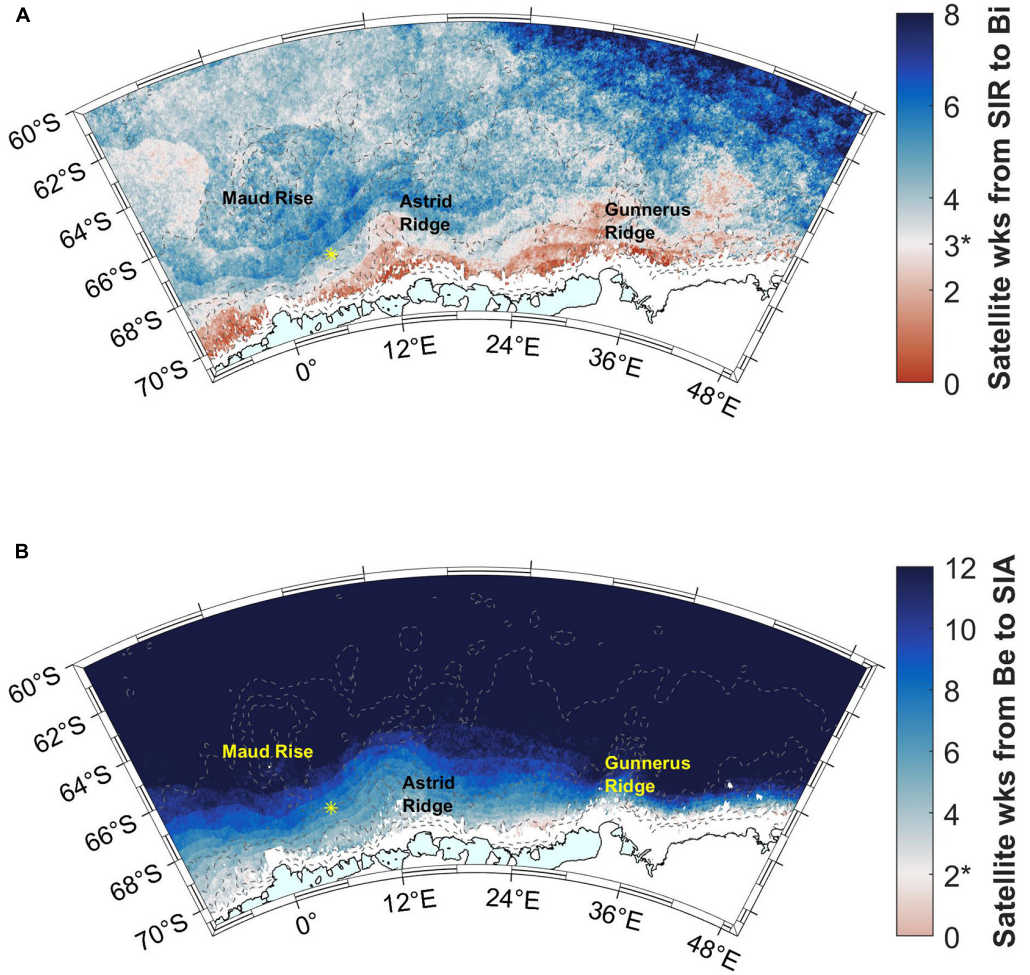

FIGURE 9 | (A) Time (in 8-day satellite weeks) from sea ice retreat (SIR) to bloom initiation. Time difference of 3 satellite weeks is highlighted with a color change and asterisk in the color scale legend (see the text for choice of the time period). **(B)** Time (in 8-day satellite weeks) from bloom end to sea ice advance (SIA). Time difference of 2 satellite weeks is highlighted with a color change and asterisk in the color scale legend. Station 53 is shown with a yellow asterisk.

Mixed layer depth is shallowest in December fairly uniformly across the area (**Figure 10A**) and ranges between 15 and 75 m (Pellichero et al., 2017). The MLD averaged for the entire study area for November, December, January, February, and March is 56 (±21), 25 (±6), 27 (±5), 37 (±6), and 49 (±9) m, respectively. When comparing March values from this product to the estimated MLDs from the cruise (coordinates of the latter ones rounded to the nearest whole degree), the MLD product values are on average 10 (±13) m deeper than the cruise values (range from 33 m deeper to 28 m shallower). This may suggest that the comparison to ZEu is a conservative estimate regarding light availability. Especially the Maud Rise stations during the cruise had deeper MLDs than the MLD product, whereas the opposite was true for Astrid Ridge and 6°E transect, which may in part reflect the sampling time: Maud Rise was sampled at the very end of the month, and the MLD product has a monthly resolution.

ZEu is deeper than the MLD throughout the productive season and across the study area (only February is shown in **Figure 10B**) thus indicating sufficient light availability. ZEu is affected by the algal biomass and shows geographical differences with shallowest values in the western part of the study area (resulting in smaller differences between ZEu and MLD), however, ZEu is still deeper than MLD.

Ocean Currents

Tidal currents along the coast are highest at the base of both Astrid and Gunnerus Ridges (**Figure 11A**). The highest MKE occurs along the coast, indicating the Antarctic Slope Current (**Figure 11B**). The current direction in the Antarctic Slope Current is from east to west, based on the surface current velocity vectors. Both these patterns coincide with the areas of the highest bloom magnitude (**Figures 6C**, **11C**), where the area east of Gunnerus Ridge has throughout low bloom magnitude and the area east of Astrid Ridge has low bloom magnitude in areas away from the coast. Conditions for high productivity are thus met at the west side of Gunnerus Ridge, then transported by the westward flowing Antarctic Slope Current, and further

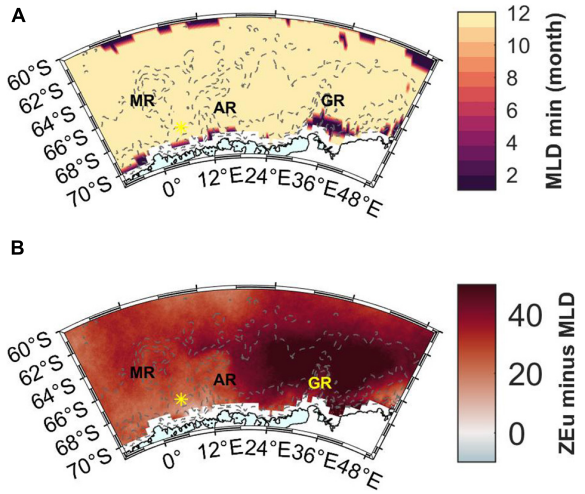

FIGURE 10 | (A) The month in which the annual minimum MLD occurs according to the data product by Pellichero et al. (2017). **(B)** Light availability expressed as the difference between ZEu and MLD in February. Red color indicates that MLD is shallower than ZEu. MR, Maud Rise; AR, Astrid Ridge; GR, Gunnerus Ridge. Station 53 is shown with a yellow asterisk.

amplified at Astrid Ridge. Small coastal areas at Gunnerus and Astrid Ridges have the highest bloom mean concentration values (>1 mg Chl *a* m^{-3}; **Figure 11C**). The western part of the study area (north and west of Astrid Ridge), also have a considerable mean concentration during the bloom (>0.5 mg Chl *a* m^{-3}), whereas the eastern part of the study area shows low values (<0.5 mg Chl *a* m^{-3}). MKE is elevated also in the north-eastern corner of the study area, indicating the southern ACC. Somewhat higher values can also be seen around Maud Rise, corresponding to the area with medium bloom magnitude.

DISCUSSION

Geographical Differences in Bloom Phases and Patterns

During the cruise, we observed phytoplankton blooms in different bloom phases. Phytoplankton biomass differed between the sampling areas, where the highest values (1.1 mg m^{-3}) were close to the lower range of summer bloom values (1.5 mg m^{-3}) in the Weddell Gyre (Vernet et al., 2019). Bacterial concentrations were in general similar to other studies reporting 2–4 × 10^5 cells mL^{-1} between January and March 2008 at similar latitudes at the prime meridian (Evans and Brussaard, 2012) and 1.5 × 10^4 to 1.1 × 10^6 cells mL^{-1} at the Antarctic Peninsula in January (Church et al., 2003; Straza et al., 2010). They were the highest at Astrid Ridge and 6° E transect which may implicate remnants of a bloom as bacterial abundance increases with bloom magnitude (Richert et al., 2019).

Based on the observations, Astrid Ridge and the 6° E transect were characterized as a post-bloom scenario due to low phytoplankton biomass, higher bacterial numbers, and satellite data indicating that this area typically has a strong bloom. Maud Rise had a terminating bloom with a visible export of biomass, i.e., a deep Chl *a* maximum (60–85 m) below the MLD, and clearly elevated fluorescence signals from the base of the MLD down to 200 m (e.g., the average Chl *a* value at Maud Rise at 150 m was 0.04 mg m^{-3}), as well as the lowest surface nutrient concentrations between the areas. The bloom observed at CTD station 53 was also past the peak bloom, based on the relatively low photosystem II fluorescence maximum quantum yields (<0.3; not shown), the sharp Chl *a* maximum right below the MLD, and microscopy pictures of surface samples that showed chlorotic cells (P. Assmy, personal communication). The surface Chl *a* concentration was still relatively high for mid-March, above 0.5 mg m^{-3}, and the underway measurements showed that this bloom covered a larger area west of the station 53. This latter bloom will hereafter be referred to as the open-ocean bloom, and will be studied in more details in a separate study (Moreau et al., in prep.).

The results we obtained at sea are compatible with the results of the satellite-based phenology analysis, with blooms ending earlier in Astrid Ridge than the open-ocean bloom. However, at least in the year the cruise took place, the Astrid Ridge and 6° E transect blooms ended earlier than the Maud Rise bloom. Such level of detail on bloom phenology may not be captured by satellites observing ocean color at the sea surface. Surface Chl *a* concentration during the cruise was similar at Maud Rise and Astrid Ridge, however, high biomass was observed at depth in Maud Rise, whereas it was low throughout the water column at Astrid Ridge and 6° transect. It should be noted, however, that Astrid Ridge was sampled in mid-March whereas Maud Rise was sampled at the end of March, thus the difference in bloom end timing may have been observable earlier given cloud-free conditions. Similarly, the open ocean bloom was sampled earlier than Maud Rise which may have contributed to differences in bloom phase observations between these areas.

The observed differences in the bloom phase between the sampling areas suggested that geographical differences in bloom patterns exist in the area. The phenology indices indeed showed differences across the study area. Five different bloom regimes emerged, which are made visible in **Figure 12** by combining bloom magnitude and timing patterns (see section "Bloom Phenology"). The regimes, with their main characteristics described in parentheses, are: coastal areas west of Gunnerus Ridge affected by the Antarctic Slope Current (1; highest bloom magnitudes, bloom initiation follows sea ice retreat); the open ocean bloom area (2; late bloom with a high magnitude); open ocean areas west of Astrid Ridge including Maud Rise (3; medium to high bloom magnitude, bloom initiation possibly controlled by sea ice cover); open ocean areas east of Astrid Ridge (4; low-magnitude blooms); and the southern ACC (5; long-lasting blooms but with a low magnitude). In the following sections we discuss the environmental control of bloom timing and magnitude across the regions. We do this in a chronological order going from bloom initiation, magnitude to bloom end.

Bloom Initiation

Bloom initiation in January in the majority of the study area corresponds well with earlier studies of Southern Ocean

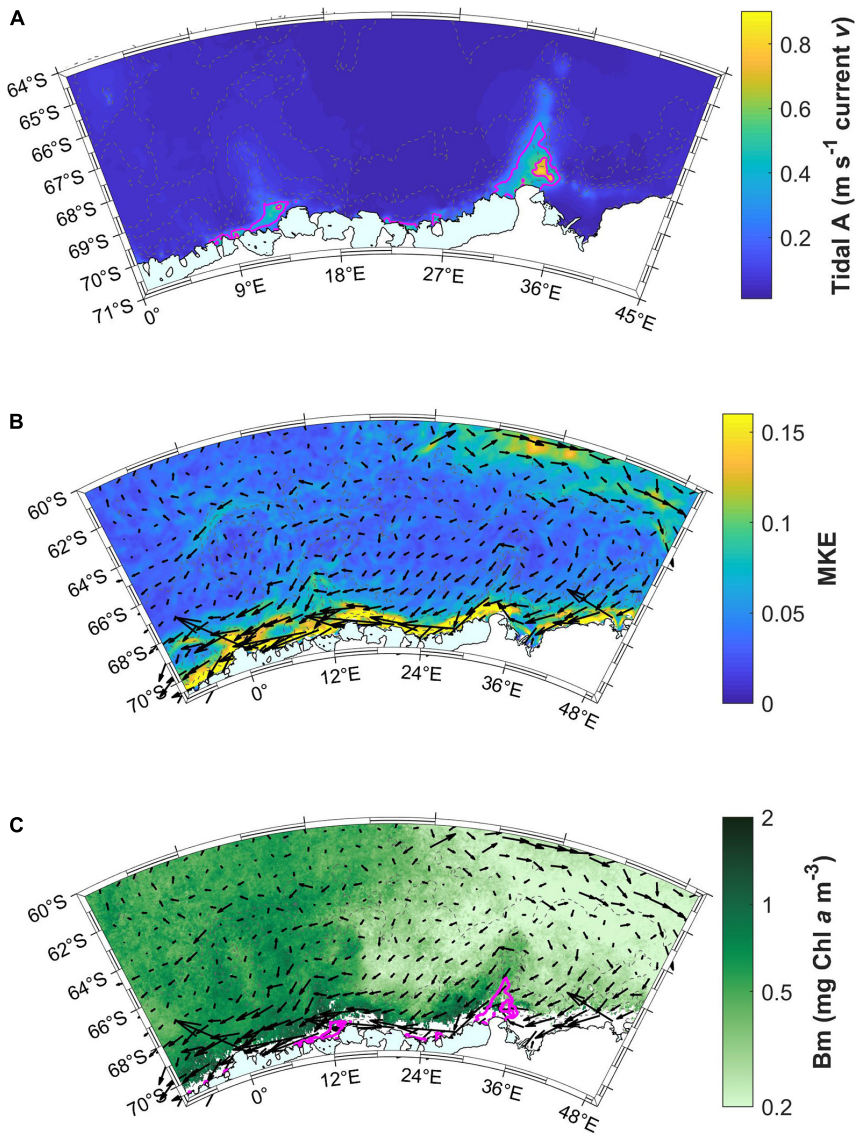

FIGURE 11 | (A) Tidal model results showing the sum of the major axis tidal amplitude (A) in current velocity (*v*) for the diurnal (Q1, O1, P1, K1) and semi-diurnal (M2, S2, K2) constituents. The magenta lines are 0.3 m s^{-1} contours of tidal currents. Note the smaller geographical area compared to the other maps. **(B)** Mean kinetic energy (MKE) and surface current velocity (relative; black vectors) in the area averaged over December to March. **(C)** Mean Chl *a* concentration during the bloom (Bm) together with the tidal amplitude contours (magenta lines) and current velocity vectors (black).

phytoplankton bloom phenology that included our study area. Thomalla et al. (2011) indicate bloom initiation in December–January for the majority of our study area (their **Figure 2**) using the same threshold value as in this study (but different pre-analysis of the data). In addition, Soppa et al. (2016), who studied diatom phenology in the Southern Ocean with the help of remote sensing and modeling and used the same threshold value as in this study, showed that bloom initiation mainly takes place in January in our study area (their **Figure 3**). Finally, the analysis of Ardyna et al. (2017) also suggests bloom initiations in January – February for the bioregions that correspond to our study area, even if using a different processing of the satellite-derived data (i.e., normalized annual bloom cycles and clustering).

It should be noted that the detected bloom initiation may be regarded as the bloom climax if considering the bloom biomass as vertically integrated estimates instead of surface observations, and that the winter ("strict") onset of the vertically integrated bloom could occur earlier (Llort et al., 2015; see **Table 1** and **Supplementary Material section 2** for definitions). A recent study concentrating on biogeochemical (BGC) Argo floats providing vertical profile observations every 10-days at Maud Rise, from 2014 to 2019, indeed shows that biomass seemingly increases as early as in November with rapid increases in December (the bloom onset is not marked in their **Figure 2**), and that bloom climaxes in December–January (von Berg et al., 2020). Further, the detected bloom initiation in this study

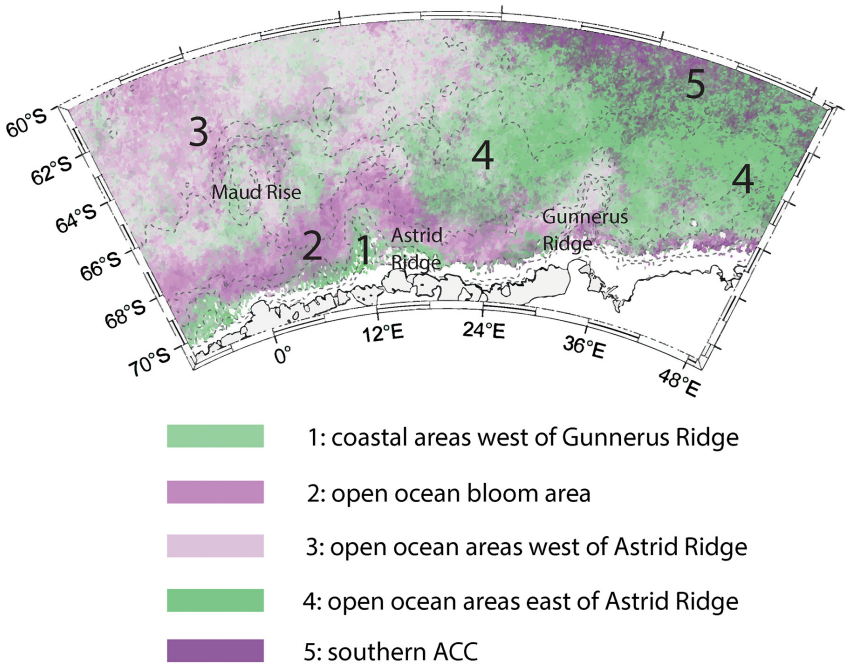

FIGURE 12 | The suggested bloom regimes: 1. coastal areas west of Gunnerus Ridge affected by the Antarctic Slope Current; 2. the open ocean bloom area; 3. open ocean areas west of Astrid Ridge including Maud Rise; 4. open ocean areas east of Astrid Ridge; and 5. the southern ACC.

(i.e., climax) should correspond to favorable environmental conditions (bottom-up control) (Brody et al., 2013; Llort et al., 2015), which are discussed in the next subsections.

Environmental Control: Sea Ice Concentration

In our study, blooms occur after the annual maximum in daily PAR and the summer solstice. ZEu is deeper than MLD during the productive season. Therefore, sufficient incident irradiance, and sufficient light in the water column in open waters (thus where the Chl *a*-based ZEu was possible to calculate) are available well in advance of the blooms. Light limitation thus likely occurs primarily via sea ice cover, delaying bloom initiation. This effect was studied by separating areas where blooms occur within 3 satellite weeks from sea ice retreat (**Figure 9A**), as ice edge blooms can be expected to develop within this time (Wright et al., 2010; Perrette et al., 2011; Taylor et al., 2013). Followingly, sea ice cover seems to play an important role for the bloom initiation along the coast and at the ridges, based on the temporal proximity (less than 3 satellite weeks) of sea ice retreat and bloom initiation. The rate of change method indicated that bloom initiation follows sea ice retreat in a somewhat larger area, namely the western – south-western part of the study area (**Supplementary Material section 2**). Sea ice retreats early in the areas around Maud Rise (de Steur et al., 2007; and **Figure 8B**). A recent study concentrating on Maud Rise also concludes that sea ice retreat controls the bloom climax timing (von Berg et al., 2020). Whereas other studies using BGC Argo floats show that bloom onset (Arteaga et al., 2020) or growth initiation (approximately corresponding to the bloom onset described here, thus preceding bloom initiation and climax; Hague and Vichi, 2021) can occur well before sea ice retreat (possibly due to unconsolidated ice relieving light limitation; Hague and Vichi, 2021).

Due to the possible delays in detecting bloom initiation with the threshold method (Brody et al., 2013) and due to data gaps (Cole et al., 2012), sea ice could play a role in bloom initiation in a larger area than shown in **Figure 9A** with areas of bloom initiation within 3 satellite weeks of sea ice retreat. If a 4-week time frame is considered for the sea-ice retreat control on bloom initiation, the majority of the area would be impacted, except for a band around Astrid Ridge (the open-ocean bloom area) and the southern ACC. On the other hand, blooms can develop at sea ice concentration above the retreat threshold of 15% used here (Lancelot et al., 1993; Assmy et al., 2017). Taylor et al. (2013) estimate that blooms in partial sea ice cover and thus not visible for optical satellites contribute significantly (up to 2/3) to the net primary production of the marginal ice zone, and state that sea ice edge blooms start decaying when sea ice disappears completely because of increased wind mixing. In an Arctic, remote sensing-based study, the majority of the pixels (77–89%, depending on the sensor) showed a bloom (defined there as Chl *a* concentration above 0.5 mg m^{-3}) within 20 days from sea ice disappearance (i.e., sea ice concentration permanently below 10%) where data was available for this time period, and half of these blooms also terminated within this 20-day period (Perrette et al., 2011). These studies indicate that bloom initiation should follow sea ice retreat closely in time if connected, despite the methodological challenges mentioned here.

The pattern at the coastal areas and the north-eastern part of the study area (southern ACC) is nevertheless robust: bloom initiation follows closely after sea ice retreat in the former and

not in the latter. In other words, in the southern ACC conditions are not suitable for phytoplankton blooms when sea ice retreats (despite the ZEu and MLD comparison presented here indicating sufficient light availability), and this area lacks a sea-ice related bloom. Blooms co-located with the ACC have been shown to occur later than could be expected from the seasonal cycle in irradiance and neighboring bio-regions, presumably due to spring light limitation caused by deep mixed layers (Ardyna et al., 2017), except in Scotia Sea where shallow MLDs persist (Prend et al., 2019).

In summary, phytoplankton blooms closely follow the sea ice retreat (within 3 satellite weeks) in coastal areas and in the western part of the study area (the latter based on the rate of change method), which we conclude indicates that bloom initiation is controlled by the length of the sea ice period in these areas.

Environmental Control: Mixed Layer Depth

In our study area, mixed layer is at its deepest latest in October (Pellichero et al., 2017), a time period when ocean color data is not available because of the sea ice cover. Whether this coincides with the bloom onset is thus unclear. The mixed layer is shallowest in December, i.e., shortly before the bloom (**Figure 10A**), and is already deepening, albeit first with small increments in the study area average, when blooms initiate in January (i.e., bloom initiation based on surface observations). The shallow mixed layer in December could aid the bloom development to initiation/climax by initially concentrating the phytoplankton cells closer to surface and light. MLD is still fairly shallow in January and shallower than ZEu, showing continued favorable light conditions. In the satellite-based phenology study by Thomalla et al. (2011), the maximum Chl *a* concentrations coincided with the shallowest MLDs (<50 m) over a transect in the Atlantic sector (overlapping with our study area) and based on satellite data and a different MLD product (2° and monthly resolution). Similarly, von Berg et al. (2020) concluded that mixed layer shoaling contributed to the bloom development at Maud Rise (based on BGC-Argo data). The MLD in their data (mainly below 50 m during the blooms) corresponds well with the product we used here. The bloom onset date is not depicted in their **Figure 4**, but the mixed layer is deepening during the blooms and when biomass is seemingly at its highest level – similar to our observations.

The observed mixed layer deepening during the blooms could further aid bloom development by the dilution effect (fewer encounters with grazers; Behrenfeld, 2010) or by entrainment of new nutrients, counteracting deteriorating light conditions and dilution of phytoplankton biomass. Considering that we lack zooplankton grazing or abundance estimates for the whole seasonal cycle, it is undecided whether the dilution effect caused by the mixed layer deepening can play a role for the bloom initiation, but not for the bloom end as mixed layer is deepening during both events and grazing likely has a role in the control of the bloom end (see section "Bloom End"). In addition, although bloom development during MLD deepening is seemingly similar to the North Atlantic spring bloom (considering, however, the difference between bloom onset and initiation), this happens at a different time of the MLD phenology; following the shallowest spring/summer MLD, as opposed to approaching the winter maximum in the North Atlantic. As blooms happen rather late in the season in our study area because of the sea ice cover and compared to the rest of the Southern Ocean (Ardyna et al., 2017), we can characterize our study area as having summer blooms rather than spring blooms. Indeed, a study based on BGC Argo floats concerning the Southern Ocean (but with very limited float coverage in our study area) suggests that the extremely low light levels under the sea ice prevented the early winter onset of the blooms in the seasonal ice zone, as opposed to the other zones (Arteaga et al., 2020).

Phytoplankton growth enhancement due to entrainment of new nutrients in connection with deepening mixed layer has been suggested in several studies. In the macronutrient-poor subtropical region of the Southern Ocean, nutrient entrainment during mixed layer deepening was considered to be controlling the bloom onset in the winter (Sallée et al., 2015). Wind-induced mixed layer deepening was found to be correlated with elevated Chl *a* levels in the summer in the Southern Ocean, which was suggested to be due to nutrient entrainment (Carranza and Gille, 2015), further supported by modeling studies (Nicholson et al., 2016). It should, however, be noted that MLD is still relatively shallow when blooms end (the study area MLD average is 37 m in February).

In summary, blooms are observed in the area during moderate mixed layer deepening in January and February. The mixed layer deepening can contribute to growth by entrainment of deep nutrients, including iron. The MLD evolution in relation to the exact bloom onset and the possible role of mixed layer shoaling in November–December for bloom initiation or climax should be studied further.

Bloom Magnitude

The highest bloom magnitude in our study area is linked to bathymetry and ridges in particular (**Figures 6C**, **11C**). High-resolution modeling results showed that the tidal mixing hot spots in the area correspond with high bloom magnitudes, likely due to enhanced upward flux of nutrients and trace metals. The area of high bloom magnitude is, however, larger than the tidal mixing hotspot, thus the enhanced nutrient, and/or tracer metal concentrations are probably transported with the Antarctic Slope Current toward the west. To confirm that these areas have also the highest primary productivity, we obtained the level 4 monthly primary productivity product (based on satellite-derived observations) from Copernicus Marine Services[3] and averaged it over the years to get the monthly climatology. The geographical pattern outlined above is confirmed in this dataset (not shown). We thus conclude that tidally induced mixing is a major mechanism in creating higher biomass and primary production along Gunnerus and Astrid Ridges.

The common view of Southern Ocean phytoplankton dynamics is that continental shelves and coasts are areas of enhanced productivity (e.g., Arrigo et al., 2008), but here we see spatial differences within this province, with the coastal areas

[3]https://marine.copernicus.eu/

east of Gunnerus Ridge having a low bloom magnitude. Adjacent to the coastal regime is the open-ocean bloom area, with high biomass. The offshore waters have otherwise lower biomass than the shelf areas. Smith and Comiso (2008) suggested deeper mixed layers of deeper waters as the reason for the lower productivity of the open ocean compared to shelf waters, likely due to the co-limitation of iron and nutrients in a deep mixing state and higher iron requirements at lower irradiances, though this hypothesis has been challenged (Strzepek et al., 2012). MLDs are, however, shallow in most parts of our study area in the productive season. Regarding the pelagic province, the main observation is that the bloom magnitude is higher in the west than the east side of the study area. This west side is part of the Weddell Gyre and corresponds to the eastern part of the Weddell Gyre where currents from the north turn westward, which results in nutrient entrainment from Circumpolar Deep Water and redistribution into the area (the Weddell Gyre characteristics are reviewed in Vernet et al., 2019). Furthermore, the gyre flow pattern fosters upwelling and therefore enhanced nutrient levels.

Within this western area lies the Maud Rise sea mount, with relatively enhanced bloom magnitude surrounding it compared to the other parts of the western area. We also observed during our cruise a strong, though likely terminating, bloom with deep-lying biomass. A study focusing on BGC-Argo floats in the area shows that the Maud Rise blooms have higher biomass than the ones recorded further north in the Weddell Gyre (von Berg et al., 2020). The sea mount topography of Maud Rise and the Taylor column circulation likely contribute to upward (micro)nutrient fluxes (de Steur et al., 2007; Jena and Pillai, 2020; von Berg et al., 2020) enabling enhanced biomass, as suggested also for Pine Bank in the Scotia Sea (Prend et al., 2019).

Coastal polynyas could not be studied in detail because the heavy sea ice conditions during the cruise prevented us from reaching the polynyas for sampling, and because of higher uncertainty in the satellite remote sensing data in these areas. The coastal polynyas are not highly productive regions in our study area (Arrigo and van Dijken, 2003), contrasting with many other parts of the Southern Ocean, although regional variability is high (Arrigo and van Dijken, 2003; Moreau et al., 2019). Regional differences have been attributed to strength of basal melt of the adjacent ice shelf and associated overturning circulation (Dinniman et al., 2020), polynya size (Arrigo and van Dijken, 2003), and water mass distribution (Moreau et al., 2019). Another region that does not seem to be particularly productive is the southern ACC, in the north-eastern corner of the study area, where blooms have a long duration but low magnitude. In fact, Sokolov and Rintoul (2007) found that the ACC mainly enhances productivity in combination with topographic features and associated upwelling, and consequently not in the area described here.

In conclusion, multiple processes and environmental factors seem to control the bloom magnitude in our study area. In particular, the interactions of tides and oceanic currents with bottom topography and the associated water column mixing seem to play a major role in enhancing phytoplankton biomass. It should also be noted that zooplankton grazing likely affects the observed bloom magnitude (see following section "Bloom End"), however, we do not have data to assess this on such large scale.

Bloom End

The bloom end in February results in bloom duration of mainly 2–4 weeks, except for the southern ACC (**Figure 7B**). Soppa et al. (2016) found a similar duration of blooms in a study concentrating on Southern Ocean diatom blooms. Neither sea ice, light or nutrient conditions seem to determine the bloom end and thus its limited duration, leaving grazing as a suggested controlling factor.

Sea ice does not seem to play a strong role in bloom end, based on the long time-interval (several weeks) between the bloom end and the sea-ice advance (**Figure 9B**). However, this cannot be excluded in the areas very near to the coast which were not included in the analysis. Sea-ice advance is also variable between the years along the coast (higher standard deviations are observed in this area than elsewhere in the study area; **Supplementary Figure 5C**), which may imply a larger role in some years. Light availability in general also does not seem to be the main cause for the bloom termination as blooms end mainly during February, i.e., before autumn, and the euphotic layer remains deeper than the mixed layer throughout the productive season (including March).

Nutrient exhaustion is a common contributor to bloom decay by limiting the growth rate. However, during our March cruise, when phytoplankton blooms were recently past the peak phase, the macronutrient concentrations even in the surface waters were well above the half-saturation constant ranges or average reported in literature. Growth rate is half of its maximum at half-saturation constant concentrations, which is considered to indicate nutrient limitation. Observed minima for silicic acid, nitrate and phosphate were 33.0, 20.7, and 1.4 μM, respectively, whereas the half-saturation constants reported for diatoms are up to 22 μM for silicic acid, up to 10.2 μM for nitrate, and on average 1.2 μM (up to 8.9 μM) for phosphate (reviewed in Sarthou et al., 2005). Furthermore, iron addition experiments conducted during the cruise in the southern cruise area showed minimal iron limitation of the phytoplankton communities, as observed through short-term changes in photophysiology (A. Singh, personal communication). Whilst these results only confirm the situation for 1 year as opposed to the long-term satellite data, they seem to indicate that neither macronutrient nor iron limitation terminates phytoplankton blooms in the western part of the study area. For the post-bloom areas such as Astrid ridge, remineralization of nutrients may have happened considering the higher bacterial numbers (thus increasing the nutrients concentrations after the bloom), but even the more active blooms such as at Maud Rise had surface nutrient concentrations exceeding the half-saturation constants, although they were the lowest over the whole cruise area. Another possible process supplying nutrients after the bloom end (thus contradicting the conclusion above) is autumn mixing, but deep winter mixing is needed to fully replenish the iron reservoirs (Tagliabue et al., 2014), which was not the case given the shallow MLDs measured during our cruise.

Another important factor controlling phytoplankton blooms is grazing. Lancelot et al. (1993) observed that protozoan grazing exerted a strong control on an ice-edge phytoplankton bloom in the western Weddell Sea, and was responsible for the decrease in phytoplankton concentration together with physical factors (e.g., dilution due to mixed layer deepening). In addition, an episodic krill passage was able to graze the phytoplankton (from 2.5 to 0.3 mg Chl *a* m^{-3}) within hours. On the contrary, macronutrients or trace metals were not observed to play a major role for the bloom magnitude in the study of Lancelot et al. (1993). In addition, other field (Dubischar and Bathmann, 1997; Whitehouse et al., 2009; Hoppe et al., 2017) and modeling studies (Llort et al., 2015; Le Quéré et al., 2016) from the Southern Ocean indicate that grazing controls phytoplankton biomass and bloom decline at least in certain areas. In the Weddell Gyre, for example, microzooplankton grazing is a major controlling factor and more important than larger zooplankton, while viral infections are suggested to be of less importance (reviewed in Vernet et al., 2019). Regarding total losses, a recent study partly concerning our study area and based on bio-optical observations from BGC-Argo floats, concluded that grazing (including viral lysis) was responsible for 83% of the losses on average and was by far more important than phytodetritus sinking (Moreau et al., 2020). In addition, grazing was found to be more important in the later part of the production season.

Sampling and observations of zooplankton and micronekton during the cruise revealed that grazers were present in the autumn, but also showed large regional variations in both abundances and composition. The high concentrations of krill swarms in the vicinity of 6° E transect (yellow – red colors in **Figure 5**) and, to a lesser extent, Astrid ridge, indicated strong herbivorous grazing of the phytoplankton community. Mesozooplankton abundances and biomass were highest at Maud Rise, however, the zooplankton community composition with high proportions of small copepods and carnivorous zooplankton does not necessary lead to a strong grazing pressure. This together with the absence of krill may indicate a lower grazing pressure on bloom-forming, large phytoplankton in Maud Rise compared to the other stations. However, it is dependent on the phytoplankton community composition, and morphological defenses (e.g., spines), whether grazing from the zooplankton community of this composition was of importance (Smetacek et al., 2004).

Similarly to the bloom initiation discussed earlier, detecting the bloom end from satellite data may suffer from data gaps. Maud Rise phytoplankton blooms ended presumably much later compared to the analysis presented here in the study of von Berg et al. (2020) who used BGC-Argo floats and water column vertical profiles (their **Figure 2**). The surface satellite observations used here cannot capture deep features such as deep Chl *a* maxima, which often occur when surface nutrients are being depleted, thus the analysis could artificially indicate early bloom termination. However, deep Chl *a* maxima can also indicate biomass export to depth rather than an actively growing bloom, when observed below the mixed layer or as a narrow band close to the pycnocline. The bloom we observed at Maud Rise at the end of March was considered to be exporting due to Chl *a* maxima well below the MLDs and high Chl *a* values in depth (below 100 m). Finally, the export of phytodetritus observed at Maud Rise could indicate that grazing has a smaller role for the bloom end in this area than elsewhere in the cruise area, which would be consistent with the observed patterns in zooplankton and micronekton abundance as discussed above. Iron limitation could not be excluded as a termination cause for the surface bloom as there were no incubation experiments available from Maud Rise during our campaign. Our sampling was condensed in the relatively isolated and stationary water column on top of Maud Rise (de Steur et al., 2007) where growth conditions may differ from the areas around.

In summary, we hypothesize that top-down control by zooplankton and micronekton contributes strongly to blooms termination in the area, possibly excluding Maud Rise. Grazing may, however, act in concert with other controlling factors. As Behrenfeld and Boss (2018) point out, growth does not have to stop for a bloom to terminate, but to decelerate so that loss rates such as grazing can exceed growth rates. Therefore, at least theoretically, any growth condition that is deteriorating (although still sufficient to enable growth) could also contribute to bloom end. Regarding light availability, although still sufficient, the temporal patterns of deepening of the mixed layer (which circulates algal cells deeper, i.e., to lower light conditions) and the shortening day length mean it is continuously diminishing. In addition, cloudiness increases after the seasonal minimum in the summer, which also decreases light availability (Verlinden et al., 2011).

Methodological Challenges

Remote sensing is inherently less precise than other methods because the measurements are indirect, restricted to the upper ocean and, e.g., in the case of ocean color must be disentangled from atmospheric influence. No other method can, however, offer the long-term dataset with high spatial coverage used here, but it is important to bear in mind some of the caveats. The polar oceans have in addition specific challenges (reviewed in IOCCG, 2015), including low sun angles affecting, e.g., the quality of atmospheric correction, frequent cloud cover (especially along the ice edge) and ice cover. Sun elevation is sufficient at the latitudes described here in the productive season, but both the latter issues result, among other things, in gaps in data, and with regard to sea ice in addition to possible biases in data because of the adjacency effect (Bélanger et al., 2007). To account for the adjacency effect, we excluded data close to the sea ice. Interpolation of the data reduced the gaps but cannot eliminate them. Phytoplankton blooms may in reality start earlier than detected due to (1) challenges related to the bloom definitions, the phenology method used and vertically integrated vs. surface observations (see **Supplementary Material section 2**), (2) data gaps affecting the threshold value (Cole et al., 2012) or masking parts of the bloom development, and (3) the lack of early observations due to partial sea ice cover. The literature (Taylor et al., 2013; von Berg et al., 2020) and primary productivity product indicate primary production and bloom development already in December, thus it is wise to recognize December as part of the productive season, despite the analysis here showing bloom initiation in January. Likewise, blooms may extend to March. In any case, January–February is the

main period for phytoplankton blooms and primary production, particularly January. In addition, against this background, we consider that the shorter duration of the blooms when data are less or not interpolated (**Supplementary Figure 2**) suggests that the interpolation methods are not creating unrealistic results but rather improve the data quality. Finally, it is also important to bear in mind that variability between years is fairly large, but primarily concerns the exact timing of the bloom which may vary, and less so the bloom duration.

The MLD product from Pellichero et al. (2017) uses a variety of data sources, but unfortunately in our study area the data coverage is somewhat poorer than in other more studied regions (see their Figure 1D), therefore our use of this data product could suffer from local uncertainty. The product corresponds, however, reasonably well with the cruise data and with a recent study using Argo floats (von Berg et al., 2020). Furthermore, errors in satellite Chl *a* concentration will also affect the estimation of ZEu, because the algorithm is based on satellite-derived Chl *a* (Morel et al., 2007). Validation studies for remotely sensed Chl *a* in the Southern Ocean have divergent conclusions ranging from good agreement (Moutier et al., 2019) to underestimation (with overall magnitudes and geographical patterns depending on the algorithm used; Johnson et al., 2013) when using standard algorithms. While the underestimation didn't affect the results of a phenology study (Sallée et al., 2015) and would also in this study be less of an issue because of, e.g., relative thresholds, it would mean that ZEu is in reality shallower than indicated in the data product. These uncertainties could affect the conclusion that ZEu is always deeper than MLD in the productive season. Note, however, that the critical depth (concerning average light absorbed in mixing conditions) is deeper than ZEu, i.e., the zone where net photosynthesis occurs (compensation depth).

SUMMARY

Based on the presented analyses and the available data, we suggest the following bloom regimes in the study area: coastal areas west of Gunnerus Ridge affected by the Antarctic Slope Current (1); the open ocean bloom area (2); open ocean areas west of Astrid Ridge including Maud Rise (3); open ocean areas east of Astrid Ridge (4); and the southern ACC (5) (**Figure 12**).

In addition, coastal polynyas and other areas very close to the coast may form their own regime, but had to be excluded from this analysis. To understand the controlling factors of bloom development in these areas, direct sampling, e.g., through tagged seals and field campaigns, is needed.

In the coastal areas and at the ridges the bloom initiation is controlled by sea ice retreat. In the areas west of Gunnerus Ridge, bloom magnitude is enhanced by tidal current interaction with ridge topography.

In the open ocean areas west of Astrid Ridge the bloom initiation is likely controlled by sea ice retreat especially in areas surrounding Maud Rise. The bloom magnitude is enhanced by flow patterns in the Weddell Gyre and current interaction with topography (the latter especially concerning areas around Maud Rise). The open-ocean bloom falls geographically between these two areas, occurs later in the season and shows to have to some extent its own environmental control (S. Moreau, personal communication), that will be studied in a separate paper.

In the open ocean areas east of Astrid Ridge the bloom magnitude is low, resulting at least partly from the absence of upstream topographic features, where interactions with oceanic currents could enhance upward nutrient fluxes. The MLD evolution may play a role for bloom initiation, as sea ice retreat does not seem to play a strong role, although this cannot be fully excluded.

In the Southern ACC, the blooms last longer (more than 4 weeks) but have a low magnitude as the ACC does not interact with major topographic features in this area.

Regarding the end of the bloom (and followingly, the bloom duration), grazing is seemingly the most plausible controlling factor based on the cruise results and literature. Sea ice advance is considerably later than the bloom end in the majority of the area. Although other environmental conditions such as those affecting light availability are not adverse when blooms end, the deteriorating conditions (MLD deepening, day length shortening, increasing cloudiness) could slow down the growth rates (although still enabling growth) and allow loss rates (e.g., grazing) to overcome, resulting in decreasing phytoplankton concentrations. The control of the bloom timing is likely dependent on several factors and their relative importance may vary between years.

It is also important to note that the bloom initiation used here, based on exceeding a threshold value in surface observations, denotes a time of rapid biomass accumulation and may correspond to the bloom climax of a vertically integrated bloom, whereas the bloom onset can occur considerably earlier and have a different environmental control. Lastly, this study shows the complementariness of satellite-based, ship-based (this study) and autonomous profiler observations (related studies). Further research is needed to confirm these hypotheses, especially the role of grazing in connection with MLD evolution. In addition, studying the control of interannual variability especially in the exact timing of the bloom would improve our understanding. This study can function as a basis for understanding the phytoplankton dynamics in the area.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories in Kauko et al. (2021), Moreau et al. (2021) (Norwegian Polar Data Centre, Norwegian Polar Institute, https://data.npolar.no/dataset/5e510f85-29e1-42c3-89a5-8766f5c5948c, https://data.npolar.no/dataset/28fbddd2-0fb2-41c9-9f42-60146e28617f), and in Chierici and Fransson (2020) (Norwegian Marine Data Centre, https://doi.org/10.21335/NMDC-1503664923). The satellite data are available from the providers described in Section "Materials and Methods."

AUTHOR CONTRIBUTIONS

HK conceptualized the study, conducted the main data analysis, and wrote the manuscript draft. SM, HK, TR-K, AS, TH, LS, AF, MC, TF, and EH planned and conducted the field work. SM, HK, TR-K, and AS processed the Chl *a* samples and AF and MC the nutrient samples. TF was responsible for the zooplankton sampling and analysis. EH processed the acoustics data. TB provided the FlowCam data. HK and AS analyzed the FCM samples under supervision by GB and TT. HK processed the *in situ* Chl *a* fluorescence profile and satellite data with the help of TH and SM. TH processed the CTD data from the cruise. QZ conducted the tidal simulations. All authors contributed to the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.623856/full#supplementary-material

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Stakeholder Engagement in Decision Making and Pathways of Influence for Southern Ocean Ecosystem Services

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Southern Ocean ecosystem management is characterized by a unique and complex international network of stakeholders and stakeholder relationships (a 'transactional landscape') relating to the globally significant services that these ecosystems support. This transactional landscape spans governments, industry (fishing and tourism), scientific research, conservation non-government organizations, civil society, and international decision-making forums. We used a network approach for stakeholder mapping to provide the first description of the transactional landscape for Southern Ocean ecosystem management – both in terms of the connections between stakeholders and ecosystem services, and directly between stakeholder groups. We considered 65 stakeholders and their relationships to 12 provisioning, regulating, supporting and cultural ecosystem services. An analysis of the connections within this network reveals differences in the degree of connectivity between stakeholders and ecosystem services. Notably, ecosystem science facilitates high connectivity between stakeholders and provisioning services, but there is little connectivity between stakeholders and supporting services. We then applied a formal 'values-rules-knowledge' framework to a set of case studies to analyze the decision-making process in relation to Southern Ocean ecosystem services, as well as the relative importance of different stakeholder groups which were considered in the network analysis. Our analyses suggest that emphases for decision making have been on knowledge and rules, but that wider consideration of values across the broader stakeholder landscape – together with science (knowledge) and governance (rules) – might better support decision making for Southern Ocean ecosystem conservation and management, and provide a stronger foundation for sustainable provision of ecosystem services into the future.

Keywords: stakeholder engagement, Southern Ocean, ecosystem services, knowledge values rules, transactional landscape, network mapping

INTRODUCTION

Southern Ocean ecosystems support a range of ecosystem services that are significant at a global scale (Grant et al., 2013; Rogers et al., 2020; Trebilco et al., 2020). Ecosystem services are the benefits that people derive from functioning ecosystems (Costanza et al., 1997; Millennium Ecosystem Assessment [MEA], 2005), and are generally classified as provisioning, regulating, supporting and cultural. For the Southern Ocean, these include, amongst others, fisheries products, genetic resources, biochemical and pharmaceuticals (all provisioning services); climate and air quality regulation (regulating services); photosynthesis, primary production and nutrient cycling (supporting services); tourism, recreation, and spiritual, religious and aesthetic value (cultural services) (Grant et al., 2013). These services are managed at an international level. This management is characterized by stakeholders from governments, the fishing and tourism industry, scientific researchers and advisors, conservation non-government organizations, civil society, and international decision-making forums. Importantly, the Southern Ocean is amongst the most rapidly changing oceans of the world, with consequences for global-scale storage and cycling of heat and carbon, major changes in habitats, and combined flow-on effects for habitats and ecosystems (Meredith et al., 2019). In order to manage these future dynamics, it will be critical to have approaches that are flexible and adaptive to the changing pressures and can meet the challenges of satisficing the competing needs of the stakeholders whilst conserving biodiversity and ecosystem function in the Southern Ocean (Constable et al., 2017). Understanding the relationships between stakeholders and the services they wish to sustain is fundamental to meeting the challenge.

The Southern Ocean is governed by the Antarctic Treaty System (ATS), which encompasses a series of international agreements that protect ecosystems south of 60°S and recognize the importance of Antarctic ecosystems to people in terms of their wilderness and aesthetic value, and value to scientific research (Antarctic Treaty System, 2020). The main governance structure within the ATS is the Antarctic Treaty Consultative Meeting (ATCM), with the aim of formulating and recommending further measures to their respective governments in accordance with the goals of the ATS (Antarctic Treaty System, 2020). This meeting is held annually, consisting of 29 Consultative Parties (including original 12 signatories to the ATS, and 17 additional countries who have conducted substantial research in Antarctica), 25 Non-Consultative Parties, observers, including the Convention of the Conservation of Antarctic Marine Living Resources (CCAMLR) and the Scientific Committee on Antarctic Research (SCAR), and invited experts (Antarctic Treaty System, 2020). While all these groups may be present in the ATCM, only Consultative Parties play a role in decision-making (Antarctic Treaty System, 2020).

Within the ATS, CCAMLR, takes an ecosystem approach to the management of fishing activities in the Southern Ocean (Constable et al., 2000; Constable, 2011), and extends to the north the jurisdiction of the ATS to include biota and ecosystems south of the Polar Front. CCAMLR is generally recognized as having a strong foundation of decision-making based on best available science and using a precautionary approach to ecosystem management (Parkes, 2000; Miller, 2011). In 2016, CCAMLR declared the world's largest marine protected area in the Ross Sea, measuring 1.5 million square kilometers in size (Dodds and Brooks, 2018). However, in recent years progress has stalled in meeting the CCAMLR Commission's commitment to the implementation of the network of marine protected areas in the Southern Ocean, and progress toward determining approaches to incorporate climate change into ecosystem management has also been slow (Brooks et al., 2019). While the continued uptake of scientific information through the ATS and CCAMLR will be critical to progressing these issues, attention to understanding stakeholder values and needs has been lacking; this is despite the fact that decision making in the ATS must be achieved through consensus, which is dependent upon satisfactorily negotiating these requirements.

Recent assessments have helped to build a clearer understanding of the links between environmental change, ecological process and functions, and associated risks for continued delivery of Southern Ocean ecosystem services; these assessments were conducted in the contexts of anticipated changes in demand and climate change impacts (Rogers et al., 2020; Trebilco et al., 2020; Cavanagh et al., 2021). However, the human dimensions that determine how and where ecosystem services are valued and used are arguably much less well understood. Stakeholder mapping is an approach increasingly used in environmental management and governance to consider the various parties interested in a system, and to analyze their relationships both with the system and with each other (Raum, 2018). The stakeholders which were considered include all individuals or groups, whether formal or informal, "who affect, and/or are affected by, the policies, decisions and actions of the system" (Grimble et al., 1995, p. 3). To date, there has been no systematic stakeholder mapping for the Southern Ocean and only scattered information is available regarding connections between stakeholders and their relationships to ecosystem services, which we refer to as a 'transactional landscape.' This is somewhat surprising given the unique nature of the Southern Ocean stakeholder landscape, in that there are no permanent residents of the Southern Ocean and the Antarctic continent, and no Traditional Owners (Aboriginal peoples) for Antarctica or most subantarctic islands. As a result, strategies for sustaining all ecosystem services within an international governance framework need to understand how governments interact and the role that different stakeholders may play in influencing outcomes.

In this study we use structured approaches to develop a network representation of the transactional landscape of the Southern Ocean. This network representation of the transactional landscape enables us to visualize parts of the landscape that are most and least connected. We then consider how this mapping relates to decision making processes for Southern Ocean ecosystems using case studies and the values-rules-knowledge (*vrk*) framework (Gorddard et al., 2016). Through applying this framework, we expect to identify the influence of values, rules and knowledge on decision making,

and whether any of these three systems has been excluded from decision making processes. We expect that this will provide useful information for identifying ways in which stakeholder values, scientific knowledge and governance frameworks might be more effectively combined to overcome issues currently facing ecosystem management for the Southern Ocean.

MATERIALS AND METHODS

Our methodology followed four steps, detailed in the subsections below. Namely:

(1) Identifying stakeholders for Southern Ocean ecosystems and the ecosystem services they have an interest in.
(2) Creating an interest-influence matrix to explore the relationship between stakeholders and ecosystem services.
(3) Analyzing the relationship between the stakeholders and ecosystem management decision-making through a network mapping approach.
(4) Applying the values-rules-knowledge framework to three case studies of Southern Ocean ecosystem management, to contextualize the relationships between stakeholders and ecosystem services and test our network mapping.

Data Collection

We developed an initial list of stakeholders for Southern Ocean ecosystems from the stakeholder list for the Marine Ecosystem Assessment for the Southern Ocean (MEASO) Science Network (Constable et al. in preparation). Other stakeholders were added iteratively to the stakeholder list if they were mentioned in the strategic reports and websites of stakeholders already on the list. Key players in unrepresented industries on the MEASO Science Network, such as the largest private fisheries in the Southern Ocean, and governing bodies in the fisheries and tourism industries, were also added to the list (Commission for the Conservation of Antarctic Marine Living Resources, 2019). In total, 64 stakeholders with an interest in Southern Ocean ecosystem management were identified. Of these, 29 stakeholders are sub-groups or sub-organizations of a parent stakeholder (e.g., SC-CAMLR is part of CCAMLR but plays a significant role as a specific body), but were analyzed separately due to their own interests in, or influence over, specific ecosystem services.

We identified the ecosystem services present in the Southern Ocean based on research by Grant et al. (2013), which explored provisioning, regulating, supporting and cultural ecosystem services (following the Millennium Ecosystem Assessment framework for ecosystem services; Millennium Ecosystem Assessment [MEA], 2005; **Table 1**).

We then conducted a thorough analysis of the stakeholders' motivations, interests, aims, actions and strategies, to understand their connection to ecosystem services in the Southern Ocean. This was done through close reading of annual reports, strategic plans, and key documents listed on organizational websites for our list of stakeholders (these resources are detailed in **Supplementary Table 1**). The scope of webpages and documents examined to understand each stakeholder's motivations, interests, aims, actions and strategies varied; this depended on each stakeholder's information management on their website, and where specific information was located.

TABLE 1 | A summary of the ecosystem services in the Southern Ocean, adapted from Grant et al. (2013).

Provisioning services	Fisheries products; genetic resources; biochemicals, medicines, pharmaceuticals; fresh water
Regulating services	Air quality regulation; climate regulation; waste treatment
Supporting services	Photosynthesis and primary production; nutrient cycling
Cultural services	Spiritual and religious value; tourism and recreation; aesthetic value

Note that biodiversity is considered to underpin ecosystem services rather than as an ecosystem service of itself (following Seddon et al., 2016; Cavanagh et al., 2021).

We linked each stakeholder to the specific ecosystem services they have an interest in. Stakeholders were defined as having an interest in an ecosystem service if they have one or more of the following relationships with it: produce, use, regulate, research, monitor (note here that the 'regulate' relationship refers to management, and can be for any ecosystem service, not just 'regulating' services). The 'produce,' 'use,' and 'regulate' relationships were determined following the methodology used by Raum (2018) in categorizing forest management stakeholders into these three groups based on their functional roles. The 'research' and 'monitor' categories were added for our Southern Ocean context to differentiate stakeholders whose relationship to ecosystem services is purely research, versus those who do not undertake research directly (i.e., non-research scientific organizations) but instead undertake monitoring and assessment activities.

Interest-Influence Matrix

We created an interest-influence matrix to explore in greater depth the relationships between stakeholders and ecosystem services (following Raum, 2018; see **Supplementary Table 2**). Stakeholders' levels of interest and influence were categorized as low, medium, or high. The level of interest in an ecosystem service was determined by how closely stakeholders' actions aligned with a particular ecosystem service (following Raum, 2018). The level of influence was defined as the ability a stakeholder has to affect specific ecosystem services, either directly or indirectly, through use, production, regulation, research and/or monitoring.

To summarize the interest-influence matrix, we categorized stakeholders under their broad industries, as science organizations (research, ecology, or monitoring organizations), regional bodies and regulators, international bodies and regulators, fisheries, lobby groups, or tourism and the public. Using the interest-influence matrix, we also assigned them functional roles based on their work with particular ecosystem services, as producers, users, regulators, researchers, or observers, following Raum's (2018) process:

- *Producers* were defined as those stakeholders who produce goods or services through particular ecosystem services.

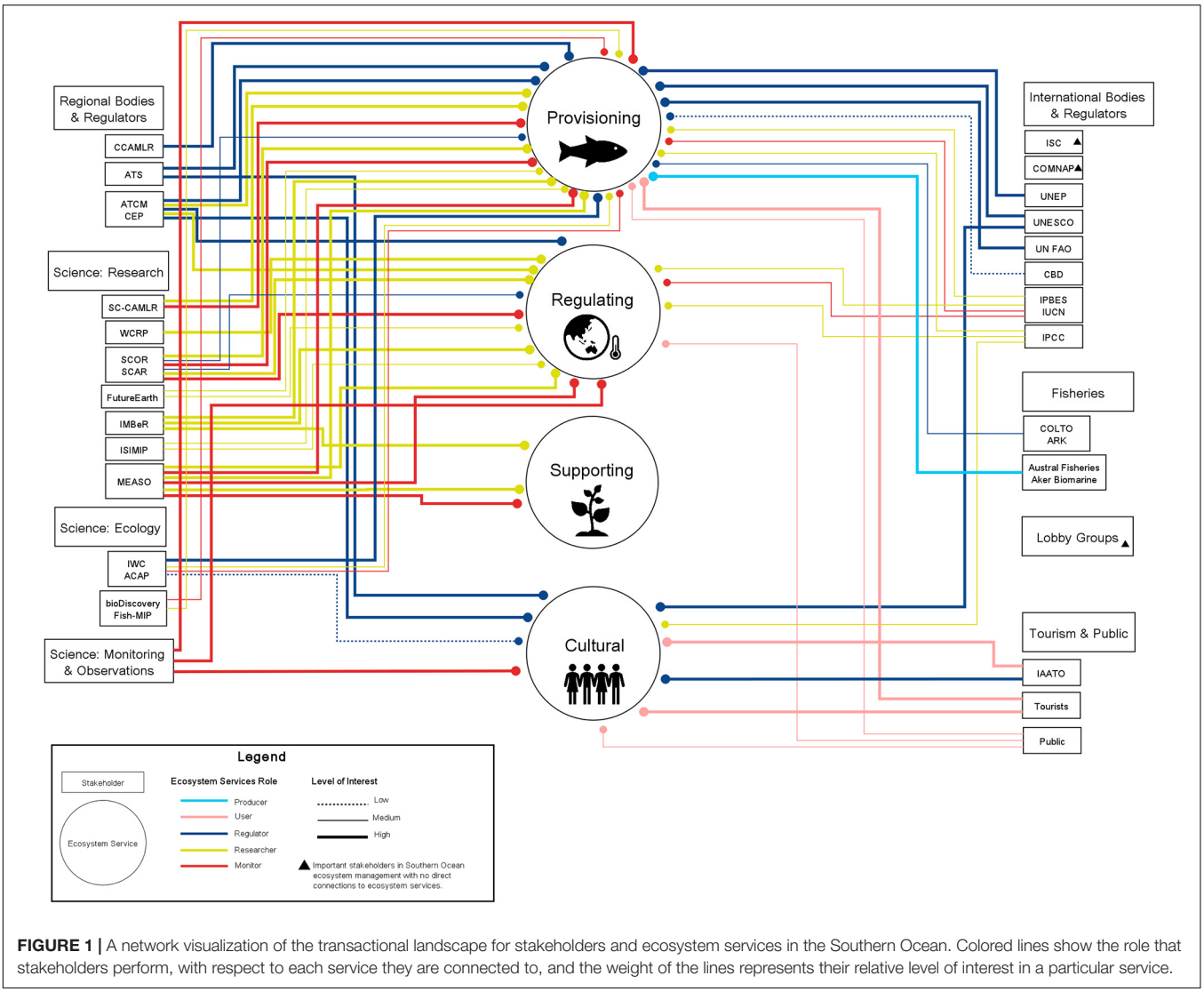

FIGURE 1 | A network visualization of the transactional landscape for stakeholders and ecosystem services in the Southern Ocean. Colored lines show the role that stakeholders perform, with respect to each service they are connected to, and the weight of the lines represents their relative level of interest in a particular service.

- *Users* are the stakeholders which passively use or benefit from the use of particular ecosystem services.
- *Regulators* are those stakeholders with the ability to set either formal or informal rules to govern the actions of other stakeholders in relation to ecosystem services.
- *Researchers* were defined as any stakeholder which engages in science research and understanding, including modeling, but excluding monitoring and observing.
- *Monitors* are the stakeholders which engage in scientific monitoring and observing of particular ecosystem services, and inform other stakeholders.

Relationship Mapping

We used a network mapping approach to visualize the relationship between stakeholders and ecosystem management, in particular the decision-making process. First, stakeholders in their broad industries were mapped against the four key types of ecosystem services – provisioning, regulating, supporting, and cultural – based on their functional role toward, and level of interest in, these ecosystem services (**Figure 1**). The aim of this network visualization was to identify: (i) the relative strength of connectivity between stakeholders and each of the four key ecosystem services, and (ii) whether any services were under-represented or over-represented in terms of connection to stakeholders.

We then visualized the relationship between stakeholders to understand how various stakeholders regulate, advise, fund, and support one another. Individual stakeholders were separated based on their functional role to understand how stakeholders with different roles interact with each other. To reduce overlap in the network visualization, some stakeholders were grouped together with their parent stakeholders when they performed the same roles and had the same level of interest in ecosystem services (for example, the SC-CAMLR scientific working groups WG-EMM, WG-SAM, and WG-FSA were grouped together with their parent stakeholder, SC-CAMLR). As a result, 38 different stakeholders or stakeholder groups, including some stakeholders which are sub-groups of others

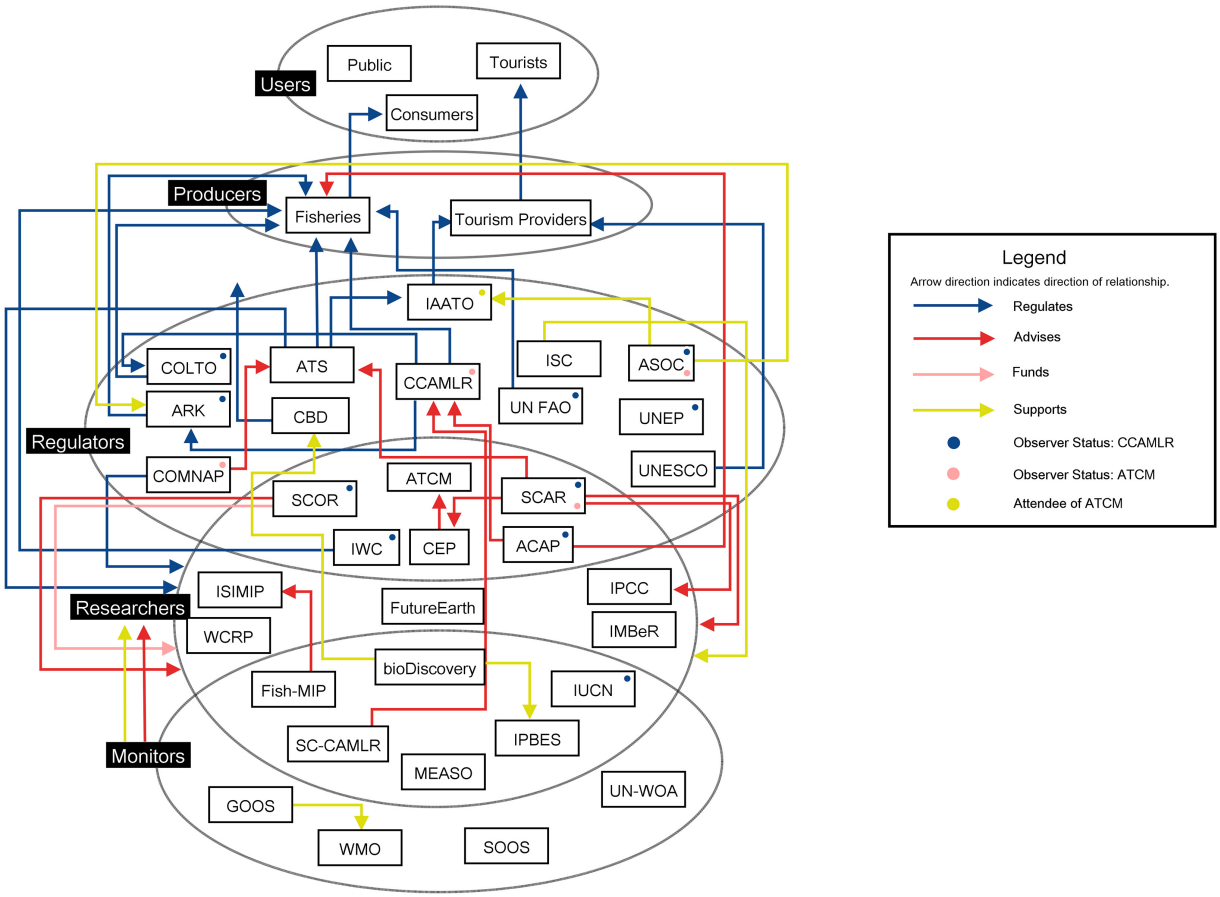

FIGURE 2 | Network visualization of relationships between key stakeholders in Southern Ocean ecosystem management, grouped by their functional role in ecosystem management as per methods. Some individual stakeholders do not have direct connections to other stakeholders, although their parent stakeholder groups, labeled as black text boxes, are connected with other stakeholder groups or with individual stakeholders.

but which perform different roles or have a different level of interest to their parent groups, were included in the network visualization.

Based on these two visualizations, we created a conceptual diagram (**Figure 2**) to demonstrate the influence pathway between key stakeholder groups, and how ecosystem services influence decision-making.

Applying the *Values-Rules-Knowledge* Framework

To contextualize the relationships between stakeholders and ecosystem services, we applied the *vrk* framework to three case studies of Southern Ocean ecosystem management, following Gorddard et al.'s (2016) approach. The *vrk* framework, aims to explore the interconnections between values, rules and knowledge in decision-making, to identify assumptions and gaps in decision-making systems and processes (Gorddard et al., 2016). It also explores *vrk* interactions, allowing for the analysis of the relationship and impact between values and rules, values and knowledge, and rules and knowledge (Gorddard et al., 2016; **Table 2**).

We selected three diverse examples relating to Southern Ocean ecosystem management as case studies, to understand gaps in decision-making through the *vrk* framework.

(1) Commission for the CCAMLR Working Group on Incidental Mortality Associated with Fishing (WG-IMAF), which aimed to reduce seabird bycatch and death through fishing in the Southern Ocean (Commission for the Conservation of Antarctic Marine Living Resources, 2007). This example is subsequently referred to as IMAF.
(2) CCAMLR Marine Protected Area (MPA) declaration for the Ross Sea Region (Commission for the Conservation of Antarctic Marine Living Resources, 2017), subsequently referred to as Ross Sea MPA.
(3) Work to consider the biophysical, governance, and policy dimensions of potential iron fertilization in the Southern Ocean research as a geo-engineering approach for climate change mitigation (Charette et al., 2013; Institute for Marine and Antarctic Studies [IMAS], 2019), referred to as Fe fertilization.

TABLE 2 | A summary of the key terms used in the *vrk* framework (Gorddard et al., 2016).

Term	Definition
Values	The guiding principles of the decision-making process, including economic, environmental, ecological, political, and social principles
Knowledge	The evidence, both formal and informal, that is used in the decision-making process
Rules	The norms, practices, heuristics, regulations, legislation, and treaties which govern the actions and behaviors of others
Values-rules (*vr*) interactions	How the favoring of particular values impacts the implementation or interpretation of rules, and vice versa
Values-knowledge (*vk*) interactions	How the under-representation or over-representation of particular values restricts or enhances knowledge, and vice versa
Rules-knowledge (*rk*) interactions	How the rules system is built upon knowledge systems, and how the rules system includes or excludes knowledge, and vice versa

These case studies were chosen to contrast different approaches in Southern Ocean ecosystem management, pertaining to different ecosystem components (1-seabirds, 2-whole-of-ecosystem, 3-primary production). The first two case studies were also selected due to high information availability. We note that while the third case study is not ecosystem management *per se*, it has a strong link to regulating services provided by Southern Ocean ecosystems, as well as complex challenges for governance and policy, and so was selected as a useful complement to the first two case studies.

We explored each case study by reviewing a combination of primary documents published by the respective body, as well as academic literature evaluating any relevant management decisions. The case studies were analyzed to understand their aims, methods, motivation, social-political context, participants and roles, following the recommended approach of Gorddard et al. (2016). We used this information to then ascertain underlying values, rules and knowledge implicit in the decision-making process. Finally, *vr*, *vk*, and *rk* interactions were explored by critically examining the values, rules and knowledge used in each case study. The process of case study analysis was conducted by one researcher, the *vrk* framework applied to the output by two researchers, and the overall process scrutinized by the authors' team as a whole. To visually represent this information, we developed a conceptual diagram (**Figure 4**) to connect key stakeholders and ecosystem services for each case study, framed through the role each stakeholder played in the decision-making process.

RESULTS

Stakeholders and Ecosystem Services

Our analysis of the transactional landscape for Southern Ocean ecosystem stakeholders and ecosystem services indicates that, across the different stakeholder groups, the strongest interest is in provisioning ecosystem services, followed by regulating services (**Figure 1**; see **Table 3** for a list of acronyms in this and subsequent figures). All stakeholder groups have at least some interest in provisioning services, and all groups but fisheries have an interest in regulating services. In contrast, the only stakeholders with an interest in supporting ecosystem services are science research stakeholders, and the majority of the interest in cultural ecosystem services is held by the tourism and public groups (see **Supplementary Table 2** for the full categorization of each stakeholder and details regarding their interest in and influence over ecosystem services).

86.9% of ecosystem services relationships are to regulators, researchers, and monitors, with only 13.1% of producer or user relationships between stakeholders and ecosystem services. As a result, there may be an overrepresentation of science viewpoints and values in Southern Ocean ecosystem management decision-making.

Stakeholder Relationships

Four key types of relationships were identified between stakeholders in Southern Ocean ecosystem management: regulating, advising, funding, and supporting. Producers, in particular the fisheries industry, are the stakeholder group whose actions and behaviors are most governed by the regulator stakeholder group (**Figure 2**). Some researchers, as well as regulators themselves, are also regulated by other stakeholders.

There appears to be a strong culture of advising among the stakeholders, with many researchers advising regulators, particularly CCAMLR and ATS. Several researchers and regulators have observer status at CCAMLR or ATCM. This allows them to represent their perspectives at decision-making forums. No producers and only one monitor (IUCN) has either observer status or attends CCAMLR or ATCM, suggesting a potential gap in these stakeholder perspectives in decision-making.

Decision-Making Pathways

Despite the interconnectedness of stakeholders demonstrated in the stakeholder relationships network (**Figure 2**), the decision-making pathway is distinct, and represents the way in which the value of ecosystem services feeds into decision-making via government, science, and governance, and how users and producers impact ecosystem services (**Figure 3**). This conceptual diagram is applicable to Southern Ocean ecosystem management, as well as ecosystem management on a broader scale.

Government performs two roles: as the primary funder and supporter of science, and as a regulator of users and producers. In the first instance, government is guided by cultural ecosystem services, which influence what areas of science are funded and otherwise supported. In the case of Southern Ocean ecosystem management, the influence of cultural ecosystem services on funding may differ between nations; some may be more strongly influenced by the values of the Southern Ocean, while others are likely to be more driven by domestic influences. However, the influence of different values may differ based on whether these decisions play out at a national or international level.

Governance takes three forms – policy, soft law, and regulation – and receives scientific advice based on scientific research, which is formulated through engagement with

TABLE 3 | Full list of identified stakeholders in Southern Ocean ecosystem management, including their parent stakeholder (if applicable), and definitions of acronyms for stakeholder groups as used in **Figures 1**, **2**, **4** and **Supplementary Table 2**.

Stakeholder	Acronym	Parent stakeholder
Agreement on the Conservation of Albatrosses and Petrels	ACAP	–
Agreement on the Conservation of Albatrosses and Petrels, Population and Conservation Status Working Group	WG-PCS	ACAP
Aker Biomarine	–	–
Analysis, Integration and Modeling of the Earth System	AIMES	FutureEarth
Antarctic and Southern Ocean Coalition	ASOC	–
Antarctic Climate Change and the Environment	ACCE	SCAR
Antarctic Climate Change in the 21st Century	AntClim21	SCAR
Antarctic Thresholds – Ecosystem Resilience and Adaptation	AnT-ERA	SCAR
Antarctic Treaty Consultative Meeting	ATCM	–
Antarctic Treaty System	ATS	–
Association of Responsible Krill Harvesting Companies	ARK	–
Austral Fisheries	–	
bioDISCOVERY	–	FutureEarth
Climate Impacts on Oceanic Top Predators	CLIOTOP	IMBeR
Coalition of Legal Toothfish Operators	COLTO	–
Commission for the Conservation of Antarctic Marine Living Resources	CCAMLR	–
Committee for Environmental Protection	CEP	–
Convention on Biological Diversity	CBD	–
Council of Managers of National Antarctic Programs	COMNAP	–
Expert Group on Antarctic Biodiversity Informatics	EG-ABI	SCAR
Expert Group on Birds and Marine Mammals	EGBAMM	SCAR
Fisheries and Marine Ecosystem Model Intercomparison Project	Fish-MIP	ISIMIP
Food and Agriculture Organization of the United Nations	UN FAO	–
Global Ocean Observing System	GOOS	–
Global Ocean Observing System Biology and Ecosystem Panel	EP-BE	GOOS
Integrated Marine Biosphere Research	IMBeR	FutureEarth
Integrating Climate and Ecosystem Dynamics in the Southern Ocean	ICED	IMBeR
Inter-Sectoral Model Intercomparison Project	ISIMIP	–
Intergovernmental Panel on Climate Change	IPCC	–
Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services	IPBES	–
International Association of Antarctica Tour Operators	IAATO	–
International Science Council	ISC	–
International Union for Conservation of Nature	IUCN	–
International Whaling Commission	IWC	–
International Whaling Commission Scientific Committee	SC-IWC	IWC
Marine Ecosystem Assessment for the Southern Ocean	MEASO	–
Public	–	–
Remote Sensing of Birds and Animals	Remote Sensing	SCAR
Scientific Committee for the Conservation of Antarctic Marine Living Resources	SC-CAMLR	CCAMLR
Scientific Committee on Antarctic Research	SCAR	–
Scientific Committee on Oceanic Research	SCOR	–
Southern Ocean Atlas	SO Atlas	SCAR
Southern Ocean Continuous Plankton Recorder Database	SO-CPR	SCAR
Southern Ocean Observing System	SOOS	–
Southern Ocean Research Partnership	IWC-SORP	IWC
State of the Antarctic Ecosystem	AntEco	SCAR
Tourists	–	–
United Nations Educational, Scientific and Cultural Organization	UNESCO	–
United Nations Environment Programme	UNEP	–
United Nations World Ocean Assessment	UN-WOA	–
Working Group 149: Changing Ocean Biological Systems	WG 149 COBS	SCOR
Working Group 150: Translation of Optical Measurements into particle Content, Aggregation and Transfer	WG 150 TOMCAT	SCOR
Working Group 154: Integration of Plankton-Observing Sensor Systems to Existing Global Sampling Programs	WG 154 P-OBS	SCOR

(Continued)

TABLE 3 | Continued

Stakeholder	Acronym	Parent stakeholder
Working Group on Acidification	WG Acidification	SCAR
Working Group on Antarctic Near-shore and Terrestrial Observing System	WG ANTOS	SCAR
Working Group on Ecosystem Monitoring and Management	WG-EMM	SC-CAMLR
Working Group on Fish Stock Assessment	WG-FSA	SC-CAMLR
Working Group on Statistics, Assessments and Monitoring	WG-SAM	SC-CAMLR
World Climate Research Programme	WCRP	–
World Meteorological Organization	WMO	–

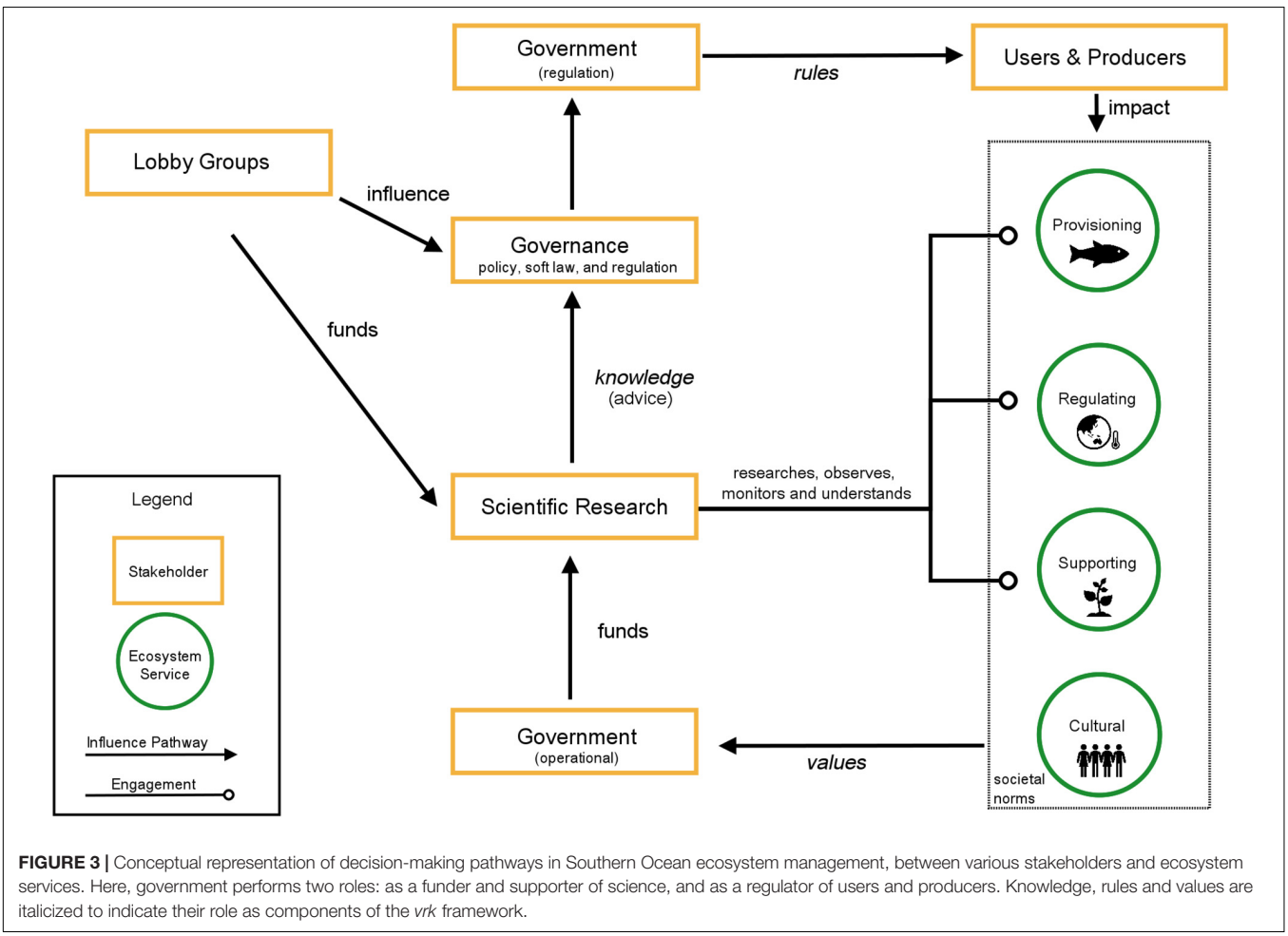

FIGURE 3 | Conceptual representation of decision-making pathways in Southern Ocean ecosystem management, between various stakeholders and ecosystem services. Here, government performs two roles: as a funder and supporter of science, and as a regulator of users and producers. Knowledge, rules and values are italicized to indicate their role as components of the *vrk* framework.

provisioning, regulating and supporting ecosystem services. Governance is also influenced by the actions and priorities of lobby groups.

Values-Rules-Knowledge (vrk) Case Studies

The *vrk* framework analysis of three Southern Ocean ecosystem management case studies is summarized in **Table 4**, and a network visualization particular to the ecosystem services and stakeholders represented in the case studies is shown in **Figure 4**. This network visualization demonstrates the dual role of science, in researching ecosystem services directly and in IMO, SCAR, and COMNAP providing scientific advice to other stakeholders. In this network visualization, researcher relationships are shown only for scientific research conducted specifically for the case study. Researchers in the Ross Sea MPA case study did not conduct any new research, but engaged only with the existing global body of scientific evidence; for this reason, science researchers are not shown to have a researcher relationship with any ecosystem service. We acknowledge the importance of individual nations as stakeholders in the Ross Sea MPA case study, so have considered four particular CCAMLR member states as stakeholders because of their roles in how decisions were made in this case study.

TABLE 4 | *vrk* analysis of three Southern Ocean ecosystem management case studies.

Project	CCAMLR: Working Group on Incidental Mortality Associated with Fishing	CCAMLR: MPA declaration of Ross Sea Region	Geoengineering/Iron (Fe) fertilization
Project aims	To reduce seabird death due to fishing	To protect habitat, support ecosystem services, provide reference areas for monitoring variability, conserve biodiversity, and promote scientific research	To understand how Fe fertilization in the Southern Ocean might mitigate climate change, to use this research to inform national and international policy on geoengineering, and develop a governance framework for future geoengineering research
Values	CCAMLR takes an ecosystem-based approach, emphasizing environmental values over social and economic values – the degree of risk management is dependent on the risk rating, which is calculated using environmental values. CCAMLR employs the precautionary principle in its decision-making.	The Proponent States communicated the key value of the Ross Sea MPA as being ecological conservation. A CCAMLR General Measure declares that MPAs must be established on the basis of the best available scientific evidence, indicating a theoretical prioritization of environmental values, consistent with the objective and expectation in the Convention. However, MPAs must be approved by consensus which can limit the scope of application depending on each and every Member. During its negotiation, coverage of the MPA was altered to give fishing access to areas that were argued to be important for biodiversity. There has therefore been a trade-off between political/economic values and ecological/environmental values.	Scientific research into Fe fertilization has been prioritized, and commercial implementation has been delayed. Despite the urgency to take climate action, key questions around Fe fertilization must be answered, around its effectiveness, economic feasibility, ecological side effects, ethics, and philosophical implementation frameworks.
Rules	The Conservation Measures (CMs) are mandatory, legally binding measures. The Monitoring and Review of the management decision is based on adherence to CMs and international instruments.	CCAMLR necessitates the integration of science in MPA proposals through specific scientific objectives. It also requires MPAs to have research and monitoring plans to help determine the continuing need for the MPA. How these plans will be used in reviews and in deciding to continue the MPA is not clear.	The 2008 London Protocol and London Convention agreements state that no ocean fertilization activities are allowed, apart from those that are legitimate scientific research. This follows the Haida Gwaii Fe fertilization activities, for which the contracting parties to the London Convention and London Protocol issued a statement of concern.
Knowledge	Baseline data on seabird mortality was collected to understand magnitude. The risk rating (1–5) is based on breeding and distribution, based on published scientific information and expert opinion from WGs. This risk rating is used to develop a risk management plan per location. CMs are reviewed based on increasing knowledge and technical/technological environments.	The Ross Sea MPA was proposed as the area is highly productive, has diverse species, and is one of the few places in the world which has retained its full community of top-level predators. A CCAMLR General Measure declares that MPAs must be established on the basis of the best available scientific evidence, and there is a mandate for any MPA to include elements such as a scientific management plan, and a research/monitoring plan. The MPA proposal process involved workshops, analyses, advice from WGs, and a review of the science underpinning the proposal.	Polar datasets are being used as a platform. Experiments and modeling will be used to generate new knowledge to quantify the removal of atmospheric CO_2. Fe fertilization makes use of new and emerging technology. There is existing knowledge that primary productivity in the Southern Ocean is limited by Fe availability. The Fe fertilization hypothesis is based on analysis of the dust and gas composition of ice cores, with findings revealing that low iron levels in dust corresponded to warmer temperatures. To date, in this particular example, there has been prioritization of environmental and economic knowledge, but not ethical or social knowledge.
References	Commission for the Conservation of Antarctic Marine Living Resources, 2007; Croxall, 2008; Waugh et al., 2008	Brooks, 2013; Kavanagh, 2016; New Zealand Ministry of Foreign Affairs and Trade, 2016; Commission for the Conservation of Antarctic Marine Living Resources, 2017; Commission for the Conservation of Antarctic Marine Living Resources, 2018; Dodds and Brooks, 2018; Brooks et al., 2019; Marine Protection Atlas, 2020; Sylvester and Brooks, 2020	Boyd, 2008; Powell, 2008; International Maritime Organization [IMO], 2012; Charette et al., 2013; Buck, 2014; Horton, 2017; Gannon and Hulme, 2018; Institute for Marine and Antarctic Studies [IMAS], 2019; International Maritime Organization [IMO], 2020

Framework adapted from Gorddard et al. (2016).

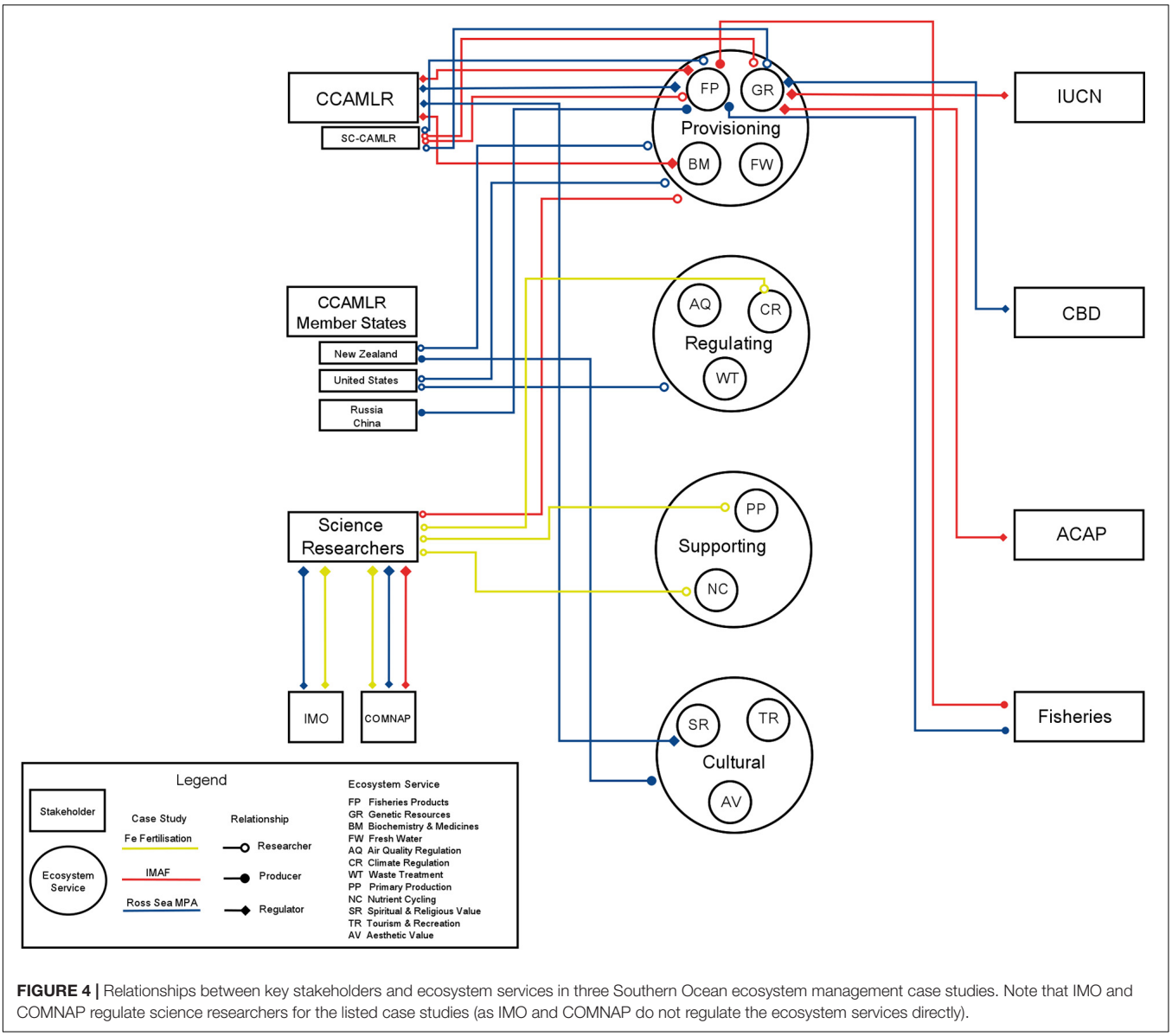

FIGURE 4 | Relationships between key stakeholders and ecosystem services in three Southern Ocean ecosystem management case studies. Note that IMO and COMNAP regulate science researchers for the listed case studies (as IMO and COMNAP do not regulate the ecosystem services directly).

Values-Rules Interactions

The remit of CCAMLR is the conservation of Antarctic marine living resources (Press et al., 2019). However, fisheries have been given most of the attention of CCAMLR since the beginning (e.g., Constable, 2011).

Case study 1 emerged with the recognition of high rates of seabird mortality in longline fisheries in the early 1990s, which coincided with rapid declines in those populations. In order to rectify this, decision-making in IMAF initially heavily prioritized ecological and environmental values over social and economic values (**Table 4**). However, as incidental mortality of seabirds was reduced to zero, conservation measures were loosened to allow fisheries more freedom in operating, suggesting a growing shift toward increasing priority for economic values, although noting that ecological values still take precedent (Croxall, 2008; Waugh et al., 2008).

Case study 2 highlighted the challenges within CCAMLR of addressing questions of biodiversity conservation and the maintenance of supporting ecosystem services. The consensus decision process in CCAMLR and the large number of fishing interests amongst its Members means that provision services have higher attention than supporting services, such as biodiversity. Although the proposal of the Ross Sea MPA was based on ecological values, there was strong prioritization of economic values in the negotiation of the MPA's boundaries, such that in its adopted form, some of the most productive areas of the Ross Sea remain unprotected, to allow fisheries to operate in these areas (Brooks, 2013; Brooks et al., 2019; Commission for the Conservation of Antarctic Marine Living Resources, 2017; Dodds and Brooks, 2018; Sylvester and Brooks, 2020).

Case study 3 provides an example external to CCAMLR but governed by an international convention that has regulatory

power – the London Convention (International Maritime Organization [IMO], 2012). The assessment process for Fe fertilization is guided by science, giving regulators time to understand how to incorporate potential Fe fertilization in the Southern Ocean into carbon markets and international laws (Powell, 2008; Institute for Marine and Antarctic Studies [IMAS], 2019). However, the scientific research framework does not directly include exploration of the important ethical considerations in intervening in the earth's biogeochemical cycles (because these were out of scope of the research project).

Values–Knowledge Interactions

CCAMLR has a remit from its Convention to use the best scientific evidence available (Constable et al., 2000; see also CCAMLR Resolution 31).

Case study 1 is an example of formal knowledge being prioritized over informal knowledge. The risk rating for seabirds in different fisheries, and therefore degree of risk management, for IMAF was based on published scientific information and expert information from CCAMLR's Scientific Committee and its working groups, particularly on breeding ranges, at-sea distribution – both ecological values – to judge potential overlap with fisheries (Commission for the Conservation of Antarctic Marine Living Resources, 2007). It did not use or rely on knowledge from fisheries or conservation NGOs.

Case study 2 shows the tension between knowledge and values and how, in a consensus environment, some values can be diminished in consideration. Most specific knowledge in the Ross Sea has been developed for advising on toothfish fisheries. Yet, there is a large body of general scientific knowledge indicating its value to global scientific research and for supporting services such as biodiversity and productivity. While the latter would be expected to be given support to be sustained, the dominance of fisheries interests meant that non-ecological values, particularly economic values, were given increasing priority as the MPA declaration process progressed (Sylvester and Brooks, 2020). Through the consensus structure of CCAMLR, Member States have the power to prioritize their own values rather than pursuing satisfactory outcomes across all values.

Case study 3 emerged from a global opposition to uncontrolled waste disposal by dumping in the ocean, recognizing the impacts that pollution has on marine ecosystem services generally. The focus on scientific modeling and critically assessing the ecological and economic dimensions of Fe fertilization gives scientists time to explore unknown variables. Under the circumstances of this convention, regulators require confidence before acting that Fe fertilization will be effective and that any environmental effects are acceptable. In this particular example, social, political, and ethical values have not been considered directly to date.

Rules-Knowledge Interactions

Case study 1 on IMAF is a clear case where the rules system was built upon the scientific knowledge system, with all reviews of the CCAMLR Conservation Measure (CM) based on satisfactory reduction (elimination) of seabird by-catch. All public discussion is therefore framed around the CMs and by-catch data (**Table 4**). Scientific and ecological knowledge is prioritized through the rule that all longline vessels fishing in the area must have an independent scientific observer on board who reports on the implementation of the CMs. This is enforced through required compliance with by-catch reduction strategies being part of some fishery permits. Existing fisheries demand a high level of proof of the need and success for new management strategies before enacting them; this knowledge was considered in the implementation of the CM, with an initial focus on enforcing the CMs on new and exploratory fisheries before targeting existing fisheries (Waugh et al., 2008).

Case study 2 on the Ross Sea MPA has a close relationship between maintenance of the MPA and scientific research and monitoring built into the long-term application of the conservation measure. It remains to be seen how science and knowledge will be used in the maintenance of the MPA.

Case study 3 on Fe fertilization has a close relationship between scientific knowledge and future regulation, where both national and international policy and future scientific research will be developed based on environmental and economic analysis. This means it may exclude sociopolitical perspectives in formulating guidelines and rules. Globally, the current focus on ocean fertilization is to generate scientific knowledge, following the 2008 London Convention and London Protocol agreement that legitimate scientific research is the only permitted ocean fertilization activity (International Maritime Organization [IMO], 2012). Although this enables scientific research, this may restrict the participation of stakeholders who bring other knowledge sources, or do not engage in traditional scientific research.

DISCUSSION AND CONCLUSION

Information about stakeholder aspirations is a fundamental requirement for effective ecosystem-based management (Cavanagh et al., 2016). A key precursor to understanding these aspirations is an understanding of who the stakeholders are for a particular context and how they are connected to ecosystems and ecosystem services. For Southern Ocean ecosystems, consideration of this 'transactional landscape' has generally been constrained to specific issues, such as the management of the Southern Ocean krill fishery (Cavanagh et al., 2016) or implementation of marine protected areas (Sylvester and Brooks, 2020). In this study we have used structured, network-based approaches to consider the full stakeholder landscape for Southern Ocean ecosystems, to consider the ways in which stakeholders relate to different ecosystem services (**Figure 1**), as well as the way in which stakeholders are connected to each other (**Figure 2**). This process has yielded important insights into how different ecosystem services are understood, valued and managed, as well as a conceptual framework for how different types of stakeholders fit into and influence decision making pathways for Southern Ocean ecosystems (**Figure 3**). By combining this analysis of the transactional landscape with consideration of the role of values, rules and knowledge in particular

examples that relate to decision making for Southern Ocean ecosystems, we are able to further highlight where gaps may exist that could be given greater consideration to support robust decision-making in the future.

Our results indicate that ecosystem science facilitates high connectivity between stakeholders and provisioning services, but that there is relatively limited connectivity between stakeholders and supporting services. This gap is likely to become increasingly important as dependencies on climate regulation services, in particular, increase in the future. Our application of Gorddard et al.'s (2016) 'values-rules-knowledge' framework to three case studies suggests that, at least in these cases, the emphasis for decision making has been on knowledge and rules. While this helps establish how to use the best scientific information in consensus decision-making, wider consideration of values across the broader stakeholder landscape (including individual nations) – together with science (knowledge) and governance (rules) – might provide greater appreciation of impediments to consensus when scientific information indicates the need to change the status quo (i.e., introduce regulations) in order to achieve agreed high-level objectives. Moreover, the type of mapping presented here can identify when some ecosystem services are being given greater short term priority, such as provisioning services, over the longer term requirements for sustaining others, such as supporting services. As a result, holistic mapping would be expected to improve whole-of-system sustainability.

We suggest that future stakeholder mapping might also usefully consider the influential role of particular nations in decision-making for Southern Ocean ecosystem services, particularly when analyzing the interests of fisheries, which all originate from nations and therefore act based on the conservation, economic and social priorities and aspirations of those nations. In the interest of keeping our analysis reasonably constrained, this nation-level analysis was deemed to be beyond the scope of our paper.

Case Study Findings With Respect to Values-Rules-Knowledge

Management to reduce incidental mortality of seabirds in the Southern Ocean (our IMAF case study) is commonly heralded as a successful collaborative conservation project (Croxall, 2008), while the MPA declaration in the Ross Sea region was arguably less successful, given its size had to be decreased in order for it to be adopted (Sylvester and Brooks, 2020). Our analyses suggest that a factor influencing this outcome was the role of social and political values in the MPA negotiation process (as opposed to values around all ecosystem services). Political and social values were successfully considered through the IMAF management process, by focusing implementation based on the values of different sub-sets of fisheries (Croxall, 2008). Although political and ethical values are acknowledged in research relating to potential geo-engineering through iron fertilization in the Southern Ocean, they are not explored directly as part of the research. Assessment of ethical and political aspects of iron, alongside ecological and economic assessment, might help ensure that scientific knowledge can be successfully implemented in rules whilst navigating trade-offs in political, ethical and economic values.

Across the three case studies analyzed, the stakeholders engaged were heavily invested in provisioning ecosystem services (**Figure 4**). This is in line with our analysis of the stakeholders across Southern Ocean ecosystem management more generally (**Figure 1**). The Ross Sea MPA process involved stakeholders who have an interest across three different ecosystem services; however, our analysis suggests that working with stakeholders who are interested in a variety of ecosystem services must be coupled with incorporating many different values in order for management decision-making to be more successful in collaboration and conserving the ecosystem.

Stakeholder Engagement for Southern Ocean Ecosystem Decision-Making Under Climate Change

The need for effective management and robust decision-making for Southern Ocean ecosystems will become more important as the global climate continues to change (Constable et al., 2017; Meredith et al., 2019; Cavanagh et al., 2021). The impacts of climate-driven environmental changes pose current and future risks for most Southern Ocean ecosystem services, and these risks will need to be managed to meet increasing demand for fisheries products, tourism and regulating services. Understanding and considering the perspectives, needs and roles of diverse stakeholders in these processes will lead to more robust outcomes for ecosystems and people. Our study is the first to characterize the full transactional landscape for Southern Ocean ecosystem services and stakeholders, and we hope that our analyses, particularly as they relate to emphases and gaps in previous processes, might help underpin effective ecosystem management under future climate change in the Southern Ocean. A remaining challenge is to determine how representative stakeholders of the Southern Ocean are with respect to the wider expectations of civil society and whether the stakeholders can keep pace with their rapidly changing norms.

Key Messages to Policymakers

(1) To gain a holistic appreciation of how Southern Ocean ecosystem services are understood, valued and managed, it is essential to consider the full stakeholder landscape.
(2) There are many connections (indicating a high level of interest) between Southern Ocean stakeholders and provisioning ecosystem services (primarily fisheries), but more limited connectivity between stakeholders and supporting ecosystem services (primary production and nutrient cycling).
(3) This suggests that short term priorities may be given precedence over longer term priorities for overall Southern Ocean sustainability (such as supporting services).
(4) Bridging the gap between stakeholders and supporting ecosystem services will become increasingly important under climate change as the world increases its reliance

on the Southern Ocean's climate regulation services (since biological supporting services play a key role in global climate feedbacks).

(5) The emphasis for decision making in the Southern Ocean has been on knowledge and rules over values. Wider consideration of values across the full stakeholder landscape may help achieve consensus through science-informed decision-making.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

JM-T and JS conceived the study. JS led the data collection and analyses. All the authors contributed to writing the manuscript.

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SUPPLEMENTARY MATERIAL

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Responses of Southern Ocean Seafloor Habitats and Communities to Global and Local Drivers of Change

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Knowledge of life on the Southern Ocean seafloor has substantially grown since the beginning of this century with increasing ship-based surveys and regular monitoring sites, new technologies and greatly enhanced data sharing. However, seafloor habitats and their communities exhibit high spatial variability and heterogeneity that challenges the way in which we assess the state of the Southern Ocean benthos on larger scales. The Antarctic shelf is rich in diversity compared with deeper water areas, important for storing carbon ("blue carbon") and provides habitat for commercial fish species. In this paper, we focus on the seafloor habitats of the Antarctic shelf, which are vulnerable to drivers of change including increasing ocean temperatures, iceberg scour, sea ice melt, ocean acidification, fishing pressures, pollution and non-indigenous species. Some of the most vulnerable areas include the West Antarctic Peninsula, which is experiencing rapid regional warming and increased iceberg-scouring, subantarctic islands and tourist destinations where human activities and environmental conditions increase the potential for the establishment of non-indigenous species and active fishing areas around South Georgia, Heard and MacDonald Islands. Vulnerable species include those in areas of regional warming with low thermal tolerance, calcifying species susceptible to increasing ocean acidity as well as slow-growing habitat-forming species that can be damaged by fishing gears e.g., sponges, bryozoan, and coral species. Management regimes can protect seafloor habitats and key species from fishing activities; some areas will need more protection than others, accounting for specific traits that make species vulnerable, slow growing and long-lived species, restricted locations with optimum physiological

conditions and available food, and restricted distributions of rare species. Ecosystem-based management practices and long-term, highly protected areas may be the most effective tools in the preservation of vulnerable seafloor habitats. Here, we focus on outlining seafloor responses to drivers of change observed to date and projections for the future. We discuss the need for action to preserve seafloor habitats under climate change, fishing pressures and other anthropogenic impacts.

Keywords: benthos, Antarctica, Southern Ocean, marine protected areas, vulnerable marine ecosystems, fishing

INTRODUCTION

The benthic habitats of the Southern Ocean are hugely variable, from ice scoured shallows to rich, dense shelf communities with many endemic species and mosaics of areas variously dominated by suspension or deposit feeders and their predators. These habitats are a store of exported carbon from the overlying pelagic productivity and habitat for commercial fish species. This paper is a contribution to the Marine Ecosystem Assessment for the Southern Ocean (hereafter termed MEASO). In this benthic assessment, we identify the pathways of impact by global drivers (Morley et al., 2020) and local drivers (Grant et al., in review, to be published in this research topic) (**Figure 1**) and discuss the observed and projected implications of those impacts on benthic communities across the Southern Ocean. Specifically, we discuss the direct and indirect impacts of increasing ocean temperature, ocean acidification, and marine ice losses (ice shelves, glaciers, and sea ice), the latter which will result in increased ice scour, light, and sedimentation, changing primary production and biogenic flux. We also consider the impacts of fishing, plastics, chemical pollution and non-indigenous species. Whilst we cannot discuss all drivers and recorded observations of change in detail, we aim to highlight the key impacts that likely influence benthic biodiversity and production.

Physical Setting

The shallowest habitat of the Southern Ocean is the intertidal zone at the very edge of the continent of Antarctica and subantarctic islands. Habitats shallower than 100 m are relatively rare and estimated to have a total area of approximately 25,000 km^2 (Clark et al., 2015). The intertidal extends into the continental shelf, which is unusually deep in a global context, averaging 450 m but exceeding 1000 m in some places, including inner shelf canyons and valleys (Harris and O'Brien, 1996; Beaman and Harris, 2005). The depth of the continental shelf is due to isostatic depression under the weight of glacial ice, and glacial erosion over geological time of the Antarctic continental shelf (Clarke and Johnston, 2003). The continental shelf covers an area of ∼4.1 million km^2; the continental shelf can reach up to 1000 km from continental margin to shelf edge, and the widest areas have large floating ice shelves (Post et al., 2014). Benthic communities of the continental shelf can underlie ice shelves and fast ice or may be ice-free with seasonally shifting ice regimes. The continental shelf joins the continental slope at the shelf break. The slope is steep, overlain by circumpolar deep water (2-2.5°C), and its gradient (generally 5-15°, with some areas up to 26°) declines toward the abyssal plain at ∼3000 m depth (Kaiser et al., 2011; Arndt et al., 2013; **Figure 2**). Seafloor areas that are shallower than 1000 m can occur in the Southern Ocean around subantarctic islands and on banks, plateau, and seamounts. For simplicity and unless otherwise specifically stated, we use the term "shelf areas" to collectively encompass these shallow areas and the Antarctic continental shelf.

Seafloor environments are influenced by different sedimentary and oceanographic processes, which in addition to depth define the habitat (Post et al., 2014). Physical seafloor features, referred to as geomorphic features, incorporate the shape of the seafloor (e.g., ridges, troughs, basins, canyons, etc.) and substratum type (e.g., hard, poorly sorted, or soft). Mapping the geomorphology of the seafloor provides a broad-scale indication of benthic habitats and associated biological communities (e.g., Beaman and Harris, 2005; Gutt et al., 2007; Post et al., 2010, 2017). **Figure 3** highlights the geomorphic features of the Southern Ocean across MEASO areas. In this assessment, we focus on the "shelf areas."

Shelf areas are not smooth areas extending from the shelf break to the intertidal (or shallowest point on a bank/seamount), instead they are broken up by deep troughs (deeps) eroded by glacial expansion during past glaciations, which form modern depocenters for sedimentation (shelf deeps). These deeps are typically associated with mobile scavengers and infauna living in the seafloor sediments. Where shelf deeps connect to the continental slope, they form cross-shelf valleys and canyons, providing a pathway for ocean circulation and food transfer between shelf and slope environments. Relatively shallow shelf banks, formed due to bypass of the mobile ice sheet around these broad features, are typically scoured by icebergs. Shelf banks usually contain communities in various stages of recolonization, from pioneer species through to later successional stages (e.g., Gutt and Starmans, 2001). Coastal terrane occurs at depths shallower than 200 m, within the photic zone unless covered by ice. Features in these areas are often rugged and rocky, consisting of deep basins, steep gullies and channels eroded by small coastal glaciers (e.g., Beaman and Harris, 2003). In nearshore areas experiencing sea ice for approximately 11 months or more annually, sessile invertebrates tend to dominate rocky and rugged seafloor habitats rather than macroalgae (Clark et al., 2013).

State of Knowledge of the Southern Ocean Benthos

Until relatively recently benthic research focused on areas within 150 km of research stations (Griffiths, 2010), however there is an increasing effort to sample slope communities and the deep

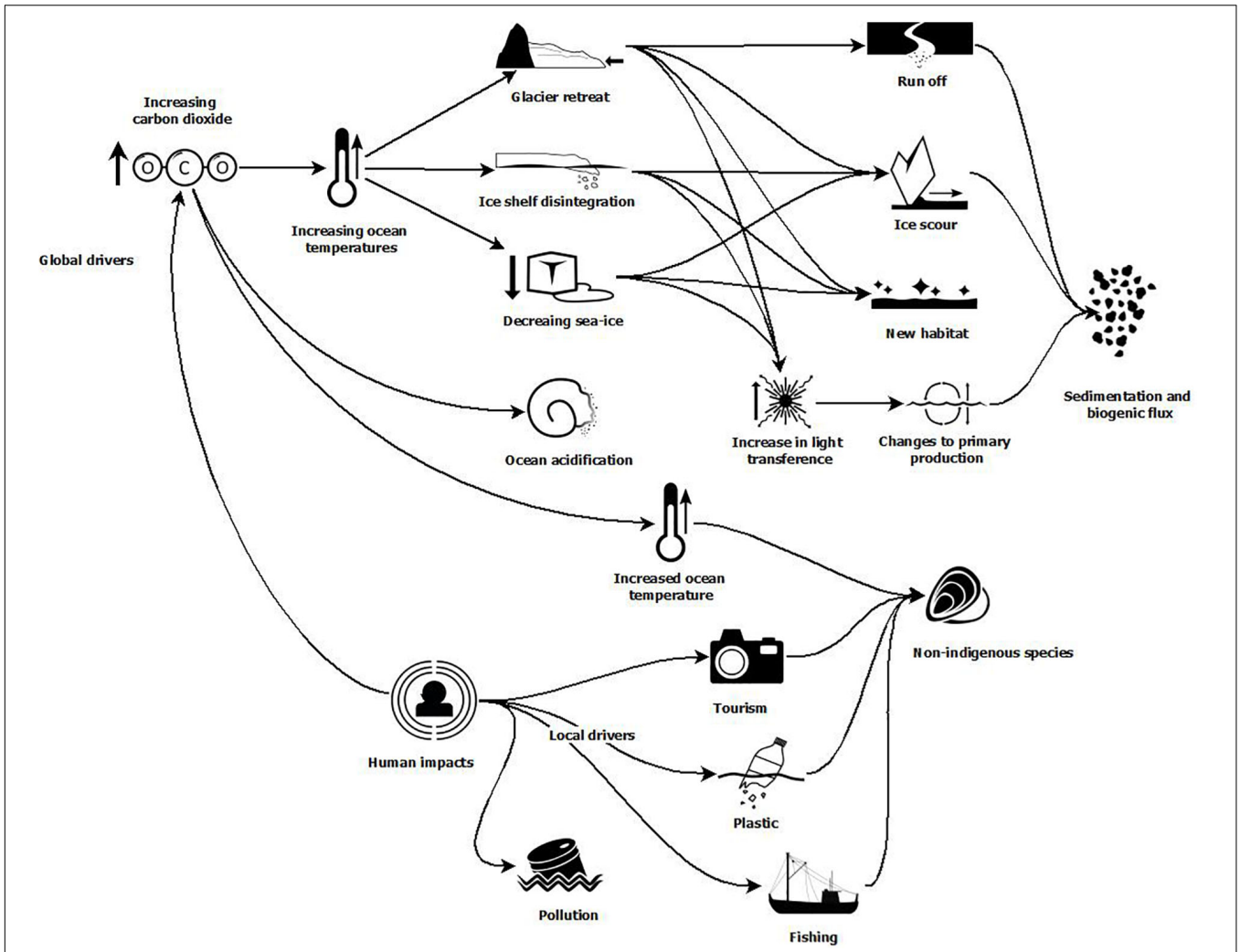

FIGURE 1 | Example pathways for impact drivers of change in the Southern Ocean that can affect benthic communities. See Morley et al. (2020) and Grant et al. (to be published in this research topic) for more details regarding global and local impact drivers within the MEASO context.

sea (e.g., Brandt et al., 2007; Kaiser et al., 2013). Observations and models that support projects like MEASO are described in Brasier et al. (2019) which includes the first Western scientific and discovery expeditions to reach Antarctica in the 1750s. Some of the earliest working research bases were established in mid-twentieth century for both scientific endeavors and territorial claims (Walton and Bonner, 1985). **Table 1** indicates the evolution of benthic research via large scale research programmes since the 1961 adoption of the Antarctic Treaty. In this paper we present observation findings and acknowledge the differences in temporal and spatial coverage across MEASO areas.

Using the Ocean Biogeographic Information System (OBIS) and Global Biodiversity Information Facility (GBIF) databases, we categorized, where possible, species distributed in the MEASO area to benthic, pelagic, and unknown (see **Supplementary Information** for more details). All the extracted data were cleaned and went through a careful quality control process (see **Supplementary Information**). The spatial coverage of 161,711 distribution records (hereafter termed the benthic records) displayed in **Figure 4** show the highest concentration of records within the Antarctic zone are in the Ross Sea (West Pacific), West Antarctic Peninsula region (East Pacific and Atlantic), and Weddell Sea (Atlantic). In the subantarctic zone benthic records concentrate in the Scotia Arc (Atlantic), Kerguelen region (Central Indian), the northern zone off New Zealand and Macquarie (West Pacific and East Indian). This is a reflection of sampling and research effort in these areas that is noted in earlier studies (Griffiths, 2010; Grant et al., 2011).

The benthic records represent 7,945 benthic species, although these results are likely an under-representation of benthic biodiversity in the Southern Ocean. The total expected number of macrozoobenthic species for the entire Southern Ocean shelf area lies between 11,000 and 17,000 species (Gutt et al., 2004). However, Gutt et al.'s (2004) estimate is conservative for Southern Ocean benthos overall, as we continue to find new species with more benthic sampling, especially in deep-sea habitats

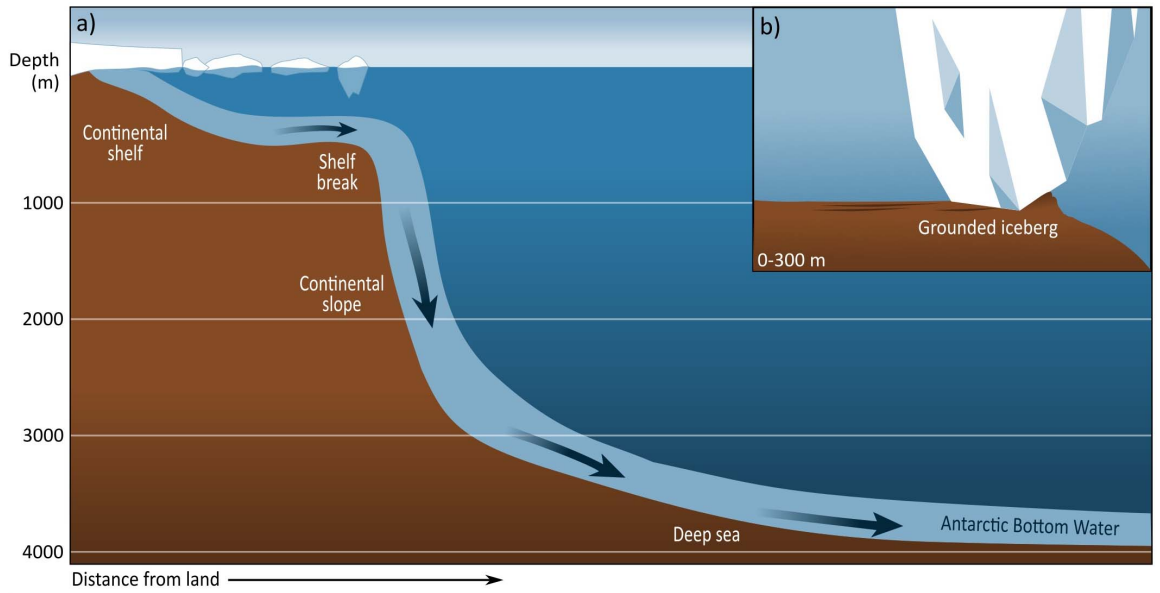

FIGURE 2 | (a) Depth profile of Southern Ocean seafloor and **(b)** grounded iceberg on the Antarctic shelf, grounding like this is most common between 0 and 300 m.

(Brandt et al., 2007, 2012; Kaiser et al., 2013). It also does not incorporate the potential for cryptic species, i.e., those that are morphologically identical but genetically distinct, which is considered a common feature of the Southern Ocean fauna (e.g., polychaetes - Schüller, 2011; Neal et al., 2014; Brasier et al., 2016; crustaceans - Held, 2003; Raupach et al., 2007; Baird et al., 2011; Havermans et al., 2011; molluscs - Linse et al., 2007; Allcock et al., 2011; echinoderms - Wilson et al., 2009; Janosik and Halanych, 2010, pycnogonids - Krabbe et al., 2010; nematodes - Thornhill et al., 2008; sponges - Vargas et al., 2017).

With an increasing amount of data for Southern Ocean benthic species, there is continuing effort to increase biological information available within species databases. For example, the Register of Antarctic Marine Species (RAMS), which was established as a standard reference for marine biodiversity research, conservation and sustainable management, contains an authoritative taxonomic list of species occurring within the Southern Ocean. Work is now underway to add additional "trait" data to RAMS, including categorical and quantitative information about species life history, habitat, diet and physiology. These data can be used for functional analyses, to help identify sensitive species or functional groups and can be combined with spatial data and climate projections to identify where and when these groups might be affected by external drivers.

Biological Traits of Southern Ocean Benthic Species

The modern Southern Ocean benthos has evolved both *in situ* and via exchange with surrounding deep basins of the Indian, Pacific, and Atlantic Oceans. *In situ* evolution and relative isolation of some benthic habitats may have driven the relatively high degree of endemism - ranging from 60 to 90% of species (Arntz et al., 1997; Brandt and Gutt, 2011). The isothermal water column has also facilitated down-slope (submergence) and up-slope migrations (emergence) of refugial populations during glacial cycles, resulting in an abundance of eurybathic species, or species able to live over a wide depth range (Brey et al., 1996; Brandt et al., 2005). Colonization of the Antarctic shelf from either deep-sea regions around Antarctica, via the Scotia Arc or caused by the breakup of Gondwana during the Cenozoic Era, has only been investigated in some taxa such as isopods, corals, echinoderms, bivalves, and bryozoans (e.g., Brandt, 1991, 1999; Brandt et al., 1999; Figuerola et al., 2014, 2017).

The Southern Ocean benthos has thrived under comparatively constant, cool conditions for millions of years. Ocean temperatures range from -1.9 at their coldest to 5°C at the northern limit of the Southern Ocean, leading to the evolution of many physiological adaptations that protect benthic organisms against, or overcome the extreme effects of, cold conditions. Examples include the presence of antifreeze in the tissues of many Southern Ocean fish that reduces their freezing point to below that of seawater (-4°C) (DeVries, 1971), and polar gigantism, where the low metabolic rates at low temperatures and the slightly increased oxygen concentration in cold water which may have resulted in some marine invertebrates becoming bigger than ecologically equivalent species from warmer environments (Chapelle and Peck, 1999). At the community level, along the continental shelf and nearshore regions, the rarity of skeleton-crushing (durophagous) predators such as bony fish, sharks, brachyuran crabs and lobsters is a key feature of the Southern Ocean benthos (Aronson et al., 2007). For some species their rarity is due to physiological implications of living in cold temperatures. For example, brachyuran crabs are unable to regulate magnesium levels in their blood at temperatures

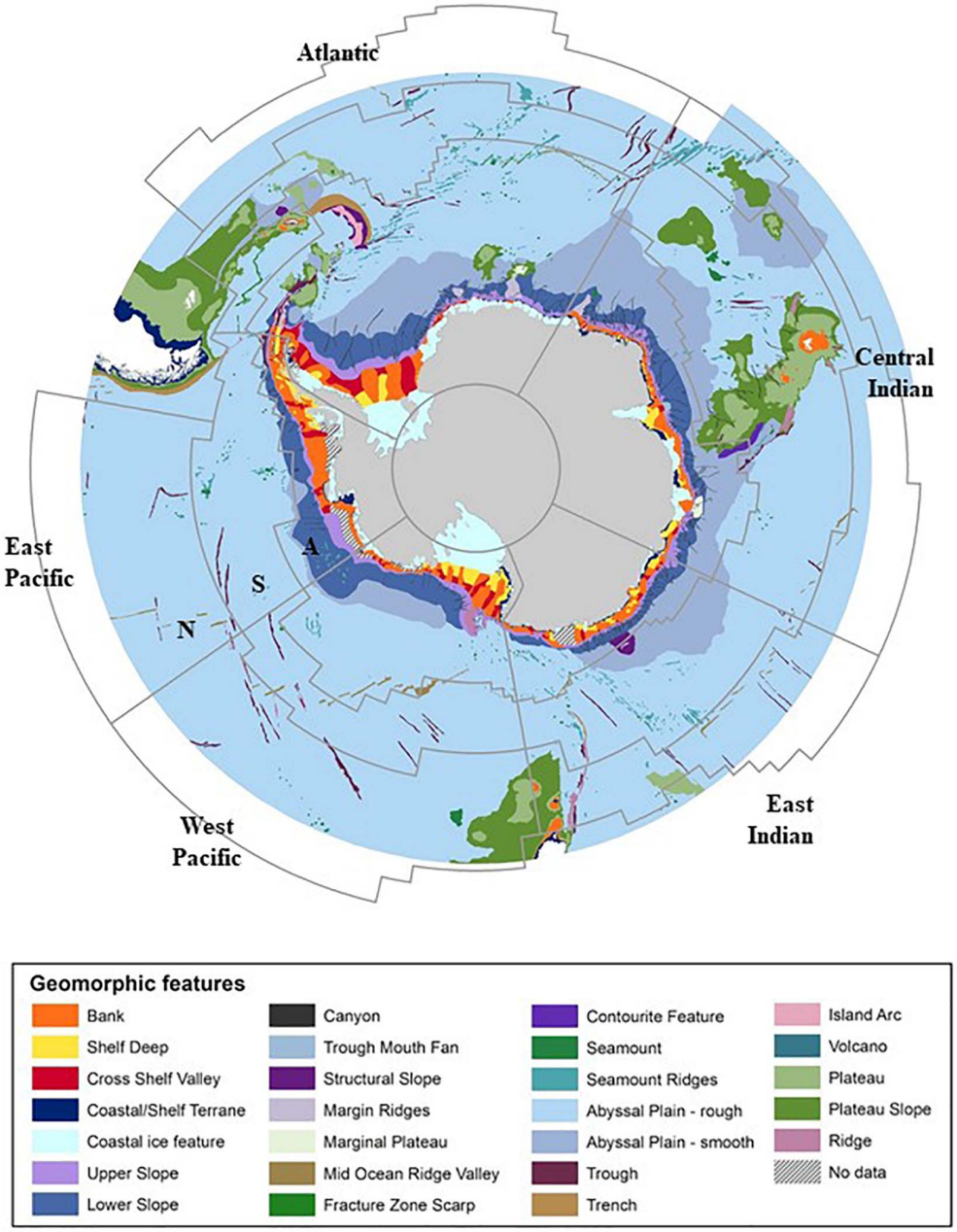

FIGURE 3 | Geomorphic features of the Southern Ocean. MEASO areas are shown (thin gray lines) including MEASO sectors (Atlantic, Central Indian, East Indian, West Pacific, East Pacific) and MEASO zones (where N = northern, S = subantarctic, A = Antarctic). Data adapted from O'Brien et al. (2009); Post et al. (2014), definitions of geomorphic features are provided in **Supplementary Information**.

<0°C, reducing the scope of aerobic activity (Frederich et al., 2001), thereby limiting their ranges.

Benthic Communities of the Southern Ocean

Benthic communities are influenced by multiple environmental factors that vary across spatial scales (e.g., Gutt et al., 2019). These can include but are not limited to depth, substrate type, food availability, temperature, salinity, oxygen availability, sea ice cover and disturbance. Generalized patterns within benthic communities are described here whilst recognizing they are subject to local and regional variation. Benthos on the Antarctic continental shelf is made up of two core communities, one is dominated by sessile suspension feeders such as sponges, bryozoans, cnidarians and ascidians, which are supported by food in strong near-bottom currents and thrive on "hard substrates" including coarse-grained sediment, gravel, rocks or dropstones

TABLE 1 | Examples of benthic species, community and ecosystem level observations within large scale research programmes including the timescale of observations and areas of study.

Topic	Study	Timescale	Spatial scale	Locations	MEASO area*	Depth**	Programmes***
Single species	Reproductive monitoring	1990s onward	Local	Antarctic Peninsula	EP-A	Shallow	AnT-ERA
Single species	Ecophysiology	2000s onward	Local	Antarctic Peninsula, Davies Sea	EP-A, CI-A, EI-A	Shallow	AnT-ERA
Single species	Molecular response	2000s onward	Local	Antarctic Peninsula	EP-A	Shallow	AnT-ERA
Single species	Thermal tolerance	1990s onward	Local	Antarctic Peninsula	EP-A	Shallow and shelf	AnT-ERA
Single species	Acidification experiments	2000s onward	Local	Antarctic Peninsula, Davies Sea	EP-A	Shallow	AnT-ERA
Single species	Ecotoxicology	2000s onward	Local	Antarctic Peninsula	EP-A CI-A, EI-A	Shallow	
Single species & community	Genetics and phylogeography	2000s onward	Local to circumpolar	Antarctic Peninsula, Amundsen Sea, Weddell Sea, Ross Sea Dumont D'Urville Sea, Davies Sea, Prydz Bay, subantarctic islands	EP-A, EI-A, CI-A	Shallow to deep-sea	CAML, AntECO
Single species & community	Non-indigenous species (benthic marine)	2000s onward	Local	Antarctic Peninsula and subantarctic islands	EP-A, AO-S, EI-S, CI-A	Shallow and shelf	AntECO, CEP
Community	Diversity and Community monitoring	1960 onward	Local to regional	Antarctic Peninsula, Ross Sea, Weddell Sea, South Georgia	EP-A, AO-A, AO-S, WP-A	Shallow and shelf	AntECO, SOOS, AntOBIS or biodiversity.aq
Community	Changing ice regimes	1990s onward	Local to regional	Antarctic Peninsula, Weddell Sea	EP-A, A-A	Shallow and shelf	ICED, SOOS, AntOBIS or biodiversity.aq
Community	Biogeography	Spatial survey only	Regional to circumpolar	Circumpolar	All	Shallow to deep-sea	CAML, AntECO
Community	VME encounters	2009 onward	Local	Mostly Scotia Arc, Antarctic Peninsula, Weddell Sea and Ross Sea	EP-A, AO-S, AO-A, WP-A	Shelf to deep-sea	FSA, AntECO
Ecosystem	Carbon sequestration	Since 1980s	Local to circumpolar	Antarctic Peninsula, Amundsen Sea, Weddell Sea, Ross Sea	EP-A, A-A, WP-A	Shallow and shelf	ICED, JGFOS, GLOBEC
Ecosystem	Food webs	no time series assessment	Regional	Weddell Sea	AO-A	Shelf	ICED, AnT-ERA
Ecosystem	Bentho-pelagic coupling	no time series assessment	Local to regional	West Antarctic Peninsula	EP-A	Shelf	ICED, AnT-ERA
Ecosystem	Distribution mapping & eco-regionalization	Spatial survey capable of future projections	Local to circumpolar	Circumpolar	All	Intertidal to deep-sea	AntECO
Ecosystem	Ecosystem models	Spatial survey capable of future projections	Local to circumpolar	Na	All	Shelf	ICED

*Whilst projects outside of these programmes are cited throughout this article, due to the very nature of small scale research this table is not entirely comprehensive but is reflective of collaborative research efforts. *MEASO area: EP: East Pacific, AO = Atlantic, EI = East-Indian, CI = Central Indian, WP = West Pacific, –A = Antarctic, -S = subantarctic. **Depths: Shallow = <100 m, shelf = beyond shallow to shelf break, deep = >3000 m. ***Internationally coordinated scientific programmes or working groups that contribute to a coordination of national programmes, where: AntECO = State of the Antarctic Ecosystem, AntOBIS = Antarctic Thematic Node of OBIS, AnT-ERA = Antarctic Thresholds – Ecosystems Resilience and Adaptation, ANTABIF = Antarctic Biodiversity Information Facility, CAML = Census of Antarctic Marine Life, FSA = Fish Stock Assessment (Commission for the Conservation of Antarctic Marine Living resources), GLOBEC = Global Ocean Ecosystem Dynamics, ICED = Integrating Climate and Ecosystem Dynamics, JGOFS = Joint Global Ocean Flux Study, SOOS = Southern Ocean Observing System.*

(Gutt, 2007; Brandt and Gutt, 2011; **Figure 5**). The second core community, which dominates soft-sediment habitats and includes infauna and mobile epifauna, is controlled by the deposition of phytodetritus, surface derived organic particles from decomposing phytoplankton that become a food resource for benthic species. Similar differences between hard- and

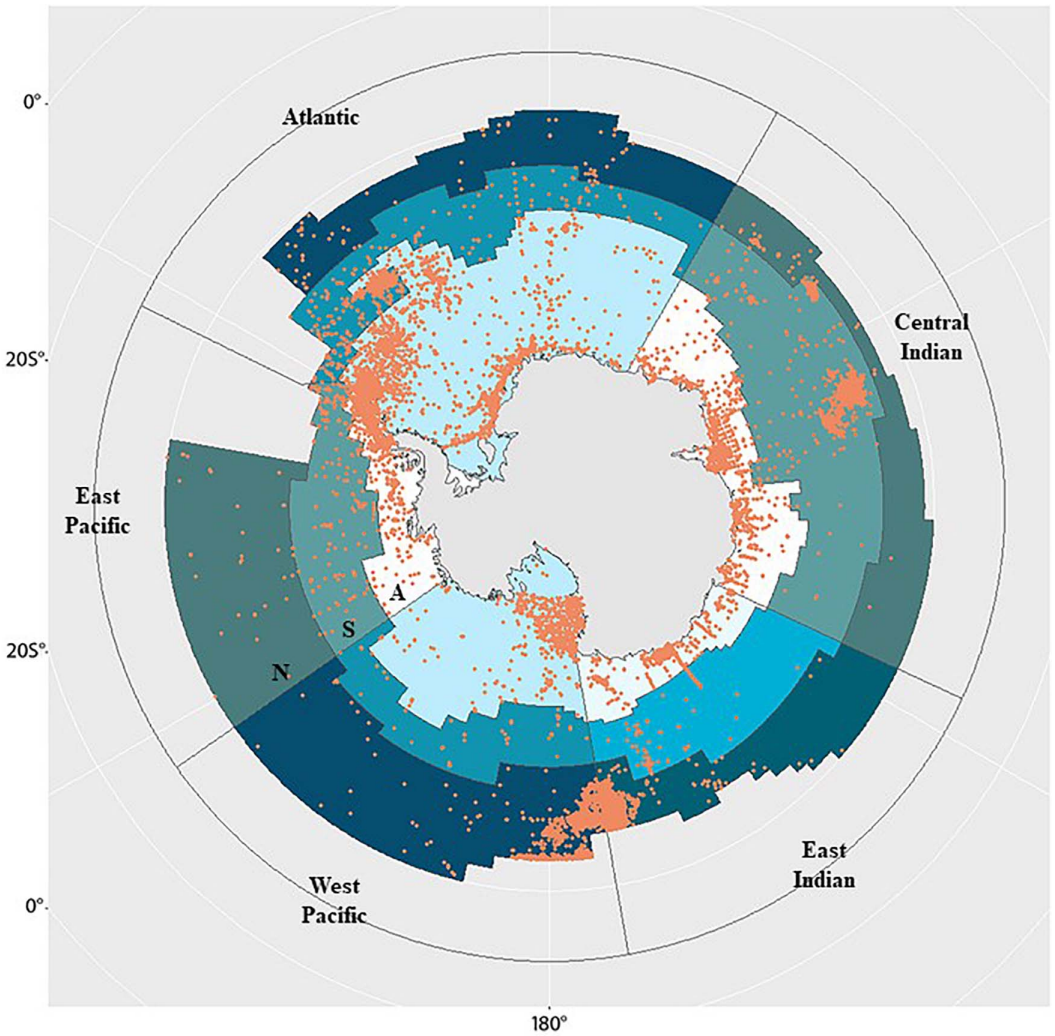

FIGURE 4 | The distribution of 161,711 distribution records (orange circles) belonging to 7,945 benthic species across size classes (macro-, mega-, meio-fauna) extracted from Ocean Biogeographic Information System (OBIS) and Global Biodiversity Information Facility (GBIF). MEASO areas are shown including MEASO sectors (Atlantic, Central Indian, East Indian, West Pacific, East Pacific) and MEASO zones (where N = northern, S = subantarctic, A = Antarctic). Details regarding data analyses are provided in **Supplementary Information**.

soft-substrates are also found in the Southern Ocean deep sea (Jones et al., 2007; Post et al., 2010; Brasier et al., 2018). Shallow water communities display high levels of heterogeneity associated with variation in habitat and sediments (Stark et al., 2003), and oceanographic processes including ice scour (Smale et al., 2008), sea ice cover and duration (Clark et al., 2013). For example, hard-substrate habitats in shallow coastal waters tend to display a gradient of benthic communities related to ice cover, whereby areas with less than 1-2 months open water per summer are dominated by marine invertebrates, while areas with longer periods of open water tend to be dominated by macroalgae (Clark et al., 2013, 2015).

In deeper water, slope and deep-sea communities are often characterized by a high number of species reaching peak diversity at lower bathyal and upper abyssal depths (Brandt et al., 2007; Menot et al., 2010). Highly specialized benthic fauna are associated with habitats such as hydrothermal vents systems, including the yeti crab *Kiwa tyleri* Thatje, 2015 (**Figure 5**) on the East Scotia Ridge vent field (Marsh et al., 2012; Rogers et al., 2012). Seamounts such as Maud Rise contain distinct faunal communities compared to nearby areas, and are characterized by a high abundance of the brooding gastropod *Onoba subantarctica wilkesiana* (Hedley, 1916), Haplomunnidae isopods and tube-dwelling suspension feeding polychaetes (Brandt et al., 2011).

RESPONSES AND PROGNOSES TO IMPACT DRIVERS OF CHANGE

In this section, we evaluate how benthic species are expected to respond to changes in global and local drivers, and then assess the prognoses for benthos in relation to those drivers.

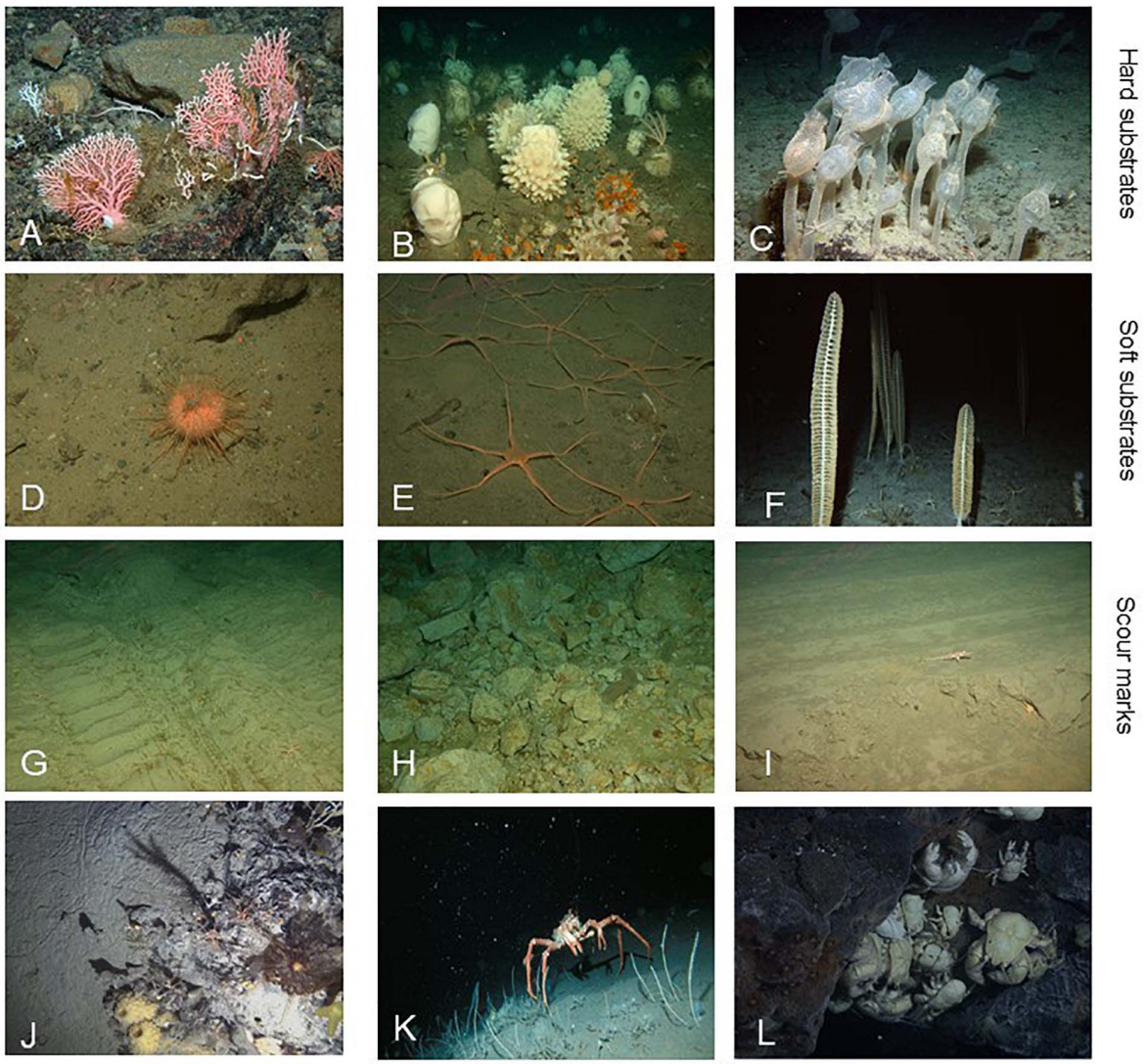

FIGURE 5 | Examples of different benthic habitats, species and scouring impacts. Where, first row = fauna associated with hard substrate on the Antarctic shelf including: A = corals, B = sponges, C = sea squirts, second row = fauna associated with soft sediments on the Antarctic shelf where D = sea urchin, E = brittle stars, F = sea pens, third row = scour marks, fourth row, J = edge of retreating glacier Marian Cove (King George Island), K = spider crab, L = yeti crabs at hydrothermal vents. Image sources: J. Gutt, A. Starmans, W. Dimmler, AWI, www.pangaea.de **(A–I,K)**, Dave Barnes **(J)**, NERC ChEsSo Consortium, Rogers et al. (2020) **(L)**.

Responses presented include *in situ* observations and laboratory analyses, whilst our prognoses use evidence from the published literature, publicly available datasets, and fisheries data within the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) to determine longer term change. Whilst we can not assess the outcomes of multiple simultaneous drivers we discuss the potential for cumulative impacts of multiple drivers on Southern Ocean benthic communities.

Ocean Temperature

Responses

As a consequence of evolving in the Southern Ocean, many benthic species are sensitive to small increases in temperature. In the most comprehensive study to date, long-term lethal temperature limits for 14 benthic species were estimated in the laboratory to be between 1 and 6°C (Peck et al., 2009). However, the thermal limits for activity are often even less, for example only 2–3°C for turning over in the limpet *Nacella concinna* (Strebel, 1908) and burying in the clam *Laternula elliptica* (King, 1832; Peck et al., 2004; Morley et al., 2012a). Overall, temperature tolerance and plasticity is species specific, however recent studies have shown that few Antarctic benthic invertebrates can acclimate to temperatures of 6°C and may have long-term limits a few degrees warmer than this (Morley et al., 2019). Some species differ in thermal tolerance between geographic areas of the Southern Ocean (Morley et al., 2009). For example, the sea star *Odontaster validus* Koehler (1906),

and the aforementioned clam *L. elliptica* in the Ross Sea had lower acute thermal limits than those in more northern areas on the Antarctic Peninsula (Morley et al., 2012b). Furthermore, *L. elliptica* has been found in intertidal habitats at James Ross Island at the northern end of the West Antarctic Peninsula, with ambient temperatures of 7.5°C within the sediment and 10°C air temperature (Waller et al., 2017b). More sensitive species, such as the Antarctic scallop, *Adamussium colbecki* (Smith, 1902) will only be able to survive if they can migrate to more southerly latitudes, or to depths below the warmer water masses (Peck et al., 2004). Other species, such as the aforementioned predatory sea star *O. validus* can continue feeding and turning over at temperatures up to 6°C (Peck et al., 2008). The differences in thermal tolerance and plasticity are likely to lead to both winners and losers, changing species distributions and therefore the composition of the benthic assemblage (Griffiths et al., 2017; Morley et al., 2019).

Prognoses

The impact of increasing ocean temperature will be population and species specific, due to both differences in thermal tolerance but also species' ability to take advantage of habitat that becomes available as the ice retreats (Morley et al., 2019). Likely due to the glacial history of the Antarctic, with ice covering much of the shelf during ice ages, many Southern Ocean marine ectotherms are eurybathic. Non-native species are expected to migrate into the Southern Ocean and establish breeding populations (Hughes et al., 2020). Similarly, deep-water species, such as reptant decapod crustaceans, which are thought to be excluded from the coldest areas within the Southern Ocean (Hellberg et al., 2019), could move into shallower water as it warms (Aronson et al., 2007; Griffiths et al., 2013). Physiological research indicates some species may perform better under limited warming while others reach thermal limits and become less competitive (Morley et al., 2019; **Figure 6**). Under altered competition and changing species distributions there are likely to be alterations in trophic interactions, food webs and the dominant species within benthic communities (**Box 1**).

Ice Shelf Disintegration, Increased Iceberg Scour, and Biogenic Flux

Responses

When ice shelves disintegrate, the ecological environment changes from allochthonous, where carbon must come from

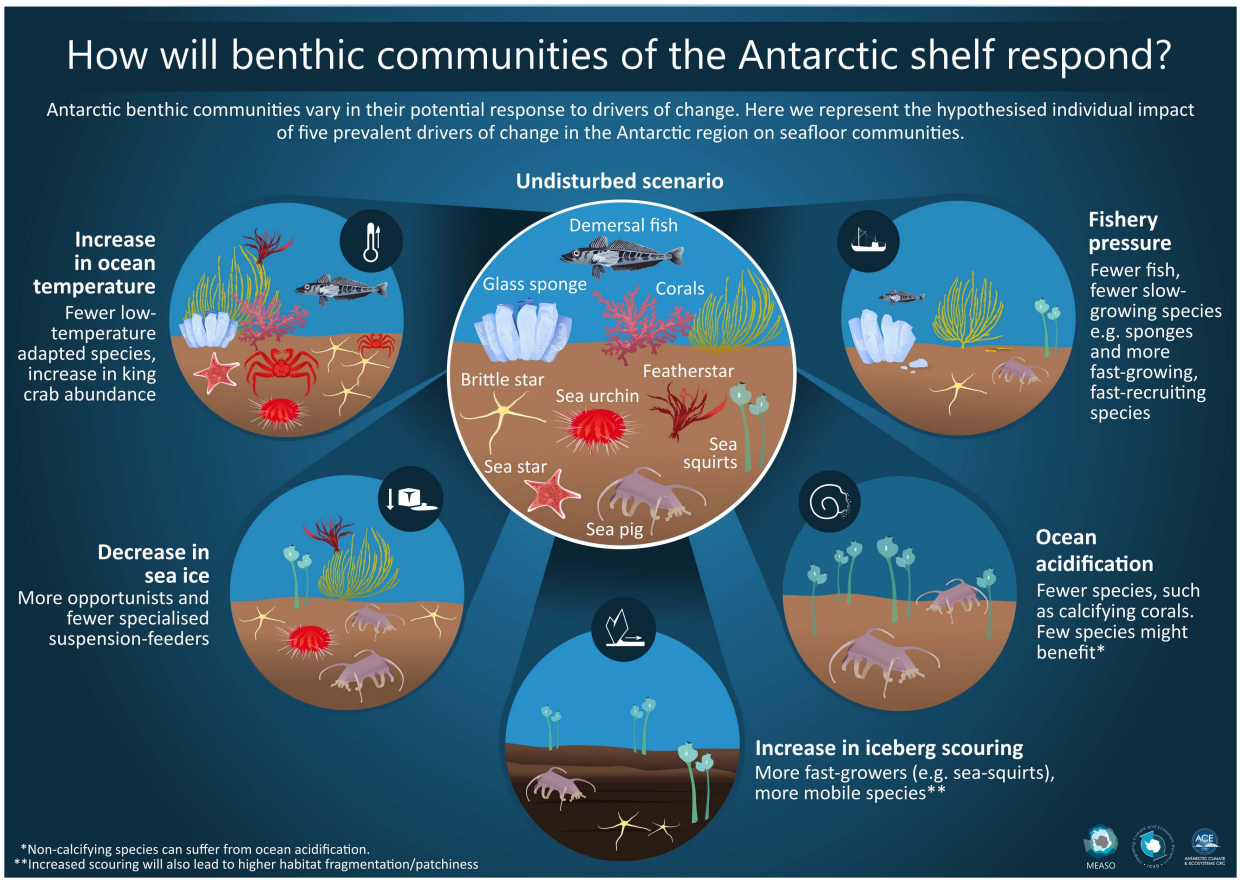

FIGURE 6 | Conceptual changes to an undisturbed seafloor community under five different impact drivers; increasing ocean temperature, decrease in sea ice, increase in iceberg scouring, ocean acidification and fishery pressure.

BOX 1 | Research gaps and priorities.

Data coverage

Most Southern Ocean benthic data have been collected within 150 km of research stations,and very few long-term data sets existfor benthic communities and habitats. Regions such as those formerly covered by the Larsen A and B ice shelves and the Amundsen Sea (Pine Island Bay and the Thwaites Glacier regions), that are currently experiencing some of the most rapid oceanographic and glaciological changes, are among the most logistically difficult to study and have only been sampled by a handful of expeditions. This leaves us with some of the most impacted areas having little baseline data for comparison.

Data sharing of both newly acquired and archived data is vital to improve spatial and temporal coverage for circumpolar assessments. Key databases include the Ocean Biogeographic Information System (OBIS, https://obis.org/about/) and the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/). Both OBIS and GBIF allow their data to be used by different gateways and repositories such as SCAR Antarctic Biodiversity Portal (the Antarctic regional Node of both OBIS and GBIF), the Register of Antarctic Species (RAS, http://ras.biodiversity.aq/), CCAMLR Geographical Information System (https://www.ccamlr.org/en/data/online-gis), and Southern Ocean interactive map (SOOSmap https://www.scar.org/data-products/soosmap/).

Knowledge gaps and projections of future change

Among the key limiting factors when projecting change within the Southern Ocean benthos are ecological variation and species-specific responses to different drivers (e.g., temperature and ocean acidification). Understanding the environmental tolerances of Southern Ocean species will enable monitoring of critical thresholds or tipping points in environmental parameters (e.g., Clark et al., 2013; Gutt et al., 2018). This, in turn, will help us understand the role of diversity in benthic resilience and vulnerability to change (Baggini et al., 2015; Dayton et al., 2016; Douglas et al., 2017). The observed environmental envelope of species and communities can be estimated to a certain extent based on historical observations, as demonstrated by Griffiths et al. (2017) in gaging the thermal tolerances of Southern Ocean species. However, realized responses to drivers may be more complex than isolated species envelopes due to competitive interactions between species within assemblages (Barnes et al., 2021).

Ongoing environmental observations and the growing capacity of the Southern Ocean Observing System to monitor oceanographic parameters such as sea ice, biogeochemical parameters, and biological variables (Newman et al., 2019) allow researchers to identify hotspots of change. However, they must be combined with biological observations to track (e.g., Gutt et al., 2011; Fillinger et al., 2013) or project (Griffiths et al., 2017; Fabri-Ruiz et al., 2020) impacts upon benthic communities. For example, Jansen et al. (2018) mapped predicted changes in food supply from surface waters to the benthos following ice-scape changes in the Mertz polynya region. They found significant changes in local oceanography and surface production, which influenced patterns of predicted seafloor food availability hundreds of kilometers from the calved glacier tongue,impacting the modeled distribution of suspension-feeder communities. Integrating this type of approach with information about benthic ecosystem structure and a better understanding of the system can highlight not only where changes are happening, but also indicate how community composition might change (Jansen et al., 2019).

Identification and management of current and future risks

Marine protected areas (MPAs) are the most significant conservation strategy under consideration in Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Vulnerable marine ecosystem thresholds, a method used to assess benthic habitat prioritization for protection, are also under consideration.However, the current weight-based thresholds are strongly biased toward sponge-dominated communities and thus may underestimate other vulnerable groups such as diverse coral communities. A re-examination of vulnerability traits is needed and other thresholds such as diversity indices or lower weight thresholds for overlooked taxa need to be considered.

Models can and are being used in Southern Ocean management (Welsford et al., 2014). Usage includes the assessment of current and proposed MPAs or networks under future scenarios; these models can be used in a robust and reproducible way and updated as new data become available (Fabri-Ruiz et al., 2020). Discussion between researchers and policy makers is needed to determine appropriate scales to inform marine conservation and management of marine living resources (Kennicutt et al., 2014; Gutt et al., 2019). Not only should these models incorporate the relevant global and local drivers discussed here and other recent syntheses (see Gutt et al., 2020), but benthic models also need to represent fine-scale patchiness and broadscale differences in community composition, as well as regional connectivity (e.g., Thrush et al., 2006; Gutt et al., 2019; Robinson et al., 2020; see Weldrick et al. to be published in this research topic).

Tourism and shipping impacts on benthic communities are currently overlooked. Investigation is required into the distribution and level of activities that make contact with the seabed (e.g., anchors, submersible, and diving) to date. Once Antarctic tourism recovers from the COVID-19 pandemic, additional measures may be needed to minimize their impact.

elsewhere, to autochthonous, where carbon is now fixed locally because light is accessible in the water column, thereby driving local primary production. This algal growth increases the food available for higher trophic levels and is exported to the benthic system, creating a new carbon sink and a possible negative feedback to climate change (Bertolin and Schloss, 2009; Peck et al., 2010; Barnes et al., 2018). However, intense phytoplankton blooms do not always occur in areas where ice shelves have disintegrated, as primary productivity also depends on the degree of permanent or seasonal sea ice cover (Cape et al., 2014; Morley et al., 2020).

Researchers investigated benthic sites that were once under the Larsen A and B ice shelves, which collapsed in 1995 and 2002, respectively (Hauquier et al., 2011; Gutt et al., 2013; Hauquier et al., 2016). Approximately five years following the collapse, the Larsen A site consisted of ascidians that had settled and grown in large numbers. Within the subsequent 12 to 16-year period of faunistic succession, most ascidians disappeared, and formerly rare species increased in abundance. Whilst suspension feeding ophiuroids halved in abundance, local populations of deposit feeding species increased (Gutt et al., 2013). A detailed discussion of ecological responses to ice shelf loss is presented in Ingels et al. (2020), including shifting food regimes associated with modified phytodetrital inputs. The retreat of glacier tongues, long and narrow sheets of ice that project out from the coastline, may also have similar benthic effects to ice-shelf disintegration. For example, around the Mertz-Glacier Tongue in East Antarctica models have predicted an increase in suspension feeder abundances "fueled by increased food supply" (Jansen et al., 2018).

Sediments in sub-ice shelf environments are typically characterized by low depositional rates. The collapse of ice shelves around the Antarctic Peninsula during the 1990s and early 2000s revealed the nature of sediments deposited beneath the ice shelves, and changes in sedimentation during and since collapse. Increased calving of icebergs at the seaward limit of ice shelves causes increased deposition of coarse sediments from ice-rafted debris (Domack et al., 1998). In addition, collapse of the Larsen A Ice Shelf caused large phytoplankton blooms in newly ice-free areas (Bertolin and Schloss, 2009), altering the deposition of phytodetritus to the seafloor (Domack et al., 2005a; Sañé et al., 2013). The increased sediment flux to the seafloor in these newly exposed areas can impact seafloor communities by providing an enhanced food source and smothering or burying existing communities. For example, suspension feeders can be excluded in areas with high sedimentation rates due to clogging of their filter-feeding structures (Pasotti et al., 2014). Disintegration of ice shelves that receive little inflow from open waters can radically change the productivity of the system and hence the seafloor ecosystem. Following the collapse of the Larsen A Ice Shelf, the flux of organic matter to the seafloor increased dramatically and resulted in a rapid growth in hexactinellid sponge biomass and abundance (Fillinger et al., 2013); researchers also recorded an increase in other species typically considered early colonizers in the recently ice-free areas of the Larsen A and B Ice Shelves (Gutt et al., 2011).

Following the collapse of the Larsen B Ice Shelf, researchers discovered a chemotrophic ecosystem 100 km from the former ice shelf front (Domack et al., 2005b; Niemann et al., 2009). The very low marine sedimentation in this sub-ice shelf environment most likely contributed to the development of this chemotrophic community by excluding competition from marine biota typical of open-water environments. Within three years of the Larsen B Ice Shelf collapse, increased deposition of phytodetritus and ice-rafted debris caused significant change to the chemosynthetic ecosystem, reducing the extent of microbial mats through partial burial and allowing colonization by benthic grazers and higher-level predators typical of Southern Ocean environments.

A consequence of increased ice shelf breakup or calving is an increase in the presence of icebergs. When icebergs drift in the open ocean they can locally fertilize the phytoplankton by releasing essential nutrients (Smith et al., 2013; Duprat et al., 2016) and stabilize the upper-water column through the local addition of freshwater (Smith et al., 2013). These processes facilitate algal growth, especially of diatoms, and contribute food to grazers such as krill (Vernet et al., 2011), which may increase storage of organic carbon (Trebilco et al., 2020). Ice scouring occurs when drifting ice, such as icebergs, contact the seafloor and will either continue drifting whilst in contact with the seabed or run aground until they are dislodged or disintegrate. The occurrence and distribution of scouring events are dependent on the rate of iceberg production, iceberg size (particularly the draught and keel), drift pathways and speed of movement (which can be influenced by oceanography and wind patterns) and melt rate (Dowdeswell and Bamber, 2007). Iceberg scour usually impacts the benthos to approximately 300 m on the shelf and effectively devastates almost all macrobenthos (Gutt et al., 2011) by direct mechanical force or indirect changes in hydrodynamic turbulence and local current patterns (Seiler and Gutt, 2007). Thus, calving, scouring and grounding often result in an immediate decline in species richness and abundances of benthic macrofaunal species (Thrush and Cummings, 2011).

Post-scouring recovery rates can be variable depending on local environmental conditions and oceanography, as well as a species' ability to relocate or settle via individual movement, advection by local currents or larval recolonization (Peck et al., 1999). Generally, scouring results in an initial increase in pioneer species including echinoid, polychaete, isopod and gastropod species, followed by successional changes resulting after 12 months in a benthic community comparable to pre-disturbed or reference communities in shallow water (<100 m) (Smale et al., 2008). While a patchwork of different successional stages with different pioneer species, e.g., ascidians, cnidarians and exceptionally fast-growing sponges, can lead to high beta-diversity (Gutt and Piepenburg, 2003), locally, intermediate stages of recolonization might also reach a structural maximum of diversity (Teixidó et al., 2004). Recently published data in, Zwerschke et al. (2021) found that it took a decade for a shallow water assemblage to 'bounce back' from major disturbance, which was only detectable with two decades of monitoring. In depths greater than 100 m succession toward a climax shelf community might require centuries due to the slow growth of adult habitat-forming species (Gutt and Starmans, 2001).

The increased frequency of iceberg scouring in the West Antarctic Peninsula region reduces the chance of such species reaching sexual maturity in between scouring events and the increased mortality of both pioneer species and climax species threatens local biodiversity (Barnes and Souster, 2011; Barnes et al., 2014). By contrast, scouring at McMurdo Sound in the East-Pacific sector has increased biodiversity following mass recruitment and the fast growth of 12 sponge species; this is possibly supported by additional environmental factors such as an increase in the size of food particles that benefit sponges (Dayton et al., 2016, 2019; Kim et al., 2019). In fact, some suspension feeders not directly hit by icebergs can benefit from scouring by gaining extra food from resuspended material (Peck et al., 2005).

In addition to direct impacts, icebergs sometimes release large dropstones as they melt, distributing additional hard substrates across the seafloor. Dropstones from previous calving episodes (e.g., during the past deglaciation) have been shown to provide habitat for sessile invertebrates in both the Antarctic and the Arctic (Starmans et al., 1999; Schulz et al., 2010). Dropstones can be associated with significant increases in the abundance and diversity of taxa (Ziegler et al., 2017) and could promote increased settlement of sessile invertebrates across areas of otherwise soft substrate (Dayton, 1990; Post et al., 2017).

Prognoses

Under ongoing climate change and increasing loss of ice shelves, we envisage two potential scenarios: (1) the ecosystem will become locally more dynamic due to higher iceberg calving rates or ongoing collapses of entire ice shelves and shorter periods

of solid ice cover; (2) a reduction in the number of icebergs as calving rates will regionally decrease since most ice shelves have disintegrated already and glaciers no longer reach the coast. The timing of these two scenarios is dependent on the intensity of future climate change and regional conditions, such as presence of ice shelves, and iceberg trajectories around the continent.

In the first scenario, elevated calving rates from ice shelves result in an increase in areas experiencing substantial ecological changes. In such areas, communities have locally reduced biomass and diversity, as well as low metabolic rates, but unique species composition (Gutt et al., 2011). Smaller areas where ice is grounded become exposed for the first time in decades to millennia for a variety of pelagic and benthic colonization (Lagger et al., 2017). It can be expected that original benthic communities under ice shelves, if they existed at all, were adapted to oligotrophic (nutrient-poor) conditions. These would be replaced by "normal" Southern Ocean shelf communities, e.g., an increased abundance of suspension feeders, following *in situ* primary production and local food supply to the seafloor. The increase in benthic biomass (Jones et al., 2014) contributes to global carbon storage and ultimately sequestration (Peck et al., 2010; Barnes et al., 2018). If a noticeable proportion of this additional biomass is buried in the sediment and not recycled in the water column to nutrients, such areas, e.g., newly emerging fjords (Barnes et al., 2020), will serve as true carbon sinks for long time scales (100-1000s of years).

An increase in floating icebergs in Southern Ocean shelf waters could lead to increased scouring events, resulting in a greater area of devastation of benthos. Subsequent recolonization develops a mosaic of patches of successional stages and leads to higher regional diversity until a certain level of disturbance magnitude is reached (Potthoff et al., 2006; Johst et al., 2006). As a result of increased iceberg calving, deposition of dropstones could increase hard substrate on the seafloor and thus could increase colonization by sessile filter-feeders and local patchiness within the benthos. However, the higher deposition of fine-grained sediments may also affect the success of filter feeders (Pasotti et al., 2014).

It is of paramount interest to know which areas and habitats of the Antarctic shelf are most at risk. The frequency and location of scouring will be influenced by seasonal sea ice duration (effecting iceberg movement) and iceberg abundance, which is dependent on regional and local calving rates, as well as their movement and pathways. It can be expected that iceberg-disturbance rates will increase in areas downstream of disintegrating ice shelves and glaciers (see next section) for months or years after collapse (Gutt et al., 2011). However, the movement and pathways of icebergs can be influenced by many factors, including the properties of the iceberg (size, draught, mass, structure etc.), oceanographic factors such as tides, wind, sea ice and currents, as well as the depth and geomorphology of the underlying seafloor. It is predicted that certain geomorphic features such as shelf banks (see descriptions of geomorphic features in **Supplementary Information**) are more likely to be struck by icebergs (Barnes et al., 2018). Whilst iceberg distribution is highly patchy, grounding hotspots have been identified for giant icebergs (>30 km^2) in the East Pacific, Atlantic, and Central Indian MEASO sectors (Barnes et al., 2018).

In the second scenario, with fewer icebergs the benthos is likely to experience less scouring which could result in reduced diversity. This is based on the "Intermediate-Disturbance Hypothesis" whereby moderate iceberg scouring enables higher benthic diversity and thus without these disturbances reduced diversity could be expected (Johst et al., 2006). Gutt and Piepenburg (2003), for example, recorded lower regional habitat heterogeneity and benthic diversity in areas of the Weddell Sea where little scouring had occurred. In the Arctic, Laudien et al. (2007) observed less diverse benthic communities at depths of low scouring impact. Without disturbance colonizing species may only exist in refuge areas as they are otherwise outcompeted by "mature" benthic fauna such as sponges.

Glacial Retreat, Sedimentation, and Newly Ice-Free Habitats

Responses

Rapid regional warming around Antarctica has driven the retreat of many tidewater glaciers which can have direct and cascading effects on surrounding ecosystems (Cook et al., 2005). Those likely to impact benthic communities can include potential ice scour, increased sedimentation rates, and the availability of newly ice-free habitats (Sahade et al., 2015).

Several studies have observed faunistic succession following glacial retreat. For example, early observations of the retreating tidewater glacier front at Anvers Island (West Antarctic Peninsula) showed high dominance of only one polychaete species near the glacier cliff in 1971 presumably due to its high stress tolerance. Within the next 18 years after the initial survey, abundances of benthic organisms showed an increase of up to a factor of 5.5 and the number of taxa doubled (Hyland et al., 1994). In newly ice-free soft bottoms in Potter Cove, King George Island at the northern tip of the West Antarctic Peninsula, sediment runoff caused by the retreating glacier was likely the main driver of a shift from an ascidian-macroalgae dominant community to a mixed assemblage (including sponges, cnidarians, ascidians and ophiuroids), with lower abundances but higher species diversity (Sahade et al., 2015). Where glacial retreat has led to new ice-free areas, the shift has resulted in macroalgal colonization of benthic habitats on the West Antarctic Peninsula (Quartino et al., 2013). However, with increased run-off reducing the depth of underwater photosynthetically active radiation, the lower depth distribution of some macroalgae species may be reduced (Deregibus et al., 2016).

As glaciers retreat plumes of sediment-laden meltwaters and terrestrial runoff can enter the marine environment, an effect that has also been observed in Arctic environments (e.g., Węsławski et al., 2011). This increased sedimentation leads to higher levels of water-column turbidity, increased rates of inorganic sedimentation and relatively low organic matter deposition (Węsławski et al., 2011). In addition, the increased turbidity of the water-column inhibits phytoplankton production, while higher sedimentation rates cause burial of some seafloor organisms. Higher rates of sedimentation have also been found to favor small-bodied, mobile surface deposit

feeders, causing low macrobenthic biomass and diversity (e.g., King George Island, West Antarctic Peninsula - Pabis et al., 2011; Siciński et al., 2012; parts of the Arctic - Wlodarska-Kowalczuk et al., 2005). Suspension feeders are typically absent in areas with high sediment loads due to clogging of their filter structures (Pasotti et al., 2014). However, it is difficult to generalize impacts between different systems. Some parts of King George Island, for instance, have responded to increased sedimentation with a shift to a more mixed benthic assemblage, highlighting differing tolerances to sediment input (Sahade et al., 2015) and the varied response to a complex array of additional variables (Pasotti et al., 2014).

Prognoses

Some shallow water marine invertebrates may be at risk of local extinction, including filter-feeding sponges, bryozoans, tunicates, corals and tube building polychaetes, all of which perform vital ecosystem functions such as water filtration, nutrient recycling and trophic transfer. Such localized impacts can be through intense local scouring (Barnes and Souster, 2011), increased sedimentation (Sahade et al., 2015), new invading non-indigenous species (Cárdenas et al., 2020) or potentially extreme warming spikes in the future. These fauna are critical components of the coastal food web, with links to pelagic and shelf ecosystems (Reid and Croxall, 2001). Future ecosystem change is likely to drive endemic shallow Southern Ocean invertebrate communities into ever shrinking refugia where longer periods of sea ice duration are maintained, further fragmenting populations and impeding genetic connectivity (Fahrig, 2003). Deep-water refugia may exist for some species on the Antarctic shelf where there is low light irrespective of sea ice, the unique invertebrate communities found under sea ice in shallow water will become threatened as periods of sea ice duration shorten.

As glaciers retreat onto land, exposing the valley floor, Arctic examples suggest that sediment discharge is captured increasingly on land, reducing turbidity to the nearshore water column (Syvitski et al., 1989). This enhances light penetration and reduces smothering of seafloor communities, these conditions can promote the development of a diverse benthic community. Insight from studies within glacio-marine fjords (fjords with tidewater glaciers) of the West Antarctic Peninsula found greater benthic megafaunal abundance within the fjord basin than control sites on the nearby open shelf (Grange and Smith, 2013). This result could be a consequence of weak meltwater influences, low sedimentation, and high food inputs during the early stages of climate warming. However, increased sediment loading to steep nearshore slopes may generate sediment slumping, contributing to longer-term smothering of benthic organisms across broader areas (Smale and Barnes, 2008).

Sea Ice Change, Light, and Primary Production

Responses

Sea ice extent varies seasonally and regionally and, within the last decade (2010-2020) there have been significant changes in Antarctic sea ice distribution; for more details see Morley et al. (2020) in this research topic. To date, due to the extreme seasonality of sea ice cover, most benthic habitats on the Antarctic shelf receive a short and intense pulse of organic material from the surface waters (Smith et al., 2006, 2012). This exchange of organic material between the pelagic and benthic zones may also be referred to as bentho-pelagic coupling. Changes to sea ice can impact the benthic habitats via altered light regimes, primary production and export to the benthos (e.g., Clark et al., 2013; Barnes, 2015). Altered light regimes such as an increased duration of photosynthetic active radiation penetrating the water column can affect the timing, intensity and duration of primary production and macroalgae on the seafloor (Vernet et al., 2008; McMinn et al., 2010).

Increased seasonal sea ice loss around Antarctica has resulted in extended phytoplankton blooms and increased export to, and production by the benthos (Arrigo et al., 2008; Barnes, 2015). Long-term studies along the West Antarctic Peninsula have also shown a change in the mean size of phytoplankton, indicating a decrease in larger phytoplankton, such as diatoms, and an increase in smaller phytoplankton, such as ciliates and flagellates, over the continental shelf of the West Antarctic Peninsula (Rogers et al., 2020). Smaller phytoplankton are important for many suspension-feeding benthic species as they are easier to consume and break down (Barnes, 2017a). At McMurdo Sound similar long-term studies observed a regime shift from large to small-sized food particles consistent with increased recruitment and growth of filter-feeding organisms and reduced populations of those that favor large particles, such as echinoderms, bivalves, crinoids (Dayton et al., 2019).

As discussed with the loss of ice shelves, detecting benthic change in response to sea ice changes is difficult because it is so variable in time and space. Increased annual growth has been detected in some suspension feeders in the Ross Sea, driven by wind strengthening creating and maintaining open-water polynyas, and in turn influencing primary production (Arrigo et al., 2008; Barnes et al., 2011). Around the West Antarctic this may have doubled benthic growth, and consequently carbon storage, on the seafloor in the last 25 years, again coincident with sea ice reduction (Barnes, 2015). However, similar losses of sea ice nearshore can increase scouring by icebergs, potentially wiping out growth and carbon gains (from longer access to phytoplankton food) and suspending the shallows in an early state of succession dominated by pioneer species (Barnes and Souster, 2011). Predicting total carbon storage of the Southern Ocean benthos is complex. Annual carbon production has been measured at well-studied sites within the Weddell Sea, West Antarctic Peninsula, Amundsen Sea, Ross Sea, South Orkney Islands and at South Georgia (Barnes, 2015). When up-scaled to the entire area of the Antarctic shelf (4.4×106 km^2), zoobenthic annual carbon production is estimated between 30 and 80 MtCyr^{-1}, depending on ice shelf losses, new growth and iceberg scouring (Barnes, 2017a, Barnes et al., 2018); this value is less than 1% of annual anthropogenic carbon emissions (IPCC, 2014). Antarctic blue carbon sequestered in the benthos around the continental shelf has an estimated economic value of between £0.65 and £1.76 billion (~2.27 billion USD), however the true value is in conserving ecosystem services and a natural negative feedback to climate change (Barnes et al., 2018; Bax et al., 2021).

Prognosis

The interaction between changing sea-ice duration and solar irradiance renders polar coastal ecosystems vulnerable to relatively rapid change. Recent changes in ice and snow cover have already altered models of annual light budgets for large areas of the Arctic and Antarctic and further predicted changes in sea-ice cover are likely to result in significant increases in photosynthetically active radiation (Clark et al., 2013). Ecological regime shifts have been observed in the Arctic (Svalbard), where rocky-reef habitats were rapidly invaded by macroalgae over a period of gradual sea-ice reduction (Kortsch et al., 2012). Increasing seawater temperatures have also been indicated as contributing to expansion of macroalgal habitats in Arctic regions, however changes in photosynthetic active radiation through decreases in sea ice cover have been identified as the primary driver in mechanistic models (Scherrer et al., 2019).

Possible shifts from invertebrate- to algal-dominated states resulting from increases in light could reduce coastal biodiversity in some Southern Ocean locations (Clark et al., 2013), and lead to alterations in ecosystem function (Worm et al., 2006; Cavanagh et al., 2020). However, the spatial variation in the duration of Antarctic sea ice cover (1979-2010) around the Antarctic margin (Maksym et al., 2012), combined with a lack of observations at appropriate spatial and temporal scales in Southern Ocean waters, prohibit drawing conclusions about changes in algal distribution.

Ocean Acidification

Responses

The process of ocean acidification within the Southern Ocean may lead to the increased dissolution of the calcium-carbonate skeletons and shells built by calcified benthic species (Fabry, 2008). In particular, skeletons/shells are composed of calcium-carbonate minerals, calcite or aragonite, and calcite can also contain varying levels of magnesium (Mg) which alters its solubility. Knowing the skeletal mineralogy of Southern Ocean calcifiers is thus essential to better understanding the vulnerability of each species to dissolution. There is a growing interest in assessing mineralogical changes in Southern Ocean taxa as a response to environmental parameters, but it is still limited to few groups (Borisenko and Gontar, 1991; McClintock et al., 2009, 2011; Taylor et al., 2009; Loxton et al., 2014; Figuerola et al., 2015, 2019; Hancock et al., 2020; Figuerola et al., 2021). The historical spatial and temporal distribution of Southern Ocean calcifiers can be also indicative of species resilience to changing ocean chemistry. For example, Margolin et al. (2014) investigated the spatial and temporal distribution of the solitary scleractinian corals within the Drake Passage from the last 35,000 years and recorded differences in age and depth distributions across taxa that could be linked to changes in carbonate saturation state, surface productivity and subsurface oxygen concentrations. The synergistic interactions between common variables recorded in these paleo-oceanographic studies hamper our ability to understand past ecosystem succession in response to decreasing saturation states (Coggon et al., 2010).

Experimental studies on benthic calcifiers in the Southern Ocean are few, and show contrasting results, which likely indicates species-specific responses to lowering pH levels. Important life processes of some benthic calcifiers appear to be resilient to pH lowering, including the physiology, growth and escape responses in gastropods (Schram et al., 2014; Zhang et al., 2016); shell crystal deposition and robustness in the scallop *A. colbecki* (Dell'Acqua et al., 2019); development and feeding energetics of the sea urchin *Sterechinus neumayeri* (Meissner, 1900; Clark et al., 2009; Morley et al., 2016; Karelitz et al., 2017); and continued shell growth and repair in brachiopods (Cross et al., 2015). Ocean acidification has been found to impact some calcifying organisms' early-life stages, reproduction and overall function, which has been recorded in sea stars (Gonzalez-Bernat et al., 2013), sea urchins (Clark et al., 2009; Foo et al., 2016), gastropods (Schram et al., 2016), and bivalves (Cummings et al., 2011).

Prognoses

The depth of the present-day Aragonite and Calcite Saturation Horizon exceeds 1,000 and 2,000 m across most of the Southern Ocean, respectively (Negrete-García et al., 2019). However, the surface is predicted to be undersaturated with respect to aragonite by the end of this century, altering its biochemistry (Orr et al., 2005; Hauri et al., 2016; Negrete-García et al., 2019). Species with aragonitic shells such as the bivalve *L. elliptica* (Bylenga et al., 2015, 2017) and high-magnesium calcite skeletons such as the sea star *Glabraster antarctica* (Smith, 1876), the bryozoan *Beania erecta* Waters, 1904, some spirorbid species (McClintock et al., 2011; Figuerola et al., 2019), and corals (Bax, 2014; Bax and Cairns, 2014), could be particularly vulnerable to global ocean surface pH reductions of 0.3–0.5 units by the year 2100 (Caldeira and Wickett, 2005). Sea stars and brittle stars are likely to be the first echinoderms to be affected by near-term ocean acidification (McClintock et al., 2011; **Figure 6**). However, species-specific mechanisms should be also taken into account in order to evaluate their vulnerability. For example, some stylasterid coral species exhibit mineralogical plasticity, whereby their skeletons contain calcite, aragonite or a mixture of the two polymorphs (Cairns and Macintyre, 1992). This mineralogical plasticity modifies the energetic cost of calcification and has been proposed as a compensatory mechanism to the lowering of pH in the oceans for calcifying organisms (Leung et al., 2017) and has been found to occur in brachiopods (Cross et al., 2019), and benthic bivalves (Cummings et al., 2011), likely improving their resilience to ocean acidification. Other species such as sea urchins and some molluscan species have external organic layers to protect skeletons/shells from ambient seawater (Ries et al., 2009). Some calcifying organisms have non-calcifying embryonic stages, and in some species, these larvae could be more robust to ocean acidification (Byrne, 2011). However, more work needs to be undertaken to understand the susceptibility of Southern Ocean species to ocean acidification.

To improve our predictions of the effects of ocean acidification on benthic calcifiers the factors that influence their vulnerability must be considered. These can include local seasonal and spatial variability in ocean chemistry, combined and interacting effects

(e.g., ocean warming), species-specific skeletal mineralogies, biological traits, physiological processes and compensation strategies (Figuerola et al., 2021). A recent literature review and meta-analysis illustrates that the response variation is largely dependent on mineralogical composition, with calcitic, aragonitic and high-magnesium calcite skeletons more vulnerable than low-magnesium calcite to future predicted carbonate chemistry conditions (Figuerola et al., 2021). Further investigation is needed to confirm these emerging trends.

Depending on acclimation time, the metabolic and reproductive physiology can be improved in certain animals, such as sea urchins (Suckling et al., 2015). For non-calcifying organisms such as multicellular algae, ocean acidification may increase production and growth (Andersson et al., 2011). This could mean the potential shift of calcifying habitat-forming organisms to macroalgae in shallow Antarctic and subantarctic coastal benthic environments, due to larval, reproductive and embryonic pH sensitivity of many calcifying organisms.

The consequences of ocean acidification over longer time scales, i.e., by 2100, are unknown. As oceanic pH decreases, the depth of the saturation horizon in the water column becomes shallower, changing the range and composition of deep-sea ecosystems (Orr et al., 2005). Guinotte and Fabry (2008) suggest the aragonite saturation horizon, which is currently estimated at ∼1000 m (Feely et al., 2004), may rise to surface waters in the Southern Ocean by 2100. The anticipated shoaling of the carbonate compensation depth could reduce the deepest depths of calcifying organisms, such as corals, and these organisms may have to "emerge" to shallower depths. Experimental results indicate that calcifying organisms do not readily acclimatize to decreasing carbonate saturation states (Orr et al., 2005; Guinotte and Fabry, 2008). Further *in situ* studies, such as using free-ocean CO_2 enrichment (FOCE) systems (e.g. Stark et al., 2019), may allow us to evaluate longer term effects of ocean acidification. However, if a lack of acclimation holds true under natural conditions, the geographical range and abundance of some calcifying species may be reduced whilst others become extinct. For more details regarding seasonal variability in pH across the Southern Ocean and how this may affect a species capacity to cope with changing ocean acidity see Morley et al. (2020), in this research topic.

Fishing

All commercial fishing operations in the Southern Ocean have been regulated by CCAMLR since 1982, before which substantial overfishing had occurred over the 1970s (Kock, 1992; Caccavo et al., to be published in this research topic) (**Figure 7**). Effective regulation did not begin until the late 1980s, with catch limits determined by assessments and decision rules coming in to play in the mid-1990s (Constable et al., 2000; Constable, 2011). Currently, the fisheries that impact benthic communities are bottom trawling for mackerel icefish (*Champsocephalus gunnari*, Lönnberg, 1905) and toothfish (*Dissostichus eleginoides*, Smitt, 1898) around Heard and McDonald Islands and toothfish fisheries (*Dissostichus* spp.) using long-lines and sometimes pots/traps. There have also been crab fisheries (e.g., for *Paralomas* spp. in South Georgia and the South Orkneys) that used pots or traps that interacted with the benthos, but to date these have been short-lived and sporadic.

Responses

The potential effects of fishing activity on seabed communities include physical damage and breakage to invertebrate fauna, scouring and structural damage to sediments and smothering of sessile fauna via sediment resuspension (Welsford et al., 2014); these impacts can be equated to iceberg scour but in deeper water (trawling occurs to about 1000 m depth while longlining can be as deep as 2000 m deep). Trawling has been the most significantly detrimental method of fishing to benthic communities globally (UNEP, 2006). In the Southern Ocean, fishing for toothfish in waters shallower than 550 m has been prohibited by a CCAMLR Conservation Measure since 2009 (CCAMLR, 2009a; Jones et al., 2016). Commercial bottom trawling in high seas areas is also restricted within the CCAMLR Convention Area (CCAMLR, 2008; Jones et al., 2016). Although some of these fisheries were large and intensive, historical fishing locations were never made public and thus, recovery assessments of affected benthic habitats are unfortunately impossible.

Established and exploratory toothfish fisheries remain a source of concern regarding their impact to benthic communities. In the first comprehensive study of the effects of demersal gears on benthic habitats in the Southern Ocean, Welsford et al. (2014) found that longlines can affect benthic habitats as well as trawls. They found a key factor in managing these effects was to measure the overlap between demersal fishing activities and benthic habitats and then to estimate the effects on the productiveness and ecologies of those habitats given that interaction. A major part of achieving this is to use cameras deployed on fishing gear to observe those interactions directly and to help quantify the distribution of habitats (Welsford et al., 2014).

The magnitude of potential demersal fishing interactions with benthic habitats was determined for MEASO areas using catch and effort data from the CCAMLR Statistical Bulletin 2019 (see Grant et al., in review, to be published in this research topic, for more details than included here). These data were allocated to MEASO areas according to evidence for fishing depths and locations in reports of the Scientific Committee, CCAMLR Conservation Measures and descriptions in the scientific literature, in particular Kock (1992), on the fishing operations. Available fishing areas in the depth ranges of the fisheries were used to spread the catch uniformly across the identified reporting area of operation. Seabed areas were calculated from the GEBCO 2014 grid at 4 km^2 resolution[1]. Catches were spread uniformly across the area identified from those sources for an individual catch based on flag state, depth range for a given target fishery and gear type and where reports allowed it, year. **Figure 7** shows the total effort in both trawl (hours) and longline (hooks) in the CCAMLR area along with time-series of that effort in the MEASO assessment areas. The time series of catches of target species (groundfish, icefish and toothfish combined) are also shown to indicate the proportion of catch for which effort data were available.

[1]https://www.gebco.net/news_and_media/gebco_2014_grid.html

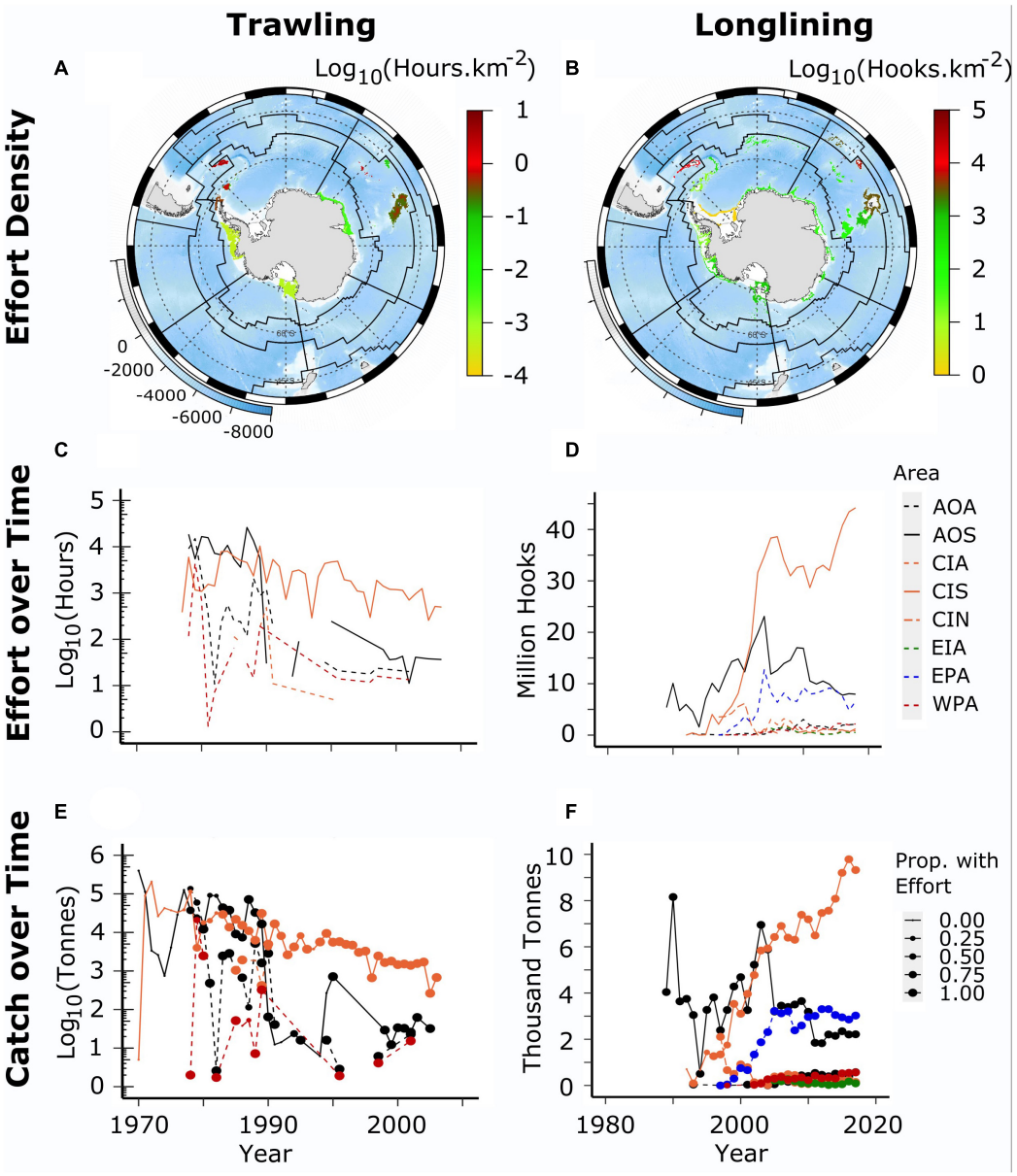

FIGURE 7 | Bottom fishing effort in MEASO areas for trawl and longline fisheries. **(A,B)** shows effort density per km^2 – hours and hooks respectively on a log^{10} scale. Background is ocean depth (bottom left legend on each map). Black lines show boundaries of MEASO areas as depicted in **Figures 3** and **4**. **(C,D)** shows effort over time (split year) in each MEASO area according to the legend at right. The first two letters correspond to the sector and the last letter to the zone. **(E,F)** shows the time series of catches in each area – color and line types according to the middle row. Catches are the total catch of targeted species in bottom fisheries (groundfish, icefish, and toothfish). The size of the points indicate the proportion of the catch that had effort data associated with it. Note the effort and catch data are plotted on different scales for each of trawling and long lining and the size of the symbol for each year indicates the proportion of catch for which we have an estimate of effort. When there is no symbol in a year then there is no record of effort. Data derived from the CCAMLR Statistical Bulletin 2019 (see Grant et al., in review, to be published in this research topic).

Until CCAMLR established limits to catches of target species, the annual catches in some areas were two orders of magnitude greater than what is now considered sustainable (Caccavo et al., to be published in this research topic). Highest catches have been in the subantarctic zone of the Atlantic and Central Indian sectors during the 1970s and 1980s, ending in the early 1990s. Effort was not reported for the very high catches in the first two decades making it difficult to estimate the total past interaction with the seafloor.

Scaling the effort to the level of disturbance of the seafloor, also known as the fishing footprint, is best done using haul data, including the location of each haul. For trawls this normally includes the swept area of the net (width of the opening of the net combined with the distance towed), and for longlines the

swept area of the line (sideways movement of the line during its deployment, fishing and retrieval). Haul data means that the footprint can be discounted by overlaps of each haul (see Welsford et al., 2014 for methods). In the absence of those data, we examine the effort density per km^2 and use information from Welsford et al. (2014) to consider the proportion of seabed that might have been affected. The densities in **Figure 7** may be lower than is experienced in local areas as a result of evenly distributing the available effort throughout the depth range of a fishery in an area. In addition, localized concentrations may also reduce the effects from repeated disturbance of the same area.

Effort densities in both trawl and longline were highest in the MEASO subantarctic zone in both the Atlantic and Central Indian sectors. Trawling also had high effort densities in the Antarctic zone of the East Pacific and Atlantic sectors, from trawling prior to CCAMLR around the Antarctic Peninsula and the islands of the Scotia Sea. Longline effort in the Antarctic zone has been greatest in the West Pacific sector associated with the Ross Sea fishery.

The greatest accumulated recorded effort for trawling has been a density of 3.1 h per km^2 ($\log_{10}$ = 0.491; noting the absence of records for the very large catches). For longlining, the greatest accumulated density has been 11,000 hooks per km^2 ($\log_{10}$ = 4.04). Using the mean estimates of swept areas for trawl gear (20 m) and longlines (6.2 m × 1 m per hook) from Welsford et al. (2014) and assuming trawling covered a conservative distance of 2 nautical miles per hour (2 knots), this equates to the proportion of area affected in these locations as 23% and 6.8% respectively.

A shortcoming of the current analysis is the lack of availability of geolocated haul data. Nevertheless, our analyses indicate that the magnitude of impact is unlikely to be trivial at a local scale, if the fisheries are concentrating in particular areas.

Marine Protected Areas (MPAs) can help offset local scale impacts on benthic habitats (Constable and Welsford, 2011; Welsford et al., 2014). To demonstrate that this may be the case, an assessment of the distribution of habitats inside and outside MPAs is needed (see Welsford et al., 2014). At present, CCAMLR has a process for identifying areas of important habitats (known as "Vulnerable Marine Ecosystems" or VMEs) based on the recovery of habitat-forming taxa during longline fishing. It has also declared some areas to be VMEs based on research data. While it now has several potential VMEs identified from fishing, there remains to be a follow-up evaluation of the nature and extent of those sensitive areas, which may be larger than the circumscribed locations.

Prognoses

The current extent of bottom trawling is restricted to areas for which there has been an assessment of how to manage bottom fisheries, while conserving benthic habitats (Welsford et al., 2014). MPAs have been shown to be an effective tool for achieving conservation while uncertainty remains regarding the environmental effects of fishing on benthos (Constable and Welsford, 2011; Welsford et al., 2014). Although CCAMLR has established two marine protected areas to date, the South Orkney Islands Southern Shelf MPA (93,751 km^2 all no take) and Ross Sea Region MPA (1.53 million km^2 open sea, 1.09 million km^2 of which are no take) (Brooks et al., 2020), these do not provide coverage of the different benthic biomes to ensure comprehensive conservation of benthos in the Southern Ocean (Douglass et al., 2014a,b).

Three additional MPA proposals, in the Antarctic Peninsula (466,000 km^2 proposed), East Antarctica (969,000 km^2 proposed), and Weddell Sea (1.97 million km^2 proposed) regions, are currently under consideration but are yet to be designated by CCAMLR as of 2020 (Brooks et al., 2020; CCAMLR, 2020). Whilst MPA proposals are in consideration, meaningful gains and essential improvements can still be made on policies that directly affect vulnerable benthic communities. For example, CCAMLR's list of VME indicator taxa is a "living document" (CCAMLR, 2009b) and requires updating (**Box 1**) to align its taxonomy with the World Register of Marine Species[2]. Following the requirements of the 2007 United Nations General Assembly Sustainable Fisheries Resolution (61/105) (UNGA, 2007), aimed at avoiding significant adverse impacts of bottom fishing activities on VMEs in high seas areas, CCAMLR implemented procedures to identify and protect these communities and habitats via adoption of several Conservation Measures (Jones et al., 2016; **Table 2**). CCAMLR has interpreted a VME to be consistent with a community that includes the presence of benthic invertebrates that significantly contribute to the creation of complex three-dimensional structure, cluster in high densities, change the structure of the substratum, provide substrata for other organisms or are rare or unique (CCAMLR, 2009b). Considering traits such as rarity, slow growth, fragility and lack of larval dispersal, CCAMLR produced a list of 27 taxa that when present in high or rare abundances indicate the presence of a VME (CCAMLR, 2009c).

The threshold for VMEs (see **Table 2**) currently in place for use by fisheries in the Southern Ocean is biased toward sponge-dominated communities, as the threshold is mass dependent and all indicator taxa are pooled and treated equally. Diverse coral communities may fail to trigger thresholds based on densities of all indicator taxa pooled (Lockhart and Hocevar, accepted), and without the availability of direct imagery, a diverse range of coral communities and vast calcareous bryozoan reefs would not be included in CCAMLR's VME registry (Jones and Lockhart, 2011). Protecting a variety of VMEs is crucial, as coral communities are not only among the most vulnerable due to their fragility, great longevity and slow growth (Roark et al., 2005; Rogers et al., 2008; Maynou and Cartes, 2012; Peck and Brockington, 2013; Martinez-Dios et al., 2016), but also because of the potential carbon storage of cold-water coral communities of the Southern Ocean, as previously discussed (Barnes, 2017b; Barnes et al., 2018).

Tourism

Responses

The number of tourists visiting the Antarctic has increased dramatically since the 1980s (Yves, 2019), the 2018-2019 season saw an 8% increase on the previous year with a total of 56,186

[2]http://marinespecies.org/

TABLE 2 | Vulnerable Marine Ecosystem (VME) encounter protocols within the CCAMLR area including evidence required and potential protection (CCAMLR, 2019a).

Notification by	Evidence	Protection	CCAMLR conservation measures
Fishery-independent research	Scientific report or proposal for VME Variety of evidence acceptable	If granted by consensus, protection from all bottom fishing to one nautical mile radius of VME encounter	CM 22-06
Fishery	Benthic bycatch exceeds 10 kg of indicator taxa per 1200 m section of long or pot line (higher threshold)	VME Risk Area Move-on rule	CM 22-07
Fishery	Benthic bycatch exceeds 1 kg of indicator taxa per 1200 m section of longline (lower threshold)	Fishing vessel notification of potential VMEs	CM 22-07

To date, 53 VMEs and 76 VME Risk Areas are recorded in CCAMLR's VME Registry (CCAMLR, 2019b). All CCAMLR Conservation measures can be viewed online at: https://www.ccamlr.org/en/conservation-and-management/browse-conservation-measures.

tourists (IAATO, 2019a). Most of this tourism is concentrated along the West Antarctic Peninsula and subantarctic regions in the West Pacific sector of Antarctica and the Atlantic and Central Indian subantarctic MEASO sectors respectively (Lynch et al., 2010; Bender et al., 2016). Whilst tourism impact assessments exist (e.g., Kriwoken and Rootes, 2000; ASOC, 2008) they tend to overlook direct impacts on benthic habitats. Tourist activities that could directly impact the benthos include small boat landings, kayaking, scuba diving, snorkeling, submersibles, remotely operated vehicles and anchoring. More specifically, landings in ice-free intertidal habitats may trample sessile species, paddles from kayaks, scuba divers and snorkelers may disturb or damage fragile species such as corals and sponges, whilst submersibles and anchoring may have the most destructive impacts if landing on or scraping the seafloor.

The International Association of Antarctica Tour Operators (IAATO) provide field operation manuals and guidelines for tourist specific activities (see IAATO, 2019b for full list). Guidelines for small boat practices, including kayaking, mostly advise on operations in the vicinity of ice and anchoring is not advised in certain areas due to poor ground holding rather than the presence of vulnerable benthic habitats (IAATO, 2012). Prerequisites for underwater activities (including diving and snorkeling) include staffing by an experienced dive master in polar waters who should advise on "wildlife awareness" during the dive briefing and all diving is limited to a depth of 20 m. Guidelines for submersibles and remotely operated vehicles specifically mention seafloor communities, stating that "when setting down on the seafloor, care should be taken to avoid areas with high concentrations of marine life, especially soft invertebrates while sitting on or hovering close to the bottom, use thrusters minimally to avoid disturbing the delicate benthic community." IAATO has also provided environmental recommendations for new activities, highlighting that those with the potential to have "more than a minor or transitory impact" should be altered or stopped.

Prognoses

There is not enough data regarding the direct benthic impacts of tourism for a full assessment of this driver. The current level of potential impact may be "low," however if the majority of this activity is repeatedly concentrated *en masse* the potential for local detrimental impacts increases (Bender et al., 2016). The potential impact of these activities grows with an evolving tourist industry; for example, the increasing number of larger vessels (over 200 passengers) for which there are fewer potential landing sites (Bender et al., 2016) could increase impacts on landing sites and at the deeper anchorages that they are limited to. At present the use of submersibles in Antarctic tourism is relatively low, only operated by two IAATO registered vessels in the 2019/2020 season (IAATO pers. comms.). This number is expected to increase, with corresponding increase in the potential damage to fragile benthic species and habitats unless operational guidelines are updated with stricter protocols.

Although nearly all Antarctic tourism operators are members of IAATO, those that are not members can and do travel to the Antarctic, and potentially lack awareness of, or regard for, IAATO vessel code of conduct. IAATO vessel code of conduct promotes environmental protection based on IAATO and Antarctic Treaty Consultative Meeting guidelines and, where appropriate, adheres to all national and international legal requirements including the International Convention for the Prevention of Pollution from Ships (MARPOL). However, whilst there has been an increasing trend in Antarctic tourism, the future of the industry post the COVID-19 outbreak is unclear.

Plastics

Responses

To date, microplastics have been found in sediments in the Ross Sea (Munari et al., 2017), Admiralty Bay (South Shetland Islands) (Absher et al., 2019), near Rothera Station (Reed et al., 2018), in the vicinity of South Georgia (Barnes et al., 2009), and the deep Weddell Sea (Van Cauwenberghe et al., 2013), at similar concentrations to microplastics within sediments in shallow and deep-sea samples outside of the Antarctic region. Whilst we do not have any records of microplastic ingestion in Southern Ocean benthic species, there are records from outside the Southern Ocean and experiments showing that microplastics are ingested across most benthic functional groups (including suspension, deposit, predatory feeders) (e.g., Wright et al., 2013; Van Cauwenberghe et al., 2015; Taylor et al., 2016). Within the vicinity of research stations, including Rothera (West Antarctic Peninsula) and Mario Zucchelli Station (Ross Sea), microplastics concentrations in sediments decrease with distance from the base (Munari et al., 2017; Reed et al., 2018). The current concentrations may be negligible on the Southern Ocean

scale, but high at local scales if concentrated at point sources (Waller et al., 2017a). However, we do not fully understand how microplastics are transported within the Southern Ocean. For more details regarding transport of plastics in the Southern Ocean via the atmosphere, cryosphere and ocean currents please see Morley et al. (2020) in this research topic.

Prognoses

Benthic habitats, including the deep sea, have become a final resting place for marine debris including microplastics (Woodall et al., 2014; Taylor et al., 2016). Thus, surface marine plastic such as the 1,794 items km^{-2} in the surface water at the Antarctica Peninsula (Lacerda et al., 2019) demonstrates the risk of increasing plastic contamination to benthic habitats in the future. At an individual level, we know that benthic organisms can ingest microplastics, for example non-selective deposit feeders have been observed to have a higher load of microplastics than other benthic feeders and therefore may exhibit the highest risk (Waller et al., 2017a). Such ingestion can have a negative impact on individual survival, however at present we do not know the risk to benthic food webs and communities, or the role of microplastics in larger-scale ecosystem changes (Browne et al., 2015). Outside of the Southern Ocean, potential microplastic pathways in benthic food webs have been observed, including the transfer from seagrasses to herbivores around the Turneffe Atoll, and microplastics appear to bioaccumulate within predatory sea stars in the Arctic (Fang et al., 2018; Goss et al., 2018). However, the transfer of microplastics through marine food webs and potential for biomagnification is not fully understood and is a key topic for global marine research (Provencher et al., 2018). Within the Southern Ocean, the habitats most vulnerable to microplastic pollution are likely to be near research stations and areas of increased greywater entering the ocean. However, the transport of microplastics and accumulation patterns needs to be better understood (Waller et al., 2017a; Reed et al., 2018). From a benthic perspective, future research should focus on the sources of microplastics, the mechanisms for transport and process of accumulation as well as the ecological effects of microplastics within the food web. In addition, given the clear link between fisheries discard and marine debris, enforcement of global fisheries to limit plastic waste is a research and policy priority (Walker et al., 1997; Sheavly and Register, 2007). These research areas reflect the key questions proposed by the "Plastics in Polar Environments" group of Scientific Committee on Antarctic Research (SCAR)[3].

Pollution

Responses

The environmental impacts of sewage and wastewater on benthic communities have been studied at McMurdo (Lenihan et al., 1990; Conlan et al., 2004; Kim et al., 2019), Rothera (Hughes and Thompson, 2004), Casey (Stark et al., 2003, 2014; Stark, 2008), and Davis stations (Stark et al., 2015, 2016). The most comprehensive study to date at Davis station found multiple lines of evidence of environmental impacts within local benthic habitats (Stark et al., 2016). This included: histopathological abnormalities in fish (Corbett et al., 2014), isotopic enrichment in fish and predatory invertebrates (Stark et al., 2016), *Escherichia coli* carrying antibiotic resistance determinants found in the local water, sediments and filter feeding invertebrates (Power et al., 2016) and community differences between control and outfall sites. Changes in benthic communities have also been detected around outfalls at McMurdo and Casey stations (Conlan et al., 2004; Stark et al., 2016) and dispersal of sewage has been studied around Rothera station (Hughes and Nobbs, 2004; Hughes and Thompson, 2004).

Former waste disposal sites on shorelines around coastal research stations, combined with meltwater runoff through such sites, has also resulted in pollution of marine sediments by metals, persistent organic pollutants and hydrocarbons, leading to localized changes in macrofaunal communities (Lenihan and Oliver, 1995; Stark et al., 2005, 2014), uptake of contaminants by biota and reduced biodiversity (Duquesne and Riddle, 2002; Stark et al., 2004). At a species level there is relatively limited knowledge on the sensitivity and bioaccumulation of pollutants on benthic species (Lister et al., 2015; Alexander et al., 2017; Brown et al., 2017). Heavy-metal studies have shown demonstrated variability within phyla and further research is required before water quality guidelines for the Southern Ocean can be established (Kefford et al., 2019; Webb et al., 2019).

Prognoses

The current minimum wastewater treatment and disposal requirements under the Protocol on Environmental Protection to the Antarctic Treaty (simple maceration where populations exceed 30 in summer) are insufficient to prevent adverse effects to benthic ecosystems (Stark et al., 2016), yet are widely practised by most nations operating in Antarctica. With the projected increase in the number of vessels and research stations in Antarctica the installation of modernized wastewater treatment systems are required to mitigate the negative impacts to benthic communities described in Stark et al. (2016). At present, an advanced treatment system has been installed at Davis station, which consists of two separate processes. First, an advanced membrane filtration technology which reduces the concentration of most contaminants and second, a purification system which treats water to produce high quality potable water, suitable for reuse. Such systems have the additional benefit of reducing power (and thus CO_2 emissions) required to melt ice for water use and increase the availability of water on stations where there are limited local resources. However, there is a reluctance or failure to adopt such technologies by national Antarctic operators, despite their proven effectiveness in remote communities. The last available survey showed that 37% of permanent stations and 69% of summer stations lack any form of treatment facility (Gröndahl et al., 2009).

Hydrocarbons represent one of the main pollution risks to coastal Antarctica. Stations are the main source of oils and fuel to the marine environment and pose a significant risk, especially where situated in catchment areas that drain to the sea. Other sources of hydrocarbons include abandoned stations and fuel depots, wastewater outfalls, former waste disposal

[3]https://www.scar.org/science/plastic/home/

sites and vehicle wrecks (Raymond et al., 2017). Hydrocarbons spilled in Antarctic marine environments have been shown to persist in sediments for long periods and undergo very slow degradation (Thompson et al., 2006; Powell et al., 2010), causing effects in marine benthic communities (Lenihan and Oliver, 1995; Powell et al., 2010; Polmear et al., 2015; Stark et al., 2017), which are likely to persist for decades. Shipping activity poses the greatest risk of fuel and oil spills. The challenges of responding to fuel and oils spills in the Antarctic have been recognized, and have led to the requirement under the Madrid Protocol (Antarctic-Environmental Protocol, 1991) for all Parties to have contingency plans for prompt and effective response to environmental emergencies. The adoption of the Polar Code for shipping also includes a ban on the use and carriage of heavy fuel oil in the Antarctic region.

Non-indigenous Species

Responses

The introduction, establishment, and impact of non-indigenous species in the Antarctic region is receiving growing attention from researchers and stakeholders. Small coastal parts of the Southern Ocean, mainly the shallows around some research stations and tourist hotspots are regularly monitored for community change, especially where there are frequent SCUBA-diving operations, such as at Arctowski, Carlini, Palmer, and Rothera research stations on the South Shetland Islands and West Antarctic Peninsula. Monitoring of such areas as well as tourism hotspots, e.g., Deception Island, has detected a few non-indigenous algae and the invasive bryozoan species *Membranipora membranacea* (Linnaeus, 1767; Avila et al., 2020). Live mytilid mussels have been recorded entering the Southern Ocean on ship hulls (Lee and Chown, 2007), and a single specimen was found in the shallows at Grytviken, South Georgia (Ralph et al., 1976) with more recent settlement and successful reproduction within the South Shetlands (Cárdenas et al., 2020). There are also established populations of the polychaete worm *Chaetopterus variopedatus* (Renier, 1804) at these shipping hotspots in the shallows around South Georgia (Hughes et al., 2020). To date it is thought that there are few if any marine non-indigenous species established on Antarctic coasts, albeit detection might be unlikely unless it was from a taxon otherwise unrepresented. However, as the polar front retreats southwards under climate forcing (Meijers et al., 2012), Antarctic species established on the current northern margins (for example on the Kerguelen Plateau) will naturally "invade" southwards – their persistence and performance could be strong indicators for how species further south will cope with predicted physical change. Modeling has shown Southern Ocean environments are currently suitable for potentially invasive benthic species such as *Asterias amurensis* Lutken, 1871 and that changes in important variables (sea surface temperature, salinity, pH and nitrate) could mean up to 13 other hull-fouling benthic species also pose an invasion risk under climate change scenarios (Holland et al., in press). For more information about the introduction and establishment non-indigenous species within the Southern Ocean and the regulatory frameworks and existing measures to limit drivers or mitigate their impacts see Grant et al. (in review), to be published in this research topic.

Prognoses

The combination of increased propagule pressure (the number of individuals of a species introduced to an area to which they are not native) (Hughes et al., 2020), increase of anthropogenic vector density (e.g., ships and plastics), sea ice losses, near surface warming and other physical changes make arrival and establishment of non-indigenous species around Antarctic coasts much more likely. Predicting which non-indigenous species are threats, which indigenous species are most vulnerable, and which vectors and locations are most likely to be involved is a difficult task, but there are obvious "usual suspects" (Hughes et al., 2020). Broadly, areas of focus for non-indigenous introductions will be north West Antarctic Peninsula and South Georgia, in hotspots of tourist ship visits, and monitoring is likely to continue within 1 km of active marine research stations (which are coincidentally also hotspots of sea ice loss and warming). However, these same parts of West Antarctica, more specifically the northern tip of the Antarctic Peninsula, South Shetland and South Georgia Islands, also have higher non-indigenous species establishment and spread risks due to stronger past, present and predicted climate change (for example reducing sea ice and warming surface waters). Nine marine species have been identified as high risk invasive non-native species that are most likely to threaten the biodiversity and ecosystems of the Antarctic Peninsula region, including three species of bivalves, two ascidians, one polychaete worm, two crabs and one type of algae (Hughes et al., 2020).

The impact of non-indigenous species is difficult to predict; whilst it could lead to reduced diversity and functional homogenization of benthic communities, it is somewhat dependent on the other interacting impact drivers (Aronson et al., 2015; Morley et al., 2019). Other than a requirement to exchange ballast water away from the continental shelf when entering the Southern Ocean, marine biosecurity measures are still in their infancy, despite the near impossible task of removing marine aliens after detection. There is widespread knowledge that hull cleaning of vessels prior to entry into the Southern Ocean could greatly reduce risks of non-indigenous transport (Lee and Chown, 2009; Hughes et al., 2020). However, this is an expensive and time-consuming step for IAATO and tourism operators. In addition, the risks of non-indigenous species on the marine environment and the impacts of anti-fouling treatments to non-target (Antarctic) species (e.g., Lewis et al., 2004) need to be considered.

CUMULATIVE IMPACTS OF MULTIPLE DRIVERS

In the previous sections impact drivers have been discussed mostly in isolation but in reality, benthic communities will experience multiple drivers of change simultaneously. Controlled laboratory experiments have considered the

synergistic impacts of temperature, ocean acidification and pollution on individual benthic species (e.g., Ericson et al., 2012; Benedetti et al., 2016; Foo et al., 2016). There have also been *in situ* experiments such as Lenihan et al. (2018) which investigated the colonization of soft-sediments exposed to multiple chemical contaminants, altered organic carbon content and predator disturbance. Significant shifts in community structure, and potential functionality, have been predicted in shallower, flatter hard substratum, which with decreased sea ice duration are likely to receive the most light and increased sedimentation (Clark et al., 2017). For other shelf habitats the greatest disturbance is most likely to be from the combined impacts of iceberg disturbance and ocean acidification (Gutt et al., 2015). **Figure 8** indicates where multiple drivers could impact specific functional groups already exposed to changing ocean conditions.

When it comes to projecting changes in benthic biodiversity and ecosystem functioning, uncertainties arise from the non-linear nature of most ecological processes, spatial differences, feedbacks and synergistic effects of multiple stressors (Gutt et al., 2015). A comprehensive quantification of such processes is still impossible due to incomplete representative datasets of physical-chemical drivers over space and time. A better quantification of ecosystem functions by state-of-the-art interdisciplinary ecological models, which include biological factors such as species-specific potentials for adaptation and acclimation (Gutt et al., 2012, 2018; Kennicutt et al., 2014) are needed to develop scenarios of Southern Ocean ecological processes in the future. The liaison between disciplines is crucial to making data collection at comparable and meaningful scales to help determine holistic biota responses to ecosystem change and inform modeling analyses (see next section). Devising strong sentinel locations, taxa (or functional groups) and important, standardized performance measures will likewise help assess biological response to environmental changes.

SUMMARY FOR POLICYMAKERS

Southern Ocean benthic ecosystems are responding to climate impacts in complex and often unpredictable ways. Isolated for millennia, benthic species have evolved to meet unique environmental challenges of life on the Southern Ocean seafloor. Climate change is poised to disrupt this habitat, altering the processes, assemblages, population dynamics, and ultimately survival rates of seafloor species. The difficulty in assessing the overall impact of climate change on benthic species is due to the challenges inherent to conducting research in the Southern Ocean, regional differences in the number and level of impact drivers, the cumulative impacts of predicted changes, and the non-linearity of multiple stressors on biodiverse benthic communities. Despite this, there are clear governance structures

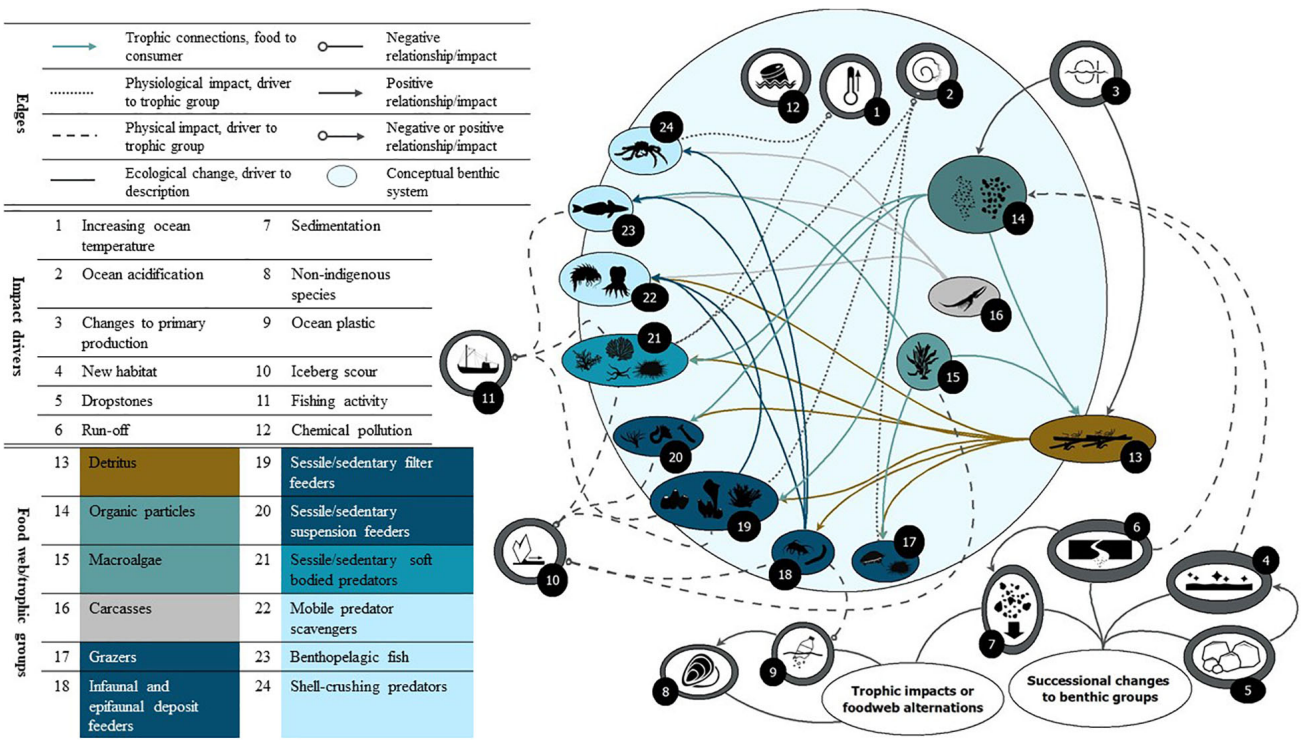

FIGURE 8 | Conceptual network diagram demonstrating multiple impact drivers acting on benthic functional groups within the Southern Ocean. Colored arrows indicate trophic connections in prey color, gray arrows indicate driver relationships. Refer to **Figure 1** of this article for driver pathways. Functional groups adapted from Barnes and Sands (2017) and listed in the **Supplementary Information**. Note that impact drivers within the conceptual benthic system circle could impact the physiology of all functional groups depending on rate or level of change but only the most sensitive groups are indicated by connecting dashed lines.

that policymakers can explore and implement to minimize the impact of climate change on benthic invertebrate ecosystems.

Governing bodies have thus far been slow to respond to the effects of climate change on Southern Ocean ecosystems, despite the urgency. Policy areas most deficient and in need of immediate attention and improvement for Southern Ocean benthos conservation include:

- International effort is needed to enforce a reduction in fishing debris and plastic waste entering the ocean that ultimately resides on the sea floor.
- A network of MPAs, including appropriate fishing restrictions, is urgently required in the Southern Ocean to help ecosystems deliver important services and allow for species to adapt to changing conditions.
- CCAMLR's VME protocols require updating, removing taxonomic bias in the implementation of thresholds, particularly for the protection of species with greater carbon-storage potential.
- Stricter protocols are needed for research and tourist vessels entering the Antarctic, to reduce the direct and indirect impacts of human activities. These include revised guidelines for the use of submarines and for direct contact by landings to benthic habitats, the introduction of marine plastics and other pollutants and the transport of non-indigenous species that could have major impacts on the diversity and functioning of benthic communities.
- Modernizing the environmental guidelines of the Committee for Environmental Protection (CEP) of the Antarctic Treaty to reflect up-to date knowledge of the status and nature of the risks of environmental change on Antarctic marine benthic ecosystems.

These actions, as well as a better understanding of benthic ecosystem dynamics (**Box 1**), can help lead to long-term management that adequately accounts for climate change impacts on Southern Ocean benthos.

AUTHOR CONTRIBUTIONS

MB, DB, SM, CW, JG, ABC, HG, and AV attended the MEASO2019 workshop in Woking (UK) where this manuscript was outlined. MB coordinated and compiled text contributions from co-authors, wrote the introductory and concluding sections, constructed **Figures 1**, **5** and **8**, and finalised the manuscript. HS reviewed and analysed the data available for **Figure 4**. AP and MS produced **Figure 3**. SM and HG provided content for the ocean temperature section. DB, JS, AP, and JG provided content for the ice shelf disintegration, increased iceberg scour and biogenic flux section. DB and AP provided content for the glacial retreat, sedimentation, and newly ice-free habitats section. JS, AP, DB, JG, and SM provided content for the sea ice change, light, and primary production. NB, BF, and RD provided content for the ocean acidification section. SL, ABC, NB, and MB provided content for the fishing section and summary for policymakers. JS and RD provided content for the pollution section. MB, CW, and HG provided content for the plastics section. JS, DB, and MB provided content for the non-indigenous species section. AB provided a deep-sea perspective throughout the manuscript providing content where relevant, JS did the same for shallow water. AJC advised on all sections, contributed to the fishing section including data analysis for **Figure 7**. All co-authors were invited to review and edit content prior to manuscript submission and during review.

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SUPPLEMENTARY MATERIAL

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Evidence for the Impact of Climate Change on Primary Producers in the Southern Ocean

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Within the framework of the Marine Ecosystem Assessment for the Southern Ocean (MEASO), this paper brings together analyses of recent trends in phytoplankton biomass, primary production and irradiance at the base of the mixed layer in the Southern Ocean and summarises future projections. Satellite observations suggest that phytoplankton biomass in the mixed-layer has increased over the last 20 years in most (but not all) parts of the Southern Ocean, whereas primary production at the base of the mixed-layer has likely decreased over the same period. Different satellite models of primary production (Vertically Generalised versus Carbon Based Production Models) give different patterns and directions of recent change in net primary production (NPP). At present, the satellite record is not long enough to distinguish between trends and climate-related cycles in primary production. Over the next 100 years, Earth system models project increasing NPP in the water column in the MEASO northern and Antarctic zones but decreases in the Subantarctic zone. Low confidence in these projections arises from: (1) the difficulty in mapping supply mechanisms for key nutrients (silicate, iron); and (2) understanding the effects of multiple stressors (including irradiance, nutrients, temperature, pCO_2, pH, grazing) on different species of Antarctic phytoplankton. Notwithstanding these uncertainties, there are likely to be changes to the seasonal patterns of production and the microbial community present over the next 50–100 years and these changes will have ecological consequences across Southern Ocean food-webs, especially on key species such as Antarctic krill and silverfish.

Keywords: phytoplankton, climate, Antarctica, biogeochemistry, deep chlorophyll maximum, ocean colour, MODIS, SeaWiFS

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Abbreviations: Chlorophyll-a / chl-a, The ubiquitous light-harvesting pigment in marine phytoplankton usually expressed as a volumetric concentration (mg m^{-3}); DCM, Deep chlorophyll maximum, a sub-surface phytoplankton bloom; ENSO, El Niño-Southern Oscillation; HNLC, High nitrate low chlorophyll water; IPCC, Intergovernmental Panel on Climate Change; ISCCP, International Satellite Cloud Climatology Project; MODIS, Moderate Resolution Imaging Spectro-radiometer (NASA); NASA, National Aeronautics and Space Administration of the United States; NPP, Net primary production is defined as the depth-integrated rate of carbon incorporation into organic (living) matter after allowing for respiration of algae (gC m^{-2} d^{-1}); PAR, Photosynthetically active radiation (light between 400 and 700 nm); pCO_2, Partial pressure of dissolved carbon dioxide; RCP, Representative Concentration Pathway; SAM, Southern annular mode (a mode of climate variability); SeaWiFS, Sea-viewing Wide Field-of-view Sensor (OrbImage/NASA); VGPM, Vertically-generalised production model.

INTRODUCTION

Primary production by microalgae communities is the foundation of Southern Ocean food-webs (Deppeler and Davidson, 2017; Boyd et al., 2019), providing the organic matter that ultimately sustains Antarctica's unique marine ecosystems (Loeb et al., 1997; Atkinson et al., 2004; Hill et al., 2006; Mock et al., 2017; Boyd et al., 2019; McCormack et al., in review). There are also important feedbacks between the microbial communities and Southern Ocean biogeochemistry, carbon sequestration and the global climate system (Siegenthaler and Sarmiento, 1993; Meskhidze and Nenes, 2006; Sarmiento, 2013; McKinley et al., 2017; Henson et al., 2019; Moreau et al., 2020).

Increases of atmospheric carbon dioxide (CO_2) from ∼400 μatm today beyond 750 μatm by 2100 will likely lead to multifaceted environmental change in the Southern Ocean, including upper-ocean warming, ocean acidification (OA), changes to incident irradiance, increased vertical mixing in the water column, less sea-ice and changed patterns of nutrient input (including iron) (IPCC, 2019; Henley et al., 2020). These environmental and oceanographic changes will affect microbial community composition, patterns of primary production and ecological pathways in Southern Ocean marine ecosystems (Le Quéré et al., 2016; Schofield et al., 2017; Deppeler and Davidson, 2017; Freeman et al., 2019; Johnston et al., in review).

Despite the importance of projecting future changes to primary production and the microbial community composition of the Southern Ocean, current modelling methods have high uncertainty (Leung et al., 2015; IPCC, 2019). The response of the Southern Ocean microbial community to multiple environmental drivers is complex and poorly understood (Petrou et al., 2016; Deppeler and Davidson, 2017). Unlike most of the world's oceans, the vast majority of the Southern Ocean is considered to be replete with nitrate and instead, silicate and iron are limiting in some areas and seasons (Banse, 1996; Boyd et al., 2012, 2001; Hiscock et al., 2003; Doblin et al., 2011). Irradiance can also be crucial to primary production (Deppeler and Davidson, 2017; Kim et al., 2018) and microbial community composition (Arrigo et al., 2010; Kropuenske et al., 2010; Van de Poll et al., 2011; Trimborn et al., 2017) in the Southern Ocean, and irradiance, iron and nutrient availability interact in ways not fully understood at present (Strzepek et al., 2012; Luxem et al., 2017; Trimborn et al., 2019). Further complexities arise from co-limitation by iron and other micronutrients (e.g., Mn; Pausch et al., 2019). Microzooplankton grazing, which can reduce NPP by facilitating nutrient loss through the sinking of particulate detritus (e.g., Cadée et al., 1992; Perissinotto and Pakhomov, 1998; Vernet et al., 2011), will be affected by climate change through changes to grazing rates (Sarmento et al., 2010; Caron and Hutchins, 2013; Behrenfeld, 2014; Biermann et al., 2015; Cael and Follows, 2016) and phytoplankton nutrient density (Finkel et al., 2010; Hixson and Arts, 2016).

Environmental changes driving these complex biological responses are, in themselves, complex and not well observed. For example, shoaling of the mixed-layer due to decreased vertical mixing can simultaneously increase mixed-layer irradiance, increase grazing, increase ultraviolet-B damage, decrease nutrient supply, and reduce 'living space' (Garibotti et al., 2005; Vernet et al., 2008; Moreau et al., 2010; Boyd et al., 2014; Zhu et al., 2016; Hoppe et al., 2017; Llort et al., 2019; Brown et al., 2019; Höfer et al., 2019). However, vertical mixing is not the only iron supply mechanism operating in the Southern Ocean; iron and nutrients (such as silicate) can be introduced into the upper water column by meltwater (from icebergs, sea ice, and glaciers), atmospheric input of iron aerosols, hydrothermal vents, and microbial recycling – Blain et al. (2007), Cassar et al. (2007), Pollard et al. (2009), Boyd and Ellwood (2010), Tagliabue et al. (2010), Treguer (2014), Lannuzel et al. (2016), Boyd (2019), and Hopwood et al. (2019).

Within the framework of the Marine Ecosystem Assessment for the Southern Ocean (MEASO), we present new analyses of the spatial and seasonal patterns of near-surface chlorophyll-a concentration (chl-a) and satellite-based proxies of primary production in the Southern Ocean from Earth-observing satellites, and relate this to information from ships, shore-stations, and autonomous instruments. We consider both primary production in the surface mixed-layer (from the surface to the depth of the seasonal pycnocline, at ∼50–150 m) and in the 'deep chlorophyll maximum' (DCM; Cullen, 2015; Carranza et al., 2018; Uchida et al., 2019). New approaches to track changes in primary production in the DCM based on satellite observations are proposed. Finally, information on future changes to primary producers from global Earth-system models are presented and discussed in the context of our present understanding of the role of multiple-drivers of changes to primary production and our ability to observe, combine and model these drivers.

METHODS

Mixed-Layer Primary Production

Both satellite observations of phytoplankton biomass (proxy of chl-a) and satellite-based models were used to describe recent changes to Southern Ocean net primary production (**Table 1**). There have been many comparisons between *in situ* and satellite estimates of chl-a in the Southern Ocean. In reprise, some studies conclude that the 'default' (i.e., globally tuned) satellite algorithm for chl-a should be adjusted to improve accuracy in the Southern Ocean (Johnson et al., 2013; Jena, 2017), whereas other studies have found that the default global chl-a algorithm was appropriate for the Southern Ocean (Arrigo et al., 2008; Haentjens et al., 2017; Moutier et al., 2019; Del Castillo et al., 2019). The reduction in absolute uncertainty in chl-a from adjusting the algorithm for the Southern Ocean tends to be small (e.g., Johnson et al., 2013) and the effect on trends will likely be even smaller, so we used the global default chl-a algorithm for SeaWiFS and MODIS-Aqua, and blended these as described in Pinkerton (2019).

For the same period, estimates of NPP are available from two widely used models: the Vertically Generalised Production Model, VGPM, Behrenfeld and Falkowski, 1997) and the Carbon Based Production Model (CBPM, Behrenfeld et al., 2005; Westberry et al., 2008). Alternative primary production

TABLE 1 | Environmental data used in analysis (in alphabetical order).

Variable	Units	Description	Reference(s)
cbpm	mgC m^{-2} d^{-1}	Net primary production from the Carbon Based Production Model (CBPM). Based on blended SeaWiFS and MODIS-Aqua measurements.	Behrenfeld et al. (2005); /ocean.productivity/www.science.oregonstate.edu/ocean.productivity/
chl	mg Chl-a m^{-3}	Near surface concentration of chlorophyll-a from MODIS-Aqua (version R2018.0) and SeaWiFS (version R2018.0) satellite sensors, blended using overlap period 2002-2010 (Pinkerton, 2019).	NASA Goddard Space Flight Center et al. (2018a,b)
kpar	m^{-1}	Diffuse downwelling attenuation coefficient in the mixed-layer for broadband irradiance, based on blended SeaWiFS and MODIS-Aqua measurements of attenuation at 490 nm (K_D490)	Clark, 1997; Relationship between K_D490 and K_{PAR} from Morel et al. (2007).
mld	m	Mixed layer depth calculated from data-assimilating hydrographic model GLBu0.08 hindcast results using a potential density difference of 0.030 kg m^{-3} from the surface: (1) *hycom*: from day 265 (2008) to present; (2) *fnmoc*: from day 169 (2005) to present; (3) *soda*: from day 249 (1997) to end of 2004; (4) *tops*: from day 001 (2005) to 225 (2010).	Metzger et al. (2007), Chassignet et al. (2007), and Wallcraft et al. (2009). Data sourced: orca.science.oregonstate.edu/1080.by.2160.monthly.hdf.mld.hycom.php;
par	μE m^{-2} d^{-1}	Photosynthetically Active Radiation (PAR) measured as broadband (400–700 nm) incident light intensity at the sea surface as a daily (24 h) average, from blended SeaWiFS and MODIS-Aqua measurements.	Frouin et al. (2012)
seaice	%	Sea ice concentration from the Scanning Multichannel Microwave Radiometer (SMMR) on the Nimbus-7 satellite and from the Special Sensor Microwave/Imager (SSM/I) sensors on the Defense Meteorological Satellite Program's (DMSP) -F8, -F11, and -F13 satellites. Measurements from the Special Sensor Microwave Imager/Sounder (SSMIS) aboard DMSP-F17 are also included. Advanced Microwave Scanning Radiometer - Earth Observing System (AMSR-E) Bootstrap Algorithm with daily varying tie-points.	Cavalieri et al. (1990), updated 2007; https://nsidc.org/
sst	°C	Optimum Interpolation Sea Surface Temperature (OISST), version 2, based on Advanced Very High Resolution Radiometer series (AVHRR) of NOAA (National Oceanic and Atmospheric Administration of the United States).	Reynolds et al. (2002)
vgpm	mgC m^{-2} d^{-1}	Net primary production from the Vertically Generalized Production Model (VGPM). Based on blended SeaWiFS and MODIS-Aqua measurements.	Behrenfeld and Falkowski (1997) and O'Reilly and Sherman (2016); www.science.oregonstate.edu/ocean.productivity/

models specifically developed for the Southern Ocean have been developed (e.g., Arrigo et al., 2008; Moreau et al., 2015) but data are not widely available and validation is scare. The accuracy of VGPM and CBPM data in the Southern Ocean is not known, so a (non-exhaustive) review of the existing NPP literature was carried out for preliminary comparison. A total of 573 measurements of (almost exclusively summer) primary production were sourced from 24 studies and each was assigned to a MEASO zone and sector based on geographical location (**Table 2**) and compared to satellite-based NPP estimates.

Deep-Chlorophyll Maxima

To explore changes in the productivity of phytoplankton at the base of the mixed layer in deep chlorophyll maxima (DCM) we propose a novel metric: irradiance at the base of the mixed layer (E_{DCM}, Equation 2).

$$E_{DCM} = par\,(1 - \rho_s)\exp\left(-kpar \cdot mld\right) \quad (1)$$

Both broadband incident irradiance at the sea-surface (*par*) and diffuse downwelling attenuation (*kpar*) were obtained from satellite observations, and estimates of mixed layer depth (*mld*) were provided from a data-assimilating hydrographic model (**Table 1**). Based on instrumented elephant seals in the Southern Ocean, Carranza et al. (2018) showed that DCM tends to occur close to the base of the mixed layer defined using a potential density threshold criterion of 0.03 kg m^{-3}. Hence, mixed layer depth (z_m) was obtained from GLBu0.08 hindcast results (sourced from orca.science.oregonstate.edu) using a potential density difference of 0.03 kg m^{-3} from the surface (Metzger et al., 2007; Chassignet et al., 2007; Wallcraft et al., 2009). A constant diffuse sea-surface reflectivity (ρ_s) of 0.07 was assumed (Campbell and Aarup, 1989).

The rationale behind this formulation is that high attenuation in the mixed layer makes it less likely that a DCM is present and vice versa. Essentially, either phytoplankton are distributed relatively evenly through the mixed layer (no DCM, higher mixed-layer attenuation), or are present in a narrow band of elevated concentration at the base of the mixed layer (typically co-located with the nutricline: Cullen, 2015) forming a DCM below a relatively oligotrophic mixed-layer. It is difficult to forecast which of these will occur without good knowledge of the factors involved (*inter alia* water column structure, nutrient supply/demand, incident irradiance, photoadaptive-capability of phytoplankton species present, loss terms including grazing and sinking; Parslow et al., 2001; Kemp et al., 2006; Cullen, 2015; Carranza et al., 2018; Uchida et al., 2019), but we hypothesize that satellite data may be able to tell us which of these situations has occurred after the event.

We recognize that although irradiance at the base of the mixed-layer is likely to be a key factor affecting whether a DCM exists and the level of primary productivity in the DCM (Cullen,

TABLE 2 | Spring-summer integrated net primary production rates (gC m^{-2} d^{-1}) retrieved from the literature and grouped by MEASO sectors and zones.

	Zone			Global per sector
Sector	**Northern**	**Subantarctic**	**Antarctic**	
Atlantic	NA	**0.86** [0.07, 3.02; 89]	**0.65** [−0.20, 4.71; 133]	**0.74** [−0.20, 4.71; 222]
East Pacific	NA	NA	**1.20** [−0.53,14.5; 154]	**1.20** [−0.53, 14.5; 154]
West Pacific	NA	NA	**0.94** [0.00, 6.22; 76]	**0.94** [0.00, 6.22; 76]
Central Indian	**0.34** [0.15,0.95; 20]	**0.44** [0.00,1.02; 29]	**0.51** [−0.13, 3.83; 72]	**0.46** [−0.13, 3.83; 121]
East Indian	NA	NA	NA	NA
Global per zone	**0.34** [0.15,0.95; 20]	**0.75** [0.00, 3.02; 118]	**0.88** [−0.53, 14.5; 435]	

Bold numbers represent mean values, while square brackets contain minimum and maximum rate as well as the number of values retrieved from the literature, respectively. Literature consulted: Saijo and Kawashima (1964), El-Sayed and Mandelli (1965), Mandelli and Burkholder (1965), Horne et al. (1969), El-Sayed (1970), El-Sayed and Taguchi (1981), El-Sayed et al. (1983), von Bodungen et al. (1986), Smith and Nelson (1990), Verlencar et al. (1990), Holm-Hansen and Mitchell (1991), Karl et al. (1991), Helbling et al. (1995), Savidge et al. (1995), Moline and Prézelin (1997), Figueiras et al. (1998), Saggiomo et al. (1998), Bracher et al. (1999), Dierssen et al. (2000), Varela et al. (2002), Uitz et al. (2009), Hoppe et al. (2017), Aracena et al. (2018), and Höfer et al. (2019).

2015), productivity and biomass of phytoplankton at depth will be affected by other factors, such as phytoplankton composition, nutrient concentrations and temperature (Sallée et al., 2015). In addition, mixed layers can contain vertical structure in optical properties (Carranza et al., 2018). To evaluate the utility of E_{DCM} as an indicator of DCM, a comparison was made between E_{DCM} and the amount of phytoplankton biomass in the DCM from three Southern Ocean Carbon and Climate Observations and Modeling (SOCOMM project; Riser et al., 2018; Uchida et al., 2019) profiling drifters between 2013 and 2018. Phytoplankton biomass in the DCM was proxied from these float measurements as the depth-integrated phytoplankton carbon biomass (C_p) minus the surface phytoplankton carbon biomass multiplied by the mixed layer depth, C_p(surf), following Uchida et al. (2019).

Spatial Summaries

Spatial variability in primary productivity was summarised using the MEASO spatial framework (Constable et al., in review; **Supplementary Information**). Briefly, MEASO defines five longitudinal sectors, three latitudinal zones (Northern between Subtropical and Subantarctic fronts; Subantarctic between Subantarctic and Southern Antarctic Circumpolar Current (ACC) fronts; and Antarctic south of Southern ACC front), and 15 areas from the sector-zone intersects.

Environmental Change in the Southern Ocean

Although autonomous profilers are delivering increasingly powerful datasets (e.g., Boyer et al., 2013; Buongiorno Nardelli et al., 2017; Uchida et al., 2019), large-area (Southern Ocean scale) and long-term (decadal) observations of environmental change in the Southern Ocean are predominantly from Earth-observation satellites (e.g., Cavalieri et al., 1990; Reynolds et al., 2002; Haentjens et al., 2017; Del Castillo et al., 2019), sometimes in conjunction with data-assimilating hydrodynamic models (e.g., Metzger et al., 2007; Chassignet et al., 2007; Wallcraft et al., 2009). To describe the oceanographic and environmental setting, this study focused on 4 key environmental data sets for which large-area, spatially resolved and long-term information is available (**Table 1**): sea-surface temperature (*sst*); sea ice concentration (*ice*); mixed layer depth (*mld*); and photosynthetically active radiation at the sea surface (*par*). Together, these describe major environmental drivers of change in the Southern but clearly do not capture all factors relevant to primary production, including nutrient supply mechanisms, acidification and grazing.

Statistical Analyses

Linear trends in monthly anomalies (differences from climatological means) for each dataset (*chl*, *sst*, *ice*, *mld*, *par*, *vgpm*) at the pixel level (smallest sampling scale) were determined using the Sen slope (Sen, 1968). This value is the median slope of all pairs of points in the time series. The insensitivity of the Sen slope to outliers means that it is generally the preferred non-parametric method for estimating a linear trend (Hipel and McLeod, 1994). Seasonal trends were calculated using anomalies from three months (spring: September–November; summer: December–February; autumn: March–May; winter: June–August).

The Sen slope was also used to describe trends at the scale of MEASO zones, sectors and areas. Satellite-based estimates of chl-a and NPP fail at low solar elevations, and we have not attempted to "fill in" the winter gaps in satellite data (e.g., as Park et al., 2019). The proportion of missing data increases with latitude and so to avoid any potential bias in area-averages, trends were only calculated when more than half of potential observations for an area were present. The statistical significance of trends was assessed using the non-parametric Mann-Kendall test (Mann, 1945; Kendall, 1975) which does not require a normal distribution assumption. We used the method of Yue and Wang (2004) to adjust the effective number of degrees of freedom for autocorrelation.

The influence of four environmental drivers (*sst*, *ice*, *mld*, *par*) on chl-a was considered by a multiple linear regression (Equation 1), where the a coefficients minimize the sum of squares of the error (ε). This analysis was not applied to satellite estimates of primary production (*vgpm*, *cbpm* or E_{DCM}) to avoid circularity: satellite measurements of chl-a are independent of observations of these environmental drivers but *vgpm*, *cbpm* and E_{DCM} are not. Here, $\widetilde{chl}$ is the monthly anomaly in *chl* (and similarly for

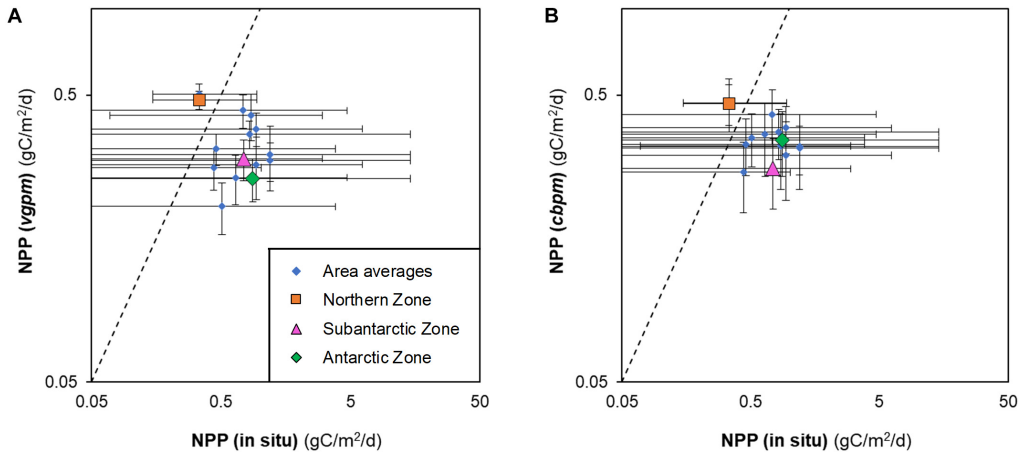

FIGURE 1 | Depth-integrated, net primary productivity (NPP) in the Southern Ocean measured *in situ* from research vessels and estimated from satellite data: **(A)** Vertically Generalised Production Model (*vgpm*); and **(B)** Carbon Based Production Model (*cbpm*). Data are combined as MEASO areas (blue) and zones (orange, pink, green). Dashed lines indicate 1:1 correspondence.

other variables).

$$\widetilde{chl} = \alpha_0 + \alpha_1 \widetilde{sst} + \alpha_2 \widetilde{ice} + \alpha_3 \widetilde{mld} + \alpha_4 \widetilde{par} + \varepsilon \qquad (2)$$

An approximation to the contribution to overall trend (Sen slope) in chl-a from each candidate driver variable (*sst*, *ice*, *mld*, *par*) is given as the product of the respective linear coefficient (α) and the trend (Sen slope) of the variable. The analysis was carried out in IDL 8.5 (Research Systems Inc., Boulder, CO, United States).

RESULTS

Mixed-Layer Primary Production

Although our compilation of *in situ* measurements of depth-integrated NPP from research vessels and shore-stations was not exhaustive, it nevertheless shows a clear pattern of where primary production has been measured more often to date (**Table 2**) and highlights the need to improve knowledge of primary productivity in the entire East Indian sector as well as the Subantarctic and Northern zones where data are scarce or non-existent. The paucity of the NPP data meant that no robust conclusions could be drawn as to the relative accuracies of VGPM and CBPM. Both NPP models look to be overestimating NPP in the Northern zone by a similar amount of ∼40% (**Figure 1**) and underestimating NPP in the Subantarctic and Antarctic zones by 55 ± 15 % (mean ± standard deviation).

Satellite observations (**Figure 2A**) show that chl-a was generally higher in Subantarctic areas, lower south of the Polar Front and that there were some areas of elevated productivity south of the southern limit of the ACC (especially in the Ross Sea and Bellingshausen Sea/western Antarctic Peninsula). Patterns of primary productivity estimated from satellite observations (**Figures 2C,E**) generally followed those of chl-a (higher values in Subantractic waters and over the Antarctic shelf) but there was a strong positive dependence of NPP on latitude. There were also significant differences in spatial variations of annual-average *vgpm* compared to *cbpm*, with *vgpm* higher to the north of the region, and *cbpm* higher to the south.

Increasing trends in chl-a between 1997–2019 were detected by satellites in most Northern and Subantarctic zones (**Figure 2B**). In contrast, decreasing trends in chl-a were observed in most Antarctic continental shelf-sea waters, especially in the Ross Sea, Weddell Sea and Prydz Bay, except along the western Antarctic Peninsula. Trends in *vgpm* (**Figure 2D**) closely followed those in chl-a. Seasonal trend analysis of chl-a and *vgpm* (see **Supplementary Information**) shows predominantly positive trends in autumn and negative trends (over the Antarctic shelf) in summer. Trends in *cbpm* were negative throughout the Southern Ocean (**Figure 2F**), including in Northern and Subantarctic zones in contrast with *vgpm*. Seasonal analysis of trends in *cbpm* suggests that changes in productivity in the summer drive these overall trends.

In terms of environmental drivers of changes in chl-a, we found that only a small amount (mean 5.6%, 5th–95th percentile range 0.9–16.8%) of the monthly anomalies in chl-a over the last 20 years was explained by a linear combination of *sst*, *ice*, *mld* and *par* (**Figure 3**). The proportions of variance explained by the individual drivers were less than 2%, with *sst* explaining most and *par* the least. The linearized contribution to the trends in chl-a from these individual environmental drivers (**Figure 4**) showed little spatial structure and were typically small, less than 0.001 mg m^{-3} y^{-1}, whereas the trends in chl-a were up to ∼0.01 mg m^{-3} y^{-1} in some areas of the Southern Ocean.

Deep-Chlorophyll Maxima in the Southern Ocean

The regression between irradiance at the base of the mixed layer and the amount of phytoplankton biomass in the DCM from three SOCCOM floats (**Figure 5**) was highly significant ($F_{95} = 82.7$, $p < 0.001$) with about half of the variance explained ($R^2 = 0.47$).

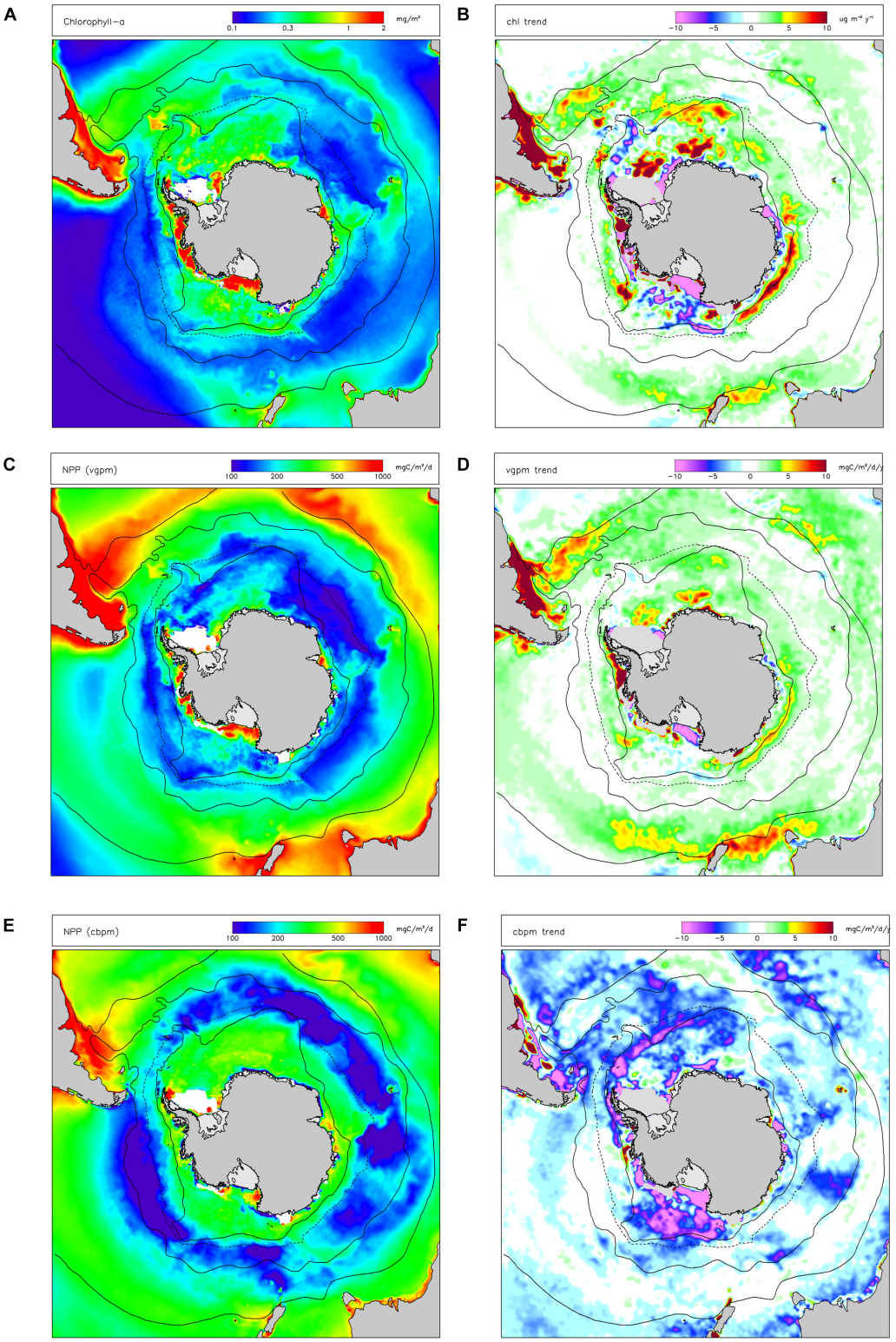

FIGURE 2 | Long-term (1997-2019) mean values of indicators for primary production: **(A)** chlorophyll-a concentration (*chl*); **(C)** net primary production in the water column estimated by the VGPM algorithm (*vgpm*) and the CBPM algorithm (*cbpm*) **(E)**. Linear trends (Sen slopes) over the same period are shown for **(B)** *chl*; **(D)** *vgpm*; **(F)** *cbpm*. White indicates missing data. Black lines are nominal positions of (from north): Subtropical Front (STF, solid line), Subantarctic Front (SAF, solid line), average maximum northern extent of seasonal sea ice (dashed line), and the Southern boundary of the Antarctic Circumpolar Current (SB-ACC, solid line).

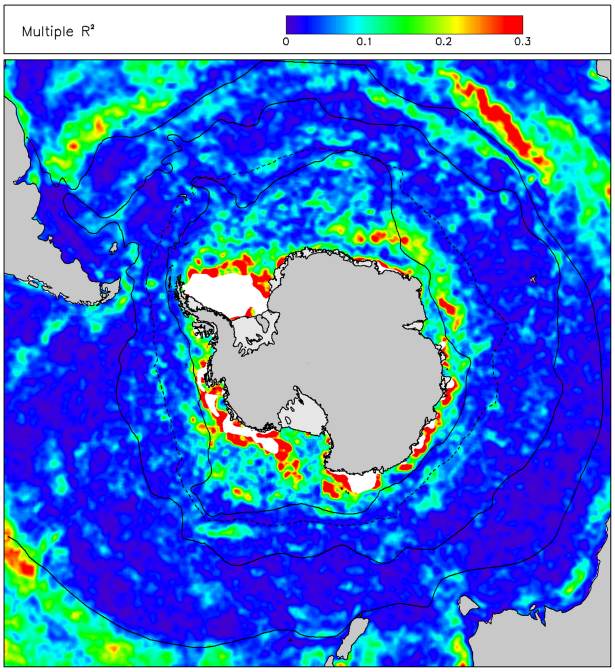

FIGURE 3 | Proportion of variance explained (R^2) in anomalies of chlorophyll-a concentration (*chl*) by a multiple linear regression of anomalies of environmental drivers: sea-surface temperature (*sst*), sea ice concentration (*sea-ice*), mixed layer depth (*mld*) and incident irradiance at the sea-surface (*par*). Other information as **Figure 2**.

Average E_{DCM} values were low through most of the Southern Ocean except in a band close to the southern boundary of the ACC and especially in the Atlantic and Central Indian sectors (**Figure 6A**). High values of mean E_{DCM} were also found in parts of the Northern zone of the Pacific sector. Trends in E_{DCM} (**Figure 6B**) were negligible north of the northern limit of seasonal sea ice, and almost exclusively negative south of this. Decreasing trends in E_{DCM} were greatest between longitude 0° and 60° (Atlantic and Central Indian sectors) and occurred almost exclusively during the summer months (December–February: see **Supplementary Information**).

Trends Summary by MEASO Areas

Significant increasing trends in chl-a and *vgpm* between 1997–2019 were found in all MEASO zones and sectors except for chl-a in the Antarctic zone (**Table 3**). Increases were highest in the Atlantic and West Pacific sectors. Significant increasing trends were also found for many (chl-a) or most (*vgpm*) MEASO areas. Positive trends in *vgpm* were almost exclusively greater in magnitude and more significant than trends in chl-a (with the exception of AON and WPA areas). In contrast, all significant trends in *cbpm* were negative, and were highest in Subantarctic and Antarctic zones. For the Southern Ocean as a whole, the mean trend and significance in *vgpm* was 0.8 % y^{-1} ($p < 0.0001$) compared to 0.5 % y^{-1} for *chl* ($p = 0.002$), whereas the overall Southern Ocean trend in *cbpm* was negative (−0.5 % y^{-1}) but not significant ($p = 0.17$). Significant trends in irradiance at the base of the mixed-layer (E_{DCM}) over the same period were exclusively negative, and substantially larger than trends in chl-a and *vgpm* especially in the Subantarctic and Antarctic zones and in the Atlantic sector (trends > 5 % y^{-1} in magnitude). At the scale of the Southern Ocean, the Sen slope in E_{DCM} was highly significant −3.2 % y^{-1} ($p < 0.0001$). Plots of time series by zones, sectors and area, and full statistics on trend analysis are given in **Supplementary Information**.

DISCUSSION

Mixed-Layer Primary Production

The present study found that chl-a and NPP were higher in the Atlantic sector than in other sectors of the Southern Ocean, likely as a result of higher iron availability due to land proximity (de Baar et al., 1995; Banse, 1996), and productivity was also elevated around the Kerguelen Plateau and Balleny Islands, consistent with enhanced supply of iron and major nutrients to surface waters (Blain et al., 2007). Annual-average values of chl-a and NPP were also high in some parts of the Antarctic zone, especially Prydz Bay (CIA), Ross Sea (WPA), and Bellingshausen Sea/western Antarctic Peninsula (EPA), likely because of persistent polynyas (Arrigo et al., 2015).

In terms of trends in chl-a, our results agreed with Del Castillo et al. (2019) who found statistically significant increases in chl-a in all sectors of the Southern Ocean, with an especially strong increase in the Northern and Subantarctic zones. Primary production in these zones are seasonally limited by the availability of silicate availability, a constraint which favours phytoplankton communities made up of small flagellates coccolithophores, cyanobacteria, and dinoflagellates (Wright et al., 2010; Balch et al., 2011; Freeman et al., 2019). In these areas, upper-ocean warming in conjunction with higher pCO_2 was anticipated to increase phytoplankton primary production (Steinacher et al., 2010; Boyd, 2019) which agrees with positive trends observed in chl-a (**Figure 2**).

Further south, silicate-rich waters in the southern Subantarctic and Antarctic zones tend to favour diatom-dominated communities (Petrou et al., 2016; Balch et al., 2016; Rembauville et al., 2017; Nissen et al., 2018; Trull et al., 2018), and here we found the trends in chl-a to be more mixed, with both increases and decreases over the last few decades. The Ross Sea was the main Antarctic area with negative trends in chl-a, but we are not aware of *in situ* measurements to confirm this.

To date, the most consistent long-term observations of phytoplankton and factors affecting primary production have been made from coastal research stations, notably along the coastal West Antarctic Peninsula as part of the Long Term Ecological Research Network (LTER; Montes-Hugo et al., 2009; Moreau et al., 2015; Kim et al., 2018; Brown et al., 2019). Over the 20-year LTER record, Kim et al. (2018) found significant positive trends in chl-a at some field stations on the Antarctic Peninsula but decreasing phytoplankton biomass at others. Our study shows increases in chl-a along the West Antarctic Peninsula (**Figure 2**) but the spatial scale of the satellite data is coarser and unreliable within a few km of the shore. Brown et al.

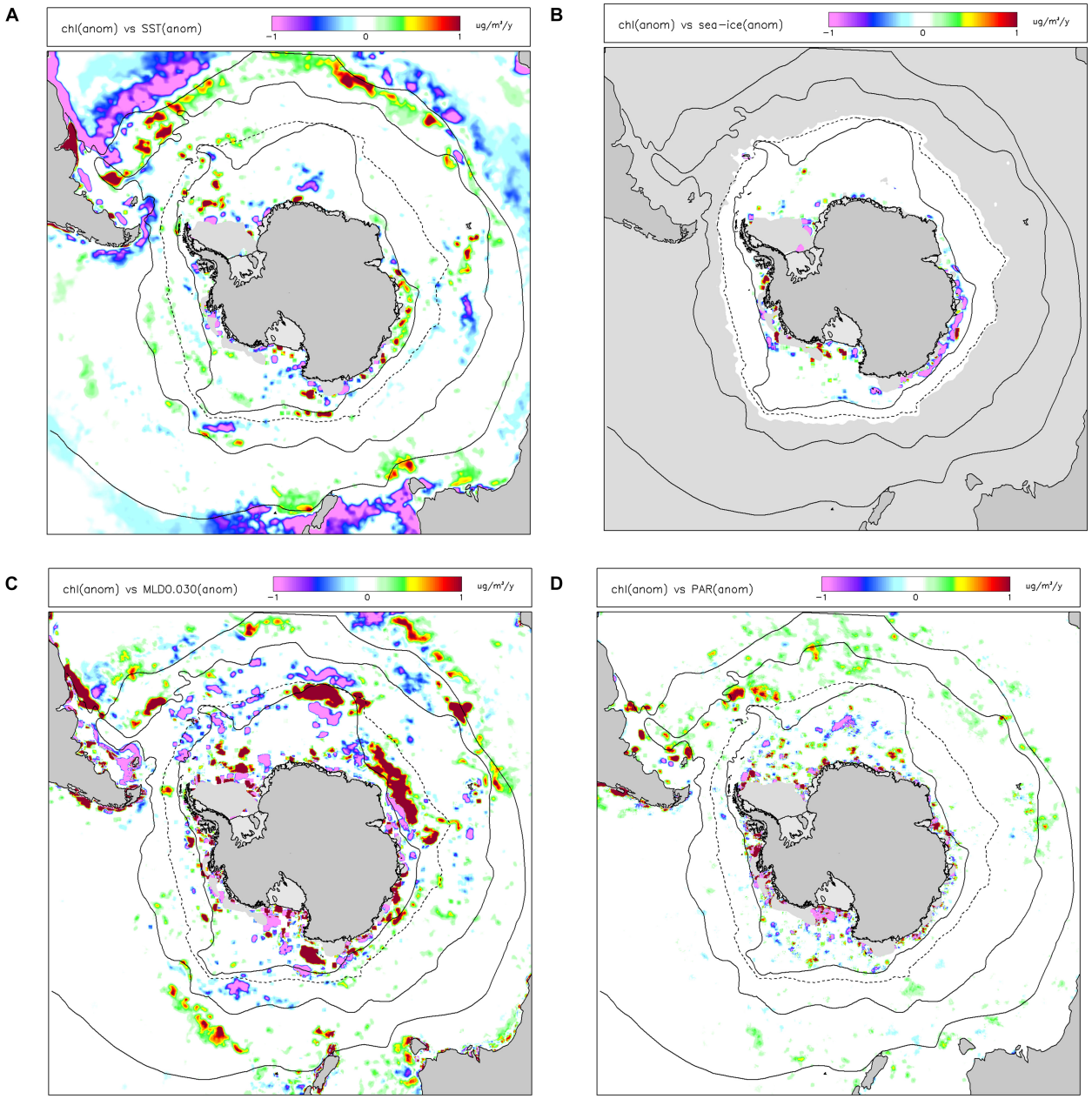

FIGURE 4 | Contribution to linear trends in chlorophyll-a concentration (*chl*) by environmental drivers: **(A)** sea-surface temperature (*sst*); **(B)** sea ice concentration (*sea-ice*); **(C)** mixed layer depth (*mld*); and **(D)** incident irradiance at the sea-surface (*par*). Other information as **Figure 2**.

(2019) found that increasing upper ocean stability along the West Antarctic Peninsula between 1993–2017 due to a combination of wind, sea ice and meltwater dynamics, led to enhanced primary production, especially of diatoms. It appears that local-scale forcing (e.g., changes to sea ice, glacier melting, changes to coastal current patterns), and large-scale climate cycles like El Niño Southern Oscillation (ENSO) and SAM both affect long-term change in Antarctic coastal productivity (Montes-Hugo et al., 2009; Schloss et al., 2014; Kim et al., 2018; Brown et al., 2019; Höfer et al., 2019).

It is notable that trends from *vgpm* were predominantly positive throughout the Southern Ocean whereas trends in *cbpm* were almost exclusively negative (compare **Figures 2D,F**). The *vgpm* data are based on chl-a, so it is expected that trends in *chl* and *vgpm* agree, whereas *cbpm* is based on satellite estimates of the C:Chl ratio and does not use chl-a *per se*. The paucity of *in situ* measurements of NPP in the Southern Ocean (see **Table 2**) means that we cannot empirically compare the accuracy of *vgpm* versus *cbpm*, or carry out independent trend analysis, but we note that the assumption of nitrate-limited phytoplankton

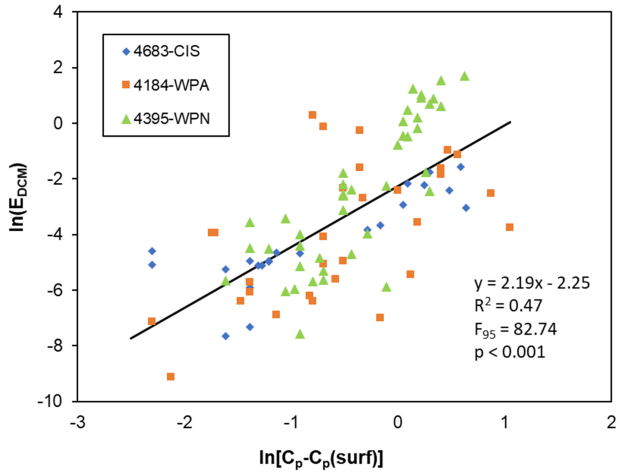

FIGURE 5 | Comparison in log-space between E_{DCM} (irradiance at the base of the mixed layer as Equation 2) and a measure of phytoplankton carbon biomass in the deep chlorophyll maximum (DCM) from profiling floats (C_p-C_p(surf): see text for details).

production implicit in *vgpm* is unlikely to be valid for the Southern Ocean, so *cbpm* may simply be more reliable than *vgpm*. Alternatively, the different patterns of change in chl-a (and *vgpm*) compared to *cbpm* may be associated with a change in community composition. Laboratory and shipboard experiments show that the responses of phytoplankton to environmental changes such as these will be species-specific (Hoppe et al., 2013, 2017; Alvain and d'Ovidio, 2014; Trimborn et al., 2017; Andrew et al., 2019; Strzepek et al., 2019). We speculate here that whereas *vgpm* is essentially showing trends in phytoplankton biomass (via the proxy of chl-a), *cbpm* could also be responding to changes in the microbial community, at least in terms of size classes. Decreases in *cbpm* compared to *vgpm* in the Southern Ocean would be consistent with a shift towards smaller phytoplankton species at high latitudes at the expense of larger species, in line with some predictions (e.g., Rousseaux and Gregg, 2015; Petrou et al., 2016; Deppeler and Davidson, 2017; Trimborn et al., 2017) and observations (e.g., Moline et al., 2004), although changes in size structure vary spatially and with climatic variability such as SAM and ENSO (Montes-Hugo et al., 2008). Higher scattering efficiencies of smaller species would likely lead to lower satellite-estimates of Chl:C ratios and tend to give lower estimates of growth rates (μ) by the *cbpm* (Behrenfeld et al., 2005). This suggestion is unproven and warrants further research.

It is increasingly clear that the response of phytoplankton to multiple stressors acting concurrently cannot be obtained by superimposing their separate responses (Boyd and Brown, 2015; Zhu et al., 2016; Boyd et al., 2016; Luxem et al., 2017; Andrew et al., 2019; Strzepek et al., 2019; Trimborn et al., 2019; Boyd, 2019). Satellite observations in the Southern Ocean show complex patterns of environmental change; surface warming in much of the Northern zone contrasts with slight cooling trends over the last 40 years further south (Maheshwari et al., 2013; Kostov et al., 2016; Sallée, 2018); average sea ice concentration has decreased in the Amundsen Sea but increased in parts of the Weddell, Bellingshausen and Ross Seas (Vaughan et al., 2013; Zhang et al., 2018; Pinkerton, 2019; IPCC, 2019); irradiance at the sea-surface has increased north of the Subantarctic Front and generally reduced to the south over the last 20 years; over the same period, mixed-layer depths have likely shallowed in the Northern zone, and both deepened and shallowed in different parts of the Subantarctic and Antarctic zones (Leung et al., 2015; Pinkerton, 2019).

Given the multifaceted and non-linear response of phytoplankton to these environmental changes, it is perhaps unsurprising that the linear model with 4 forcing factors (*sst*, *ice*, *mld* and *par*) explained only a small fraction (5.6%) of the variance in chl-a over the Southern Ocean (**Figure 3**), and the individual environmental contributions to chl-a trends were negligible (**Figure 4**). Also, we recognize that satellite observations were not available for important factors including ocean pH, pCO_2, and grazing, so these factors were not included as drivers in our empirical analyses of recent changes to chl-a.

Based on long-term sampling from research stations in the Antarctic peninsula region, Kim et al. (2018) showed that variability in chl-a is strongly linked to large-scale climate cycles (ENSO and SAM). Analyses of biogeochemical models are also providing similar insights into these climate-biology relationships acting over large areas (e.g., Hauck et al., 2015). Given the important effects of multi-decadal climate variability such as ENSO and SAM on patterns of primary production, Henson et al. (2010) estimated that ~40 years of continuous satellite ocean–color data was needed to reliably ascribe any trends in chl-a and production to climate change rather than variability. Del Castillo et al. (2019) repeated the analysis for the Atlantic sector of the Southern Ocean and found that ~34 years of continuous data were needed. We caution therefore that the satellite record is still not long enough to separate long-term trends from climate variability.

Deep Chlorophyll Maxima (DCM)

Deep chlorophyll maxima (DCM) can form and persist over several months in the Southern Ocean depending on factors including the state of the seasonal pycnocline and nutricline, rates of nutrient supply, incident irradiance, photoadaptation, grazing and sinking (Parslow et al., 2001; Kemp et al., 2006; Cullen, 2015; Carranza et al., 2018; Uchida et al., 2019). Phytoplankton in the DCM have elevated pigment concentrations, likely indicative of production being light-limited, though iron and silicic acid limitation may also be present (Parslow et al., 2001). The factors affecting when, where and how a deep phytoplankton bloom develops have been extensively studied (review by Cullen, 2015), and although observations generally agree with established hypotheses, the lack of accurate information on key drivers mean that forecasts of DCMs are unreliable (Uchida et al., 2019). For this reason, we presented a new approach to tracking changes in DCM in the Southern Ocean. Based on data from three SOCCOM floats in the Southern Ocean, about half the

TABLE 3 | Annual average mean values and long-term linear trends (1997–2019) for: phytoplankton biomass (chl-a concentration); net primary production (NPP) by the vertically-generalised production model (VGPM) and carbon-based production model (CBPM); and irradiance at the base of the mixed-layer (E_{DCM}) proxy of primary production in the deep chlorophyll maximum (DCM).

	Chl-a		NPP (VGPM)		NPP (CBPM)		E_{DCM}	
	mean	trend	mean	trend	mean	trend	mean	trend
	mg m^{-3}	% y^{-1}	mgC m^{-2} d^{-1}	% y^{-1}	mgC m^{-2} d^{-1}	% y^{-1}	μE m^{-2} d^{-1}	% y^{-1}
Southern Ocean	0.20	0.5**	222	0.8***	164	−0.5	0.10	−3.2***
Zones								
Northern	0.20	0.6***	294	0.7***	199	−0.2	0.12	−0.6*
Subantarctic	0.19	0.4*	168	0.7***	107	−1.3*	0.04	−5.4**
Antarctic	0.36	0.3	200	0.9***	223	−1.0	0.51	−5.1**
Sectors								
Atlantic	0.28	0.7*	258	1.0***	175	−0.8	0.04	−6.6***
Central Indian	0.20	0.4**	212	0.6***	125	−0.8*	0.02	−3.2**
East Indian	0.18	0.5*	223	0.7**	127	−0.4	0.04	−0.7
East Pacific	0.14	0.4**	178	0.7***	188	−0.2	0.31	−1.9***
West Pacific	0.19	0.6**	242	0.9***	191	−0.3	0.20	−0.2
Areas								
AON	0.29	0.8***	416	0.7***	242	−0.2	0.04	−0.4
AOS	0.27	0.6	204	0.8**	131	−1.7**	0.03	−8.7***
AOA	0.34	0.4	165	1.1**	193	−1.2	0.23	−7.1***
CIN	0.21	0.3*	331	0.4***	154	−0.4	0.02	−0.7*
CIS	0.18	0.4*	169	0.6***	104	−1.4*	0.03	−3.6**
CIA	0.25	0.9	157	1.4***	264	−0.3	0.74	−5.2**
EIN	0.19	0.5	299	0.6**	112	0.0	0.01	0.3
EIS	0.16	0.4	162	0.6***	132	−0.9	0.04	−2.0
EIA	0.32	1.3	180	1.7*	285	−0.4	0.49	−3.6
WPN	0.17	0.9***	281	1.0***	224	0.1	0.16	0.0
WPS	0.17	0.2	162	0.6**	103	−1.5*	0.03	−6.0**
WPA	0.40	−0.6	209	0.2	205	−2.1*	0.33	−2.7
EPN	0.12	0.4***	202	0.6***	229	−0.2	0.27	−1.3***
EPS	0.14	0.3	137	0.5*	81	−0.8	0.06	−7.0**
EPA	0.47	0.5	245	1.0	256	−1.1	0.68	−3.8**

*The magnitude of the trend is expressed as a proportion of the mean value (% year^{-1}). Significance of the trend (Mann-Kendall linear trend test corrected for autocorrelation) is shown: *p ≤ 0.05 **p ≤ 0.01 ***p ≤ 0.001.*

variability in the amount of phytoplankton biomass in the DCM was explained by our simple metric of irradiance at the base of the mixed layer (E_{DCM}). The comparison shown in **Figure 5** provides preliminary support for E_{DCM} being a useful metric for tracking changes in DCMs in the Southern Ocean.

The new E_{DCM} metric revealed a significant decrease in NPP at depth in the Antarctic sector of the Southern Ocean (**Figure 6**), but there were not co-located hotspots of trends in chl-a, diffuse irradiance attenuation, or mixed layer depth. The interpretation is that relatively small changes over time to attenuation and mixed-layer depth acting together can lead much more significant trends in E_{DCM}. Further analysis of this preliminary result is recommended as variations in DCMs could have important consequences for ecosystems and biogeochemistry because of higher efficiencies of organic matter export from sub-surface primary production (Tilstone et al., 2017; Henley et al., 2020).

PROGNOSES FOR THE FUTURE

Mixed-Layer Primary Productivity

Based on Earth-systems models, the 'Special Report on the Ocean and Cryosphere in a Changing Climate' (IPCC, 2019; Meredith et al., 2019) included a summary of observed changes in NPP and drivers, and projected future changes. Future projections were based largely on the CMIP5 (Coupled Model Intercomparison Project) which used two Representative Concentration Pathways (RCPs): RCP2.6 (low greenhouse gas emission, high mitigation future) and RCP8.5 (high greenhouse gas emission scenario, 'business as usual', in the absence of policies to reduce climate change). Key conclusions from CMIP5 model projections of NPP (Leung et al., 2015; Meredith et al., 2019) were as follows:

- In the Northern MEASO zone, higher mean underwater irradiance (from reduced mixed-layer depths) and higher iron supply were projected. Overall, this projection points to increased primary production in the mixed-layer and

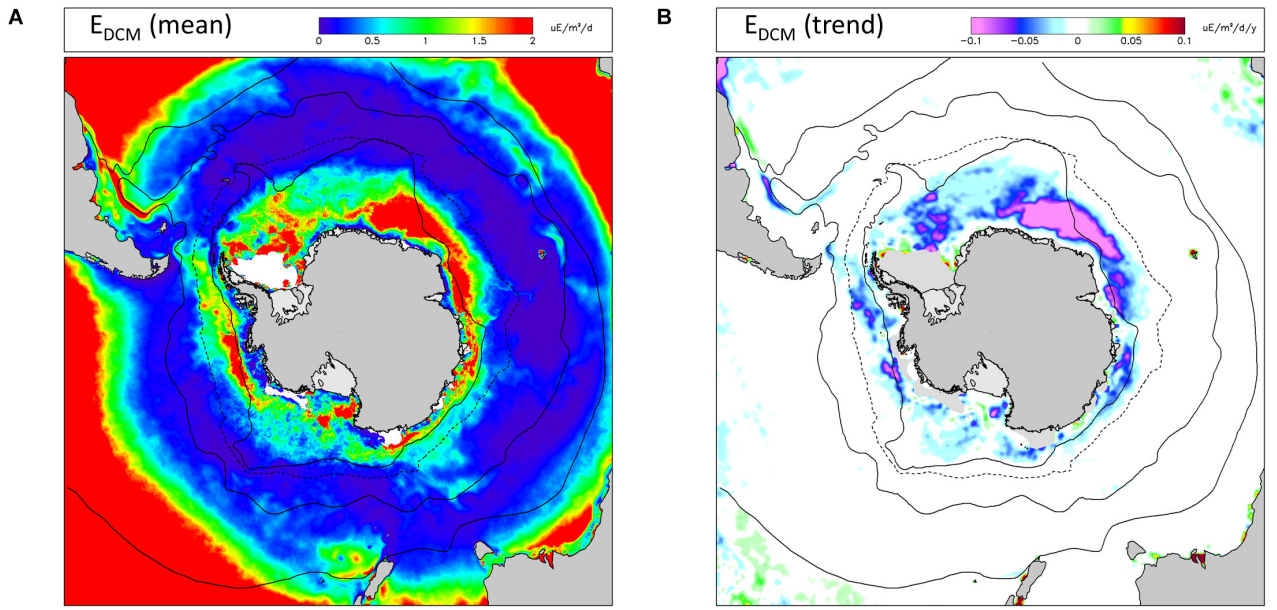

FIGURE 6 | Irradiance at the base of the mixed layer (E_{DCM}) as a proxy for potential primary production in the deep chlorophyll maximum (DCM). **(A)** long-term (1997-2019) mean values; **(B)** linear trends (Sen slopes) over the same period. Other information as **Figure 2**.

increased phytoplankton biomass (Leung et al., 2015; Meredith et al., 2019). These model projections are consistent with recent observations provided in the current study (chl-a, *vgpm*) and elsewhere (e.g., Le Quéré et al., 2005; Doney, 2006; Del Castillo et al., 2019).

- In the Subantarctic zone, deeper summertime mixed-layer depth together with increased cloud albedo were projected to lead to lower average irradiance in summer, leading to lower chl-a and NPP (Leung et al., 2015). This result agreed with a modelling study by Moore et al. (2018) which found that changes to sea ice and circulation patterns under climate warming scenarios would lead to a global reorganization of nutrient distributions and a steady decline in global-scale marine biological production. However, recent satellite observations show recent increasing rather than decreasing trends in chl-a in this zone (Del Castillo et al., 2019; present study).
- In the Antarctic zone, CMIP5 models generally suggested that less seasonal sea ice and a warming ocean will lead to greater iron supply, higher underwater irradiance and thence to increases in chl-a and NPP (Leung et al., 2015; Rickard and Behrens, 2016). These projected increases agree with recent trends in chl-a and *vgpm* (present study), except in the Ross Sea where chl-a, *vgpm* and *cbpm* all show negative trends.

Confidence in future projections of chl-a and NPP remains low (IPCC, 2019). The strongest drivers of future changes in NPP in CMPI5 models were iron availability and irradiance; acidification and temperature *per se* were less important (Leung et al., 2015). The balance between different iron-supply mechanisms (i.e., vertical mixing *versus* aeolian *versus* ice-mediated supply) are hence crucial to our ability to forecast future changes to the productivity of the Southern Ocean (Boyd et al., 2012; Boyd et al., 2014; Leung et al., 2015; Hutchins and Boyd, 2016; Hopwood et al., 2019). High spatial and seasonal variability in the relative importance of various iron-supply mechanisms, coupled with a lack of long-term observations, the simultaneous change of a number of environmental conditions, and the complexities of phytoplankton response to different environmental drivers hence severely limit our ability to anticipate these changes (Hutchins and Boyd, 2016; Mongwe et al., 2018; Freeman et al., 2019; Smith et al., 2019; Hopwood et al., 2019). In the longer term, longer-time series of satellite observations, increasingly sophisticated laboratory experiments, and more co-ordinated and extensive Antarctic observations such as the Southern Ocean Observing System (SOOS) are expected to help provide the information required to improve these future projections (Newman et al., 2019).

Deep Chlorophyll Maxima (DCM)

Prognoses of future changes in production in the DCM in the Southern Ocean are not reliable and Earth system models focus instead on depth-integrated estimates of NPP (e.g., Leung et al., 2015; IPCC, 2019). Better satellite-based observation of the occurrence of DCMs in the Southern Ocean using the simple metric described here (E_{DCM}) and better *in situ* observations using autonomous technology could improve this situation in the future. In particular, the advent of biogeochemical Argo floats (Rembauville

et al., 2017; Briggs et al., 2018; Carranza et al., 2018), the SOCOMM project (Riser et al., 2018; Uchida et al., 2019) and Southern Ocean and Climate (SOCLIM) floats[1] represent a major step forward.

Primary Production by Sea Ice Algae

Although not a focus of the present study, we note that tracking and anticipating changes to primary production in the Southern Ocean should include that within sea ice (Arrigo, 2014; Saenz and Arrigo, 2014; van Leeuwe et al., 2018) and beneath it (Arteaga et al., 2020). Although sea ice algae only contribute ∼1% of total Southern Ocean primary production, and 12–50% of total primary production in the sea ice zone (Kottmeier et al., 1987; Grossi et al., 1987; Saenz and Arrigo, 2014; van Leeuwe et al., 2018), sea ice algae are of disproportionate ecological importance because their production occurs in locations and at times when production in the water column is low (Quetin et al., 1996; Saenz and Arrigo, 2014; McCormack et al., in review). As such, sea ice algae are a crucial bridge between low and high productivity periods for many mid-trophic level species, such as Antarctic krill (*Euphausia superba*; Daly, 1990; Smetacek et al., 1990; Loeb et al., 1997; Kohlbach et al., 2017; Meyer et al., 2017), and Antarctic silverfish (*Pleuragramma antarctica*) (Guglielmo et al., 1998; Vacchi et al., 2004).

Drivers of primary production by sea ice algae include ice-extent and thickness, incident light availability, and nutrient supply (Kottmeier and Sullivan, 1990; Arrigo et al., 1998; Arrigo, 2014; Hobbs et al., 2016; Tedesco and Vichi, 2014), though temperature and salinity can be important (Tedesco and Vichi, 2014; Saenz and Arrigo, 2014). Variations in snow depth will influence both light penetration into sea ice, and nutrient input (Saenz and Arrigo, 2014). Both laboratory manipulations and *in situ* experiments indicate that sea ice algae are little affected by changes to pH (McMinn, 2017).

Complex models have been developed to simulate the large-scale primary production by sea ice algae (Arrigo et al., 1991, 1997; Arrigo and Sullivan, 1994; Saenz and Arrigo, 2012; Arrigo, 2014; Tedesco and Vichi, 2014) but these have neither been well validated to date (Meiners et al., 2012) nor used to investigate long-term changes in sea ice algae primary production. Furthermore, no future projections of changes to sea ice algae production are available in CMIP5 models (IPCC, 2019).

In the longer term (∼100 years hence) it is likely that sea ice algae primary production will decrease in line with reducing sea ice extent and concentrations throughout the Southern Ocean (IPCC, 2019), but these changes are likely to be spatially heterogenous and non-linear (van Leeuwe et al., 2018). We also note that the ecosystem consequences of a reduction of primary production in sea ice could be significant and far reaching (Atkinson et al., 2004; Meyer et al., 2017; Saenz and Arrigo, 2012; Arrigo, 2014; Tedesco and Vichi, 2014; McCormack et al., in review) so this represents a major gap in forecasting capability.

[1] http://soclim.com/index.php

SUMMARY FOR POLICY MAKERS

Summary Tables

A summary of recent observed changes and anticipated future changes (**Table 4** and **Figure 7**) shows that primary production in the Southern Ocean will likely increase over the next 100 years, with more primary production in the water column and less in sea ice. The distinctive nature of the microbial community of the Southern Ocean (i.e., the dominant species of phytoplankton, phenology (seasonality) and spatial distribution of primary production) will likely reduce, with shifts towards communities more dominated by small and flagellated species, and with endemic Southern Ocean phytoplankton species losing out to temperate species (Deppeler and Davidson, 2017). Year-to-year variability in primary production in the Southern Ocean will likely increase with increasing prevalence of marine heatwaves (Oliver et al., 2019). Recent increases in sea ice concentration (and potentially associated sea ice algae production) will likely reverse in the next few decades and decrease consistent with less ice in a warming Southern Ocean (IPCC, 2019). The importance of local-scale forcing means that forecasting the effects of climate change on coastal primary production, crucial to the reproductive success of many endemic Antarctic species, is especially challenging (Montes-Hugo et al., 2009; Kim et al., 2018). The effects of future changes to primary production are likely to be greatest for those Southern Ocean species with life-cycles intimately linked to seasonal sea ice growth and retreat, including 'keystone' species such as Antarctic krill and silverfish (Smetacek et al., 1990; Quetin et al., 1996; Loeb et al., 1997), and their predators (McCormack et al., in review).

Key Messages for Policy Makers

KM1

Satellite observations show mainly increases in phytoplankton biomass in the Southern Ocean over the last 20 years (1997–2019) (*high confidence*), but the direction of recent changes to primary production are generally not known except to say that it is likely that primary production has decreased in the Ross Sea over the recent past (*medium confidence*).

KM2

At present the satellite record is not long enough to separate long-term trends from climate variability, so we cannot say whether these observed trends will continue in the future (Henson et al., 2010; Del Castillo et al., 2019) (*high confidence*).

KM3

Over the next 100 years, Earth system models project increasing primary production in the northern and Antarctic MEASO zones but decreases in the Subantarctic zone (Leung et al., 2015; Rickard and Behrens, 2016) (*low confidence*). Low confidence in these projections arise from the difficulty in mapping supply mechanisms for the key nutrients of iron and silicate in the Southern Ocean and understanding the effects of multiple stressors on different species of Antarctic phytoplankton

TABLE 4 | Summary of recent observed changes (satellite data) and future projections by MEASO areas of the Southern Ocean.

Sectors	Recent observed trends				Future projections		
	Zones				Zones		
	Northern	Subantarctic	Antarctic	All zones	Northern	Sub-antarctic	Antarctic
Atlantic	↗↗– –	–↗↓↓	–↑– ↓	↗↗– ↓	↑	↓	↑
Central Indian	↗↗– ↘	↗↗↓↓	– ↑– ↓	↗↗↘↓	↑	↓	↑
East Indian	– ↗– –	–↗– –	–↑– –	↗↗– –	↑	↓	↑
West Pacific	↗↗– –	–↗↓↓	– –↓–	↗↗– –	↑	↓	↑
East Pacific	↗↗– ↓	– ↗– ↓	– – – ↓	↗↗– ↓	↑	↓	↑
All sectors	↗↗– ↘	↗↗↓↓	– ↗– ↓	↗↗– ↓	↑	↓	↑

*Arrows show recent trends, in order: phytoplankton biomass in the mixed-layer (chl-a concentration, 1997–2019, chl); net primary production (NPP, 1997–2019) by Vertically Generalised Production Model (vgpm) and by Carbon Based Production Model (cbpm); irradiance at base of the mixed-layer (1997–2019, E_{DCM}). The arrows show: ↑ indicates a significant increasing trend > 1% y^{-1}; ↗ significant increasing trend < 1% y^{-1}; – no significant trend over the period analysed; ↘ significant decreasing trend < 1% y^{-1}; ↓ significant decreasing trend > 1% y^{-1}. So, for example, "–↑↘–" indicates no trend in chl, strongly increasing trend in vgpm, decreasing trend in cbpm, and no trend in E_{DCM}. 'Future projections' are based on CMIP5 models (Leung et al., 2015; **Figure 1**) just for NPP: ↑ increases projected for the future; – no changes (or a mixture of increases and decreases) projected; ↓ decreases projected for the future.*

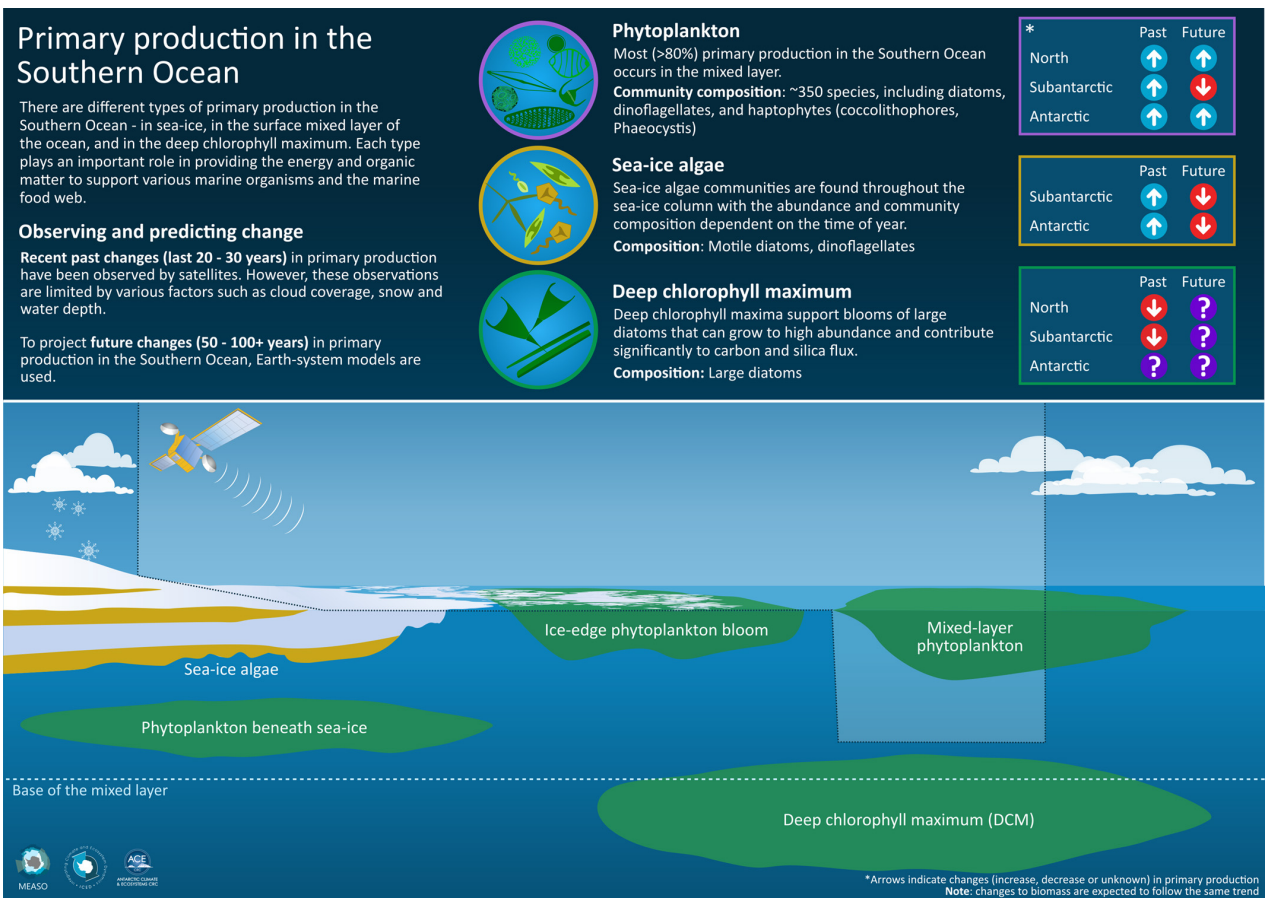

FIGURE 7 | There are different types of primary production in the Southern Ocean – in sea ice, in the surface mixed-layer of the ocean, and in the deep chlorophyll maximum (DCM). Only some of these types of primary production can be observed by satellite over the last 20–30 years. Earth-system models can project future changes to primary production in the next 50–100 years. Changes vary between the Northern, Subantarctic and Antarctic zones.

(Hutchins and Boyd, 2016; Boyd et al., 2016, 2019; Deppeler and Davidson, 2017; Freeman et al., 2019; Meredith et al., 2019; Trimborn et al., 2019).

KM4

As well as affecting the total amount of primary production in the Southern Ocean, climate change will likely alter seasonal patterns in production (phenology) and the relative abundances of different types of phytoplankton (Wright et al., 2010; Petrou et al., 2016; Balch et al., 2016; Kaufman et al., 2017; Nissen et al., 2018; Trull et al., 2018) (*high confidence*). These changes will affect zooplankton, have ecological consequences across Southern Ocean food-webs including on keystone species and top predators (Atkinson et al., 2004; Moline et al., 2004; Pinkerton and Bradford-Grieve, 2014; Johnston et al., in review; McCormack et al., in review) (*high confidence*).

KM5

Primary production by sea ice algae will likely decline in the future as sea ice extent shrinks (*medium confidence*). Because of the ecological importance of sea ice to a range of key Southern Ocean species, the reduction in Southern Ocean sea ice and its associated primary production could lead to a critical tipping point in Southern Ocean ecosystems (*medium confidence*).

KM6

Better methods of monitoring change to phytoplankton and sea ice algae are needed to improve confidence in future projections of primary production in the Southern Ocean (*high confidence*). Efforts to maintain long-term coastal observations (e.g., Palmer Long Term Ecological Research Network LTER, e.g., Kim et al., 2018), improve satellite observations, co-ordinate field sampling, and develop and deploy autonomous instrumentation in the Southern Ocean are essential to assess long-term trends (Newman et al., 2019) (*high confidence*). Long-term, multi-trophic level monitoring is required to understand the effects of changes to primary production on middle and upper level predators such as krill, salps, fish, seabirds and marine mammals (*high confidence*).

FREQUENTLY-ASKED QUESTIONS (FAQ)

What is primary production and why is it important?	Primary production is the formation of organic matter by photosynthesis. It is the process by which energy enters the marine food-web. All marine animals ultimately rely on organic matter created by primary production.
Why can't satellites see ice algae?	Ice algae typically grow within or below sea ice, so that the sea ice stops satellites seeing the colour of the algae directly.
How does climate change affect primary production?	Primary production depends primarily on the amount of light available and on the concentration of nutrients in sea-water. If the amount of cloud cover, sea ice or snow changes, this affects the amount of light entering the water column. The depth of mixing in the ocean also affects the light availability. Many processes affect nutrient supply, including those associated with water column mixing, dust input, circulation patterns, icebergs, snow and sea ice. There are lesser effects on phytoplankton due to warming, acidification, carbon dioxide concentration and indirect effects from changes to zooplankton grazers.
Why is it so hard to predict what will happen to phytoplankton?	There are many different species of phytoplankton in the Southern Ocean and all respond differently to environmental changes. The effects of multiple stressors acting on species at the same time also makes it difficult to anticipate phytoplankton responses to global change.
Why do the predictions vary with location?	Ocean physics differ drastically among regions of the Southern Ocean, which means that environmental changes in the Southern Ocean are not the same everywhere. For example, some areas are warming and other cooling; some areas have more ice and some less. Also, phytoplankton communities are not the same everywhere, and different species respond to environmental change in different ways.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: https://oceandata.sci.gsfc.nasa.gov/, http://sites.science.oregonstate.edu/ocean.productivity/, https://nsidc.org/, https://www.ncdc.noaa.gov/isccp.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.592027/full#supplementary-material

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Enabling Enduring Evidence-Based Policy for the Southern Ocean Through Cultural Arts Practices

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This paper provides a perspective on how art and cross-cultural conversations can facilitate understanding of important scientific processes, outcomes and conclusions, using the Marine Ecosystem Assessment for the Southern Ocean (MEASO) as a case study. First, we reflect on our rationale and approach, describing the importance of deeper communication, such as through the arts, to the policy process; more enduring decisions are possible by engaging and obtaining perspectives through more than just a utilitarian lens. Second, we draw on the LivingData Website [http://www.livingdata.net.au] where art in all its forms is made to bridge differences in knowledge systems and their values, provide examples of how Indigenous knowledge and Western science can be complementary, and how Indigenous knowledge can show the difference between historical natural environmental phenomena and current unnatural phenomena, including how the Anthropocene is disrupting cultural connections with the environment that ultimately impact everyone. Lastly, we document the non-linear process of our experience and draw lessons from it that can guide deeper communication between disciples and cultures, to potentially benefit decision-making. Our perspective is derived as a collective from diverse backgrounds, histories, knowledge systems and values.

Keywords: Southern Ocean, Antarctic, Indigenous knowledge, climate science, interdisciplinary, cross-cultural

INTRODUCTION

Communicating and understanding knowledge from a range of sources, views and diverse values are fundamental to making robust and enduring decisions (Gorddard et al., 2016; McElwee et al., 2020). In this era of the Anthropocene there is greater awareness of global values (Gurney et al., 2017; Martin et al., 2020), resulting in people across the globe connecting with regions other than those they inhabit. This is especially true for the global value of the Southern Ocean which

regulates key physical, chemical, and ecological processes (Grant et al., 2013; Cavanagh et al., 2021, Murphy et al. to be published in this research topic). This perspective is an invitation to enhance understanding of scientific data and knowledge from different cultural backgrounds through the arts.

Understanding does not hinge on trans-disciplinary and cross-sectoral academic communications alone, but on new and ancient evidence from people listening and responding to changing patterns in lands and waterways. This is demonstrated by artwork in everyday life, conveying messages in many different forms. In this paper we explore and highlight this more holistic approach for understanding and communication, through scientific data and art.

An increasing body of literature identifies how Indigenous perspectives move us away from a strictly utilitarian approach in the present, to a more socially and globally aware approach for the future (e.g., McElwee et al., 2020; Ogar et al., 2020). The latter approach is one that is grounded in deep knowledge of the past leading to the present, and provides a pathway toward a preferred future. Central to the approach we describe here is expression through many art media, to build on messages otherwise confined to scientific data and analyses alone; the arts are used for deep listening to the data and to Country, to expand understanding beyond specific science terminology, to appeal to the senses for deeper, more memorable engagement and relationships.

We regard the region of Antarctica and the Southern Ocean as a prime example of where deeper communication can help decision-making because of the heterogeneity of cultures and people directly involved in the Antarctic Treaty system. While nobody calls Antarctica home, the region is important globally for many ecosystem services (Grant et al., 2013, Cavanagh et al. to be published in this research topic; Murphy et al. to be published in this research topic) and its management relies on the best available science (Constable et al., 2000). While the work of the Commission for the Conservation of Antarctic Marine Living Resources is informed by a Scientific Committee, the interpretation and use of the science may be driven by different national norms and perspectives. Moreover, the world's people have a deep, often unacknowledged, connection with the region and value it greatly, despite not living there. Sound management of the region is dependent not only on the science but also an ability to understand different perspectives, cultural sensitivities and global priorities.

This paper is developed in the context of this region, to show how art and conversational processes can be used to facilitate not only understanding of science but also different perspectives that may not just be about use of the region but also about its value to life everywhere. We adopt the general approach used in Indigenous cultures to embed oral knowledge in stories that are introduced from childhood as moral tales. These tales provide a context for the growth of knowledge as the child grows. We approach this work with the moral perspective that we need to come together to share our experience and feelings around such issues in order to come to a unified action for ocean cultural management. We acknowledge that this approach is available to everyone (Shawn Wilson, 2008). This approach is not foreign to the scientific domain. Recent controversies in the scientific literature about how marine fisheries should be managed have been harmonised through workshops (conversations) of scientific experts from across the spectrum views. These workshops and joint studies have yielded important lessons, intellectual growth and understanding amongst this wide group (Worm et al., 2009).

The concepts for the paper are developed in three sections. The first section reflects our rationale and approach, describing the importance of deeper communication, such as through the arts, to the policy process; more enduring decisions are possible by engaging and obtaining perspectives through more than just immediate utilitarian outcomes but with a longer term view. The second section draws on the LivingData[1] initiative which is using art in all its forms to bridge differences in knowledge systems and their values. LivingData provides examples of how Indigenous knowledge and Western science can be complimentary, and how Indigenous knowledge can show the difference between historical natural environmental phenomena and current unnatural phenomena, including how the Anthropocene is disrupting cultural connections with the environment that ultimately impact everyone. Our perspective is derived from a group with different backgrounds, histories, knowledge systems and world views. In the final section we document the process of this experience and draw lessons from it, on how deeper communication could benefit future decision-making.

RATIONALE AND APPROACH

Antarctica and the Southern Ocean are central to global life. They are the pulsing heart of our planet, regulating, refuelling and balancing (Fraser et al., 2020; Murphy et al. to be published in this volume) [http://www.lunartime.net.au/content/library/sandtalkminds/ancestor/ocean-dance-ancestor.php Ocean dance 2020. Lisa Roberts (animation), Paul Fletcher (music), Stephen Taberber (music); http://www.lunartime.net.au/content/library/sandtalkminds/pattern/ocean-dance-poem-pattern.php Southern Ocean Dance Poem 2020. Andrew Constable (poem), Lisa Roberts (dance, motion capture), Paul Fletcher (music, animation, post production)]. The Antarctic Circumpolar Current merges with deeper, warmer, nutrient-laden waters to create the frenzy of birds, fish and whales feeding on krill, which feed on phytoplankton. In the southern regions of the world we brace against its winter weather patterns on our distant shores, and watch whales, seals and seabirds touch these more northern regions. In this way we directly experience the ongoing connection between the Antarctic, the Southern Ocean and ourselves. Though we are not always aware of it, we are all deeply connected to the southern polar region.

Since ancient times we humans have known ourselves as part of nature. We have known and respected our relationships with lands and waterways necessary for sustaining life. Indigenous knowledge of this relationship endures through experience, sharing and consensus between people. While Western science has been credited for discovering and documenting intrinsic connections between humans and the natural environment,

[1]https://www.livingdata.net.au/

such discoveries and observations are older than our Western records. They have been, and are maintained through stories, merged and layered with messages about how we must behave as custodians of Country. This knowledge is passed on by generations of communication through the arts, reflecting the diverse forms in which knowledge is expressed and remembered through all the senses.

Being so geographically removed it can be difficult for us to recognise or engage with the role of the Southern Ocean in our lives. This is exemplified by the disconnection of wider society from the issues of climate change and the melting poles. While we can be shown and told about its occurrence, and lectured on its effects, our general lack of physical relationship limits our empathy. We can create empathy by sharing scientific knowledge (as stories, narratives) using methods that facilitate connecting tangible data and abstract concepts to more deeply felt emotional responses in our audience. Storytelling through the arts has been pivotal for this purpose for millennia. Re-embracing the power of the arts for sharing knowledge may allow us to establish an emotional relationship between disparate places and diverse peoples.

In the face of increasing pressures on Earth's systems, change is happening faster than we can acquire scientific data to guide environmental management. Pattern-matching between Indigenous stories and Western data, combined with their cultural endurance through arts, demonstrates the wealth of knowledge contained within the stories (Nunn and Reid, 2016; Nunn, 2018). By using established experience-based knowledge that is contained and preserved in stories that have been echoed through time, we may uncover insights into how best to face our current environmental crises. Listening to collective knowledge, we can start to fill the data gaps that will enable sustainable decision making.

Our purpose is to bring together stories from modern science and traditional cultural knowledge systems, acknowledging that wise decisions must be made now, for sustaining humanity. We invite readers to understand (through science) and to experience (through art) diverse ways of thinking that together give a holistic view of what is necessary to assess and communicate the value of the Southern Ocean globally.

In doing so, we are endeavouring to expand scientific understanding through the arts, to more fully inform policy developers and decision makers about the health of the Southern Ocean that impacts on the health of people worldwide. Here, we introduce ourselves as co-authors of a project that will evolve over the next three years (see **Supplementary Material**). We explore the role that art plays in expressing knowledge, perception, scientific evidence and cultural values across temporal and spatial dimensions.

Our approach utilises a grounded, inclusive holistic methodology. This means that through conversation, sharing of experience, stories and art, and discussing the relationships between these stories, we develop a collaborative story that reveals connections between the different perspectives. In this way we anticipate that people will recognise their own voices as part of the process of knowledge production that is necessary for expanding understanding and adapting to climate change.

Rather than adopting the linearity of a pre-specified scientific process, we used a connected round-table discussion that brings holistic understanding. This form of knowledge sharing as a group follows an Indigenous model of yarning (Bessarab and Ng'andu, 2010) and allows further integration of knowledge across this interface.

We determined that the main method to facilitate communication, understanding and relationships between different knowledge and cultural systems is the sharing of stories on location, so we use an interactive map (MEASO Cultural Connections, 2021) which features the placement of different stories and perspectives on a world map.

The MEASO website map not only collates stories and their relationships to one another but also invites others to continue the expansion of scientific understanding in the community through experience of the stories told on virtual Country and the arts presented therein. The placement of each story (see **Table 1**) from the authors onto the map relates to whether it is a perspective of Southern Ocean ecosystems generated from within the region, or from afar, through cultural understandings. Our stories are then categorised by ways of thinking that together work to give a more holistic view (see Yunkaporta, 2019). Geographic mapping of stories on the map aims to inform and inspire policy decisions with scientific accuracy and artful engagement, to support the sustainable management of the Southern Ocean ecosystem that plays a key role in the global climate system.

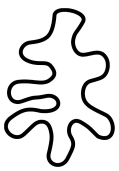
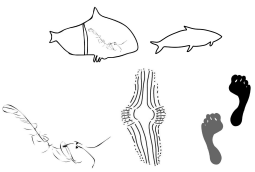
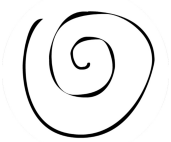
By journeying within this map people from different perspectives can see how the stories tie together and build a picture of a world that has been changing for millennia and is changing more rapidly now. Included in our group of authors are scientists, artists, scientific artists and artistic scientists. We include Indigenous authors from various countries along with stories they have shared with us and drawn significance into our work over many years.

CIRCUMPOLAR CONNECTIONS: STORIES SURROUNDING THE SOUTHERN OCEAN

Weaving provides a useful analogy for the mind's process of making sense; what often begins as a tangle of threads, once woven, creates a whole that is often both beautiful and useful. Through 'sense weaving' we create connections that together, hold the form and shape of our weave, avoiding tangling or unravelling. For the mind, interweaving of ideas or information is often assisted by their delivery through story. For this reason, throughout history, stories have been used to impart lessons, ensuring the safety and survival of successive generations.

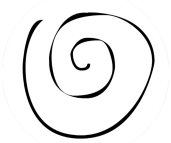
Stories are a central part of cultural identity and through continual re-telling, help awaken a broader awareness and relationship to the interconnectedness of life. Stories are formed with deep connections to place, sometimes called Country, and are typically only relevant to that area. As the environment changes between places, so too do the stories, although commonalities are often found. These commonalities

TABLE 1 | Stories conveyed through the interactive web-based map of MEASO Cultural Connections (http://measocc.teachingforchange.edu.au/).

Living Data Stories	Entities involved	Cultural knowledge, Values	Ecological concepts, Lessons
Scientific Modelling http://measocc.teachingforchange.edu.au/node/130 How can a scientific model be communicated through art? Location: Margate, Tasmania/Palawa Kani 42.9769°S, 147.3083°E	People	Since ancient times, cultural leaders have observed and recorded patterns in nature. They have predicted, experimented and gathered evidence of behaviours needed to sustain life.	Reciprocity between peoples and environments maintains balance in nature. People's failure to recognise natural patterns and disruptions to these patterns can lead to ecological collapse.
Krill Sex http://measocc.teachingforchange.edu.au/node/101 A first time look at the complete mating dance of Euphausia superba (Antarctic krill) is expressed as art and scientific data. Location: Southern Ocean/Animation (language of change and transformation) 65.87°S, 88°E	Phytoplankton, Krill, People	There are places where people must not intrude, in order to ensure that natural cycles of life endure for future generations.	Disturbing breeding grounds of keystone species threatens whole ecosystems. The arts can be used for deep listening to nature, and to combine scientific data and expressions of relationship.
Ocean Dance http://measocc.teachingforchange.edu.au/node/147 Animation brings together many meanings and understandings of the Southern Ocean: flows of ideas, currents, nutrients, waste, perspectives, temperatures, ice, global connections.	Ocean currents, Cultural flows, People	Flows of new and ancient cultural knowledge inform protocols for developing and sustaining relationships between peoples and places.	Global systems evolve through complex interactions between smaller systems. Dance, music and animation can be used to express the complex interactions that turn the clockwise Antarctic circumpolar flows into the anticlockwise flows of the Arctic.
The art of making images http://measocc.teachingforchange.edu.au/node/155 An empirical study shows relationships between First Nations people of Tierra del Fuego, the land, water and spiritual systems. Location: Tierra del fuego/Yagan, Selk'nam and Kaweskar 54.8054° S, 68.3242° W	 People, Whales, Dolphins, Pinnipeds, Birds, Fishes, Molluscs	Knowledge of balance, union and preservation of natural resources is perpetuated through arts that embody ancestral beings and spirits with deep connections to the fauna and landscape.	People co-evolve as part of environments. Eliminating waste can sustain peoples, lands and waterways. Making art that appeals to spirit connections can strengthen human identity as part of the whole natural system.
Gumbayngirr story http://measocc.teachingforchange.edu.au/node/118 Sea level rise stories from Western science and Indigenous cultural knowledge complement each other. Location: Ngambagabaga (Nambucca Heads)/Gumbaygnirr/Animation 30°S, 153°E	 Whales, Fish, Krill, Algae, People	Ceremonies maintain knowledge of natural climate patterns and reciprocity between creatures of the ocean and the land.	Life evolves through interactions between entities in waterways and on land. Artistic and mythical expressions of ancient eye witness accounts of such events as sea level rise can make these stories memorable and believable, and so better prepare people to adapt to change.
Whales return to land http://measocc.teachingforchange.edu.au/node/150 People across the globe relate to whales and so connect with the Southern Ocean which regulates key physical, chemical, and ecological processes. Location: Gulaga/Yuin 36.378°S, 150.13°E	Whales, Snakes, People	Whales come to land to regurgitate the lore so that land and sea can know each other as relations (Pascoe, 2019).	Connections endure between terrestrial and oceanic entities, physically, biologically and spiritually, as knowledge endures and expands as new and ancient knowledge systems are valued, understood and practiced.
Way of the Turtle: Exchanging Breath http://measocc.teachingforchange.edu.au/node/140 The primal spiral form calls for taking time to listen and deeply observe and to appreciate the world around us. Location: Parihaka/Mâori/Yorta Yorta 39.3°S, 173.0°E	 River, Blood, Sweat, Tears	The river represents our bloodstream, the mist represents our sweat and the rain represents our tears.	An ecosystem evolves between entities relating in ways that benefit the system as a whole. Human relationships to Earth are expressed across cultures in song, symbol and story. So the spiral can be repeated in diverse forms, times and contexts, to deepen and share individual experiences of relationships in cycles of Earth.

(Continued)

TABLE 1 | Continued

Living Data Stories	Entities involved	Cultural knowledge, Values	Ecological concepts, Lessons
Shell necklace http://measocc.teachingforchange.edu.au/node/163 Indigenous knowledge can show how the Anthropocene is disrupting cultural connections with the environment that ultimately impact everyone. Location: Cape Portland, Tasmania/Tebrakunna Country 40.782°S, 148.026°E	 Yolla (short-tailed shearwater), Kelp, Sea shells, People	Sea country traditional knowledge is disappearing as coastlines recede, and oceans become more acid.	Disruptions to natural climate patterns disrupt traditional cultural practices. Changing coastlines in Tasmania are affecting nesting of yolla, a traditional food. Rainbow kelp shell (*maireener*), an iconic shell for necklace-making by the tabrakunna women, are in decline.

These stories have Indigenous, scientific, or artistic origins, each reaching into cultural traditions and values as well as providing ecological concepts and lessons. Links are to the pages underlying the map which provide the details and background of these stories. Location provides a description of the location and the approximate Latitude (decimal degrees) and Longitude (decimal degrees) from where these stories emanate and/or of where these stories relate.

can instruct us on how to live harmoniously and sustainably with our surroundings. For example, Miriam-Rose Ungunmerr's discussion around Dadirri (deep listening) resonates not only for the Ngangikurungkurr people of the Daly River area of the Northern Territory in Australia (references to Indigenous Australia can be located on the AIATSIS Map, Horton, 1996), but provides a lesson that we can all learn from – to take the time to listen and deeply observe one's surroundings and to appreciate the world around us (Ungunmerr, 2017).

Historically, storytelling and the communication of ideas evolved through a diverse range of mediums: sand painting, dance, oral recitation, tapestry, sculpture and song, all of which enabled reliable transfer and translation of knowledge through time (Davidson, 2020). These mediums also invoke powerful emotional responses, helping us make deep empathetic connections to the elements within the story. Perhaps First Nations storytelling techniques can straddle the boundary between cultures, bringing collaboration and harmony between knowledge systems and evoke emotional engagement with environmental issues. Maybe through this lens we can effectively communicate the importance of ecological sustainability to a broader audience. There is willingness and capacity in Indigenous peoples to embrace European knowledge systems into their own where beneficial, for moving forward together for the common good. 'We are not exclusive, pushing others away. . . even in our grandparents' time, we were not a village of closed, unchanging tradition' (Bashkow, 2020, p.189). Interlacing narratives from different perspectives is generative. Melding and cross-referencing stories creates movement from fixed to evolving relational views.

Perceptions of history and culture based on traditional colonial concepts and values limit the capacity for interrelated understandings by privileging a single linear voice, thereby limiting the building of relationships. Linear story-telling on its own cuts one line of thought like an argument for possession, definitively naming and claiming through language that forms separation, not relationship; this dominant voice erases the stories of any who do not identify with this experience of history, including the exclusion of the many Indigenous voices that have for so long enabled enduring knowledge for sustaining life (Olivier, 1986; Todorov, 1987). As in nature, old and new patterns unfold in storytelling. Consider genetic conservation in the evolution of the human brain, with its layers of ancient and recent cognitive capacity enabling ". the unparalleled explosion in behavioural repertoire from tool use and language to science and art." (Bruce T. Lahn. Howard 2008. Hughes Medical Institute, Department of Human Genetics, University of Chicago, Chicago, IL, United States).

Consider the conservation of congregational ceremony of Indigenous Australians, the corroboree, where stories from far and wide are brought and shared over days through multifarious and layered forms of expression. Everyone is included in the creation of ceremony, with contributions from children through to Elders. Consider in contrast, international scientific conferences where the structure is designed to give voice only to those deemed important. Consider the power of the collaborative and coalescing practices experienced during a corroboree and how they effectively give a richness to the subject of exploration.

Pattern matching (**Figure 1**) allows us to recognise the value and endurance of stories. In the Yuin story of Guruwal (the whale, known by various names by different First Nations people), we find strong parallels (pattern matching) between Indigenous knowledge sharing and Western science. Australian Yuin Nation cultural knowledge tells us that Guruwal ". . .will come back to the land and regurgitate the lore so that the lore can be complete and the land and sea can know each other'[2]. Western science tells us whales came from the sea, evolved on land into a wolf-like creature, *Pakicetus*, before returning to the sea, first as amphibious *Ambulocetus*, and through time evolving into completely aquatic animals of the ocean, emerging as the whales we see today (Gingerich et al., 1983; Thewissen and Hussain, 1993), many of whose modern distribution patterns have been shaped by the Antarctic Circumpolar Current (Fordyce, 1980). This story illustrates the enduring link between land and sea, and how Western science can support cultural values of care for the environment, which endure through the arts. Such stories reflect patterns of relationship between the oceans and the earth on geological timescales, and knowledge of the evolution of marine mammals, propagating reverence for their nurturing and persistence.

Another example is a dreaming story by Aboriginal people in Maningrida (Arnhem Land, Northern Territory) about an island

[2]Bruce Pascoe, 2019, Pub. Black Inc., Salt p. 134

FIGURE 1 | Artwork signifies origins of this project in bringing together Australian Aboriginal perspectives and scientific data from Antarctica and the Southern Ocean. This illustrates pattern-matching between the Australian river catchments on the ice catchments and glacial flows of Antarctica.

cut off from the mainland (John Church, UNSW, pers comm.). This story was corroborated recently by modern science using scientific data on sea level changes over the last glacial period. Using records, climate scientist John Church was able to date the origin of the story to around eight thousand years ago, a time when sea level was rising following the last glacial maximum[3]. Other examples of similar phenomena were explored by Nunn and Reid (2016) and if we listen closely to the messages in the stories, we find that they also carry information on the responses of Indigenous people to the threat of rising sea levels, for example to build barriers of wood or rock (Nunn, 2020). In the age of the Anthropocene, we find ourselves facing rising sea levels once again and maybe it is within these stories that inspiration for adapting to disappearing shorelines can be found.

[3]http://www.livingdata.net.au/content/conversations/2019conversations/SeaLevelScience-and-a-DreamingStory.php

The arts have always been powerful languages for generating and expressing knowledge, because of their capacity to interact with our values and emotions. The immersive experience of artistic expression on its audiences can break down barriers that often prevent people from relating to places, data and facts. By inciting an emotional connection or bodily response, arts can enable people to imagine themselves as participants in the stories being told, and so may become more motivated to strive for a healthy planet and sustainable future.

The term 'art' remains epistemologically, politically and theoretically relevant in scholarly work related to Indigenous art, since it emphasises that all societies are capable of producing artworks of diverse features, which do not necessarily have to accommodate Western conceptions of what art is, or is not (Fiore, 2020). This perspective has been applied to the analysis of the production of engraved artefacts and body paintings from Tierra del Fuego (Southern South America). Drawing

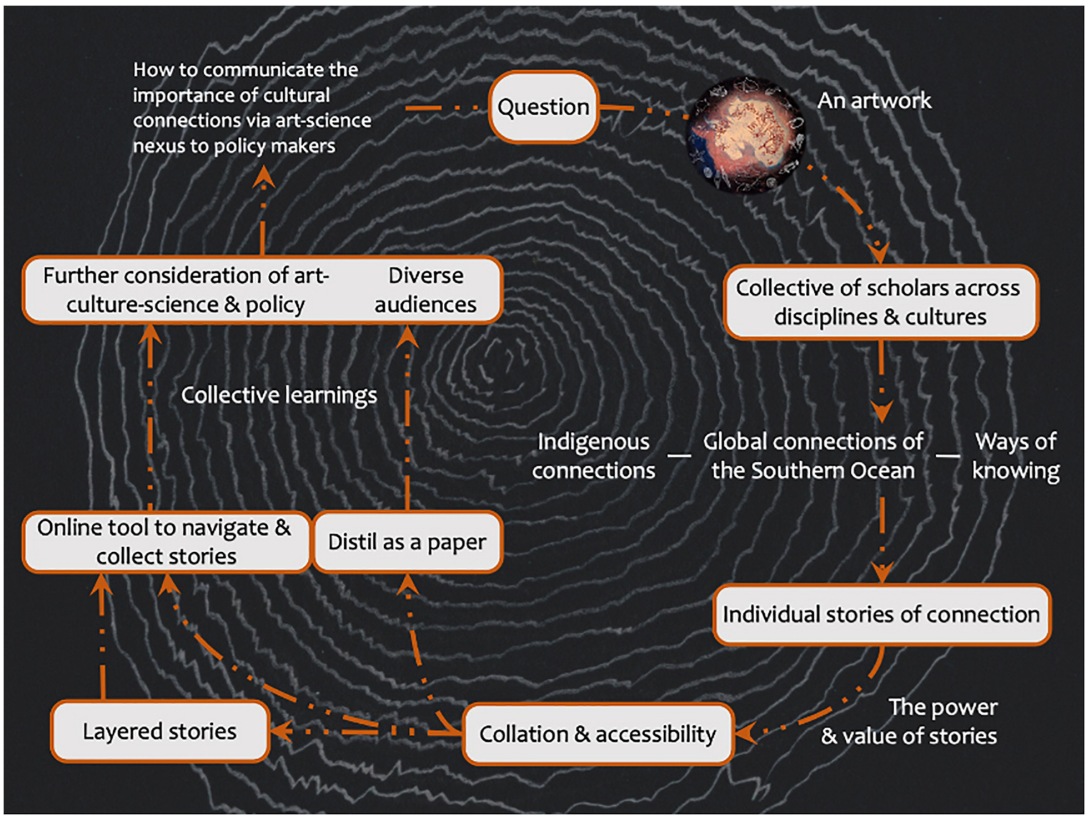


FIGURE 2 | Process used to develop this perspective based on the question of how to communicate to policy-makers the importance of cultural connections with the Southern Ocean, and the emerging values for the region, via art-science nexus.

from archaeological and ethnographic evidence of art production in Yagan territory (also known as Yamana, located in the southernmost portion of the Fuegian archipelago), Fiore (2020) presents the relationship between the First Nations people, the land, water and spiritual systems as not only represented in images applied to tools, ornaments, non-utilitarian objects and bones, but also evident in material procurement and pigment production processes to create body painting designs. The socioeconomic life of Yagan art moves through the collection of raw materials, technical and social processes of application, to storage, discard or abandonment. Gell's (1992) concept of "technology of enchantment" is applicable here, since it helps to shed light on the fact that art is not simply the end result, but the affordance gained during the alchemical power of its making. The relational nature of making undeniably connects the maker to the environment in which the making occurs.

Yagan art/making in Southern Tierra del Fuego includes technological affordances related to the labour organisation underlying portable art and body art creation, and the contexts in which they were manipulated, displayed, viewed and reacted upon (Fiore, 2020). According to ethnographic and historical records, material and pigment procurement, preparation and storage relied on mineral colouring substances as well as organic components of whale, dolphin, pinniped (seal), fish, and mussel shell. Since prehistoric times, highly geometric designs were applied to tools, domestic utensils and body adornment. The techniques used to produce these images reveal high skill and knowledge in managing production processes, as well as possessing spiritual portent. Currently, 'making' is viewed as a constant dialogue between the eye, mind, and hand, linked closely to problem-solving and critical thinking (Maeda, 2013). For the Fuegians, image creation constructed and reinforced social roles and relationships. The ephemeral performative affordance of body painting and non-ephemeral decorations engraved on bone artefacts conceptually broadcast the power of images being rooted in their making (Fiore, 2020). Moreover, several ceremonial body painting designs represented maritime animal referents. Therefore, we would be wrong to assume there is, or was, little connection between art/making and the Southern Ocean given its proximity to the ancestral territories of Tierra del Fuego's Indigenous populations.

This paper invites expanding understanding of scientific data through diverse languages of art, acknowledging ourselves as participants in the processes that govern our planet's chemistry and our human cultures. Indigenous perspectives develop depth and breadth that engender an unaffected connection with the environment, and ability to work harmoniously with Nature, to tread lightly, in terms of ecological footprint, through time. From a Fuegian perspective:

"Belonging to an Indigenous Community or First Nation is a fact that gives us a deeper vision of our environment: being part of it and not considering ourselves as its owners is what makes us have a deeper connection with Nature than other inhabitants of our cosmopolitan City [TN: the referred City is Ushuaia, capital of Tierra del Fuego]. Yagan crafts are involved in our everyday life, our children grow amongst bark canoes and reed baskets. Baskets have been made with the same Ancestral process for thousands of years, which lasted with its maximum purity. Today we make miniatures so that people from all the planet can take with them our message of balance, union and preservation of natural resources, since, in the end, we are all human and we must understand that our future depends on mother nature before it is too late. It only takes us to look at the current situation that we are facing now in August 2020, to reflect about our life in this earth. It is urgent that we look back [TN: toward our past] to replicate much of the way of life of our First Nations – Pueblos Originarios – *who lived in perfect balance with the environment: for this reason, they could carry on living for thousands of years. From the South of Tierra del Fuego, I send you a greeting in my mother tongue:* Ala Yala mamakús, hasta pronto hermanos*, see you soon brothers."*

Víctor Vargas Filgueira
Primer Consejero Comunidad Indigena Yagan Paiakoala de Ushuaia TDF
(First Chancellor of the Comunidad Yagan Paiakoala of Tierra del Fuego)
Translated from the original Spanish by D. Fiore

Linked with this paper are a selection of stories positioned on the map described above with circumpolar connections to physical and ecological processes in the Southern Ocean, told through languages of art and science (see examples of these stories in **Table 1**, with hyperlinks to these stories on the MEASO Cultural Connections, 2021, website).

We acknowledge that people have authority to share such stories through their relationship to the story and its location, so the stories are attributed to their authors. Types of authority people have to a story include the following:

1. They work where the story is located and consult with relevant cultural leaders about protocols and accuracy.
2. They are related by family to a person from that story, or to a person having close/family ties to that place.
3. They come from the country where the story is located, linked through clan, or language.
4. They are a member of the clan/group who were involved in the story.
5. They have personal involvement in the story at that place through skin or totem, and hence responsibility for the story themes and content (Povinelli, 1993).

This process ensures that knowledge is not shared by those who do not have authority on the story and may miss-tell it. This is important in the process of keeping oral knowledge 'pure' as we do in establishing expertise in written works. Through collaboration with others from the area we develop an objective knowledge viewpoint, that surpasses our individual interpretations.

DISCUSSION AND CONCLUSION

Humans have always been closely connected with the sea, as a provider, passage of transport to new places and bearer of stories. The great southern continent of Antarctica lies at the intersection of the world's oceans, where exchange between waters occurs. The heart of the planet, Antarctica pumps life throughout the global ocean, regulating temperature, transporting nutrients and oxygen to all corners of the globe (Marshall and Speer, 2012). Although there is no evidence that Antarctica has ever welcomed humans, the icy continent and its waters are part of stories and knowledge enduring through deep time and diverse cultures. This endurance is shown palpably through our animated interactive map. Through time, like the circumpolar current surrounding Antarctica, stories endure, travelling between peoples and poles, as both physical and imaginary explorations, connecting, growing and sharing knowledge of the vast Southern Ocean ecosystem.

In this perspective, we have considered how the stories and connections that bring together knowledge from Western science, Indigenous ecological knowledge and the Dreaming can promote understanding of and connection with the Southern Ocean. It has also demonstrated how deeper connections to the region and value of it are present within many cultures distant from the region. By combining new and ancient ways of expressing, embodying and passing on knowledge we hope to inspire collective ways of thinking. We encourage ways that are inclusive across diversity of experience and knowledge, and that develop deeper understanding, which will galvanise the making of a healthier future.

We came together from a range of backgrounds, with different ways of knowing and perceiving the world, to better understand the roles that Southern Ocean ecosystems play in the world and how Indigenous cultural perspectives underpin modern scientific understanding and enable enduring cultural engagement that is necessary to manage and sustain the health of the Southern Ocean and global ecosystems in these times of climate change and the Anthropocene.

Figure 2 illustrates the process that evolved as we engaged across disciplines and cultures to more deeply understand, respect, record and combine perspectives, to contribute to the holistic view that we consider necessary for best informing government policy on management of Antarctica and the Southern Ocean.

Through this process we have described how cultural arts have power to deliver, to a diversity of people, information that is based on 'hard data,' and that this is not something new – the interweaving of complementary knowledge systems is ancient and intrinsic to Indigenous cultures. Communicating stories generated through the scientific method and cultural arts in all its forms, increases accessibility across diverse audiences (from the general public to policy makers), is an important means to disseminate facts, and critically, enables people to personally engage in different ways of knowing. When compared with contemporary (and in many ways fleeting) means of communicating scientific findings (reports and papers),

the sharing of knowledge through a diversity of cultural arts practices is enduring, for co-authors and readers alike.

In this paper we have brought together ways of knowing through scientific data and the languages of arts, to more wholly engage people, through the process of first engaging ourselves in relating to the Southern Ocean ecosystems (which currently face an uncertain future), through the power of cultural connections for enduring conservation and long-term sustainability. Along the way we continue to learn about ourselves and each other, having also learnt that there is a long road ahead. It has been a journey of asking questions, listening deeply to one another and to Country as Ungunmerr teaches in Dadirri (Ungunmerr, 2017), deliberating on what transpires and develops between us, and translating that sharing into outputs for sharing with others, while inviting others to engage with us. We have laughed, we have despaired, we have felt enlivened and challenged. We have seen more deeply the complexity of the challenge. There is much still to be done.

We feel enlivened by the process that has evolved between us, for helping to build new relationships between cultural knowledge and scientific data, through the diverse languages of art, which are now constructively entangled with these written words needed for academic publication.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: http://www.lunartime.net.au/content/about/accession-numbers/001-SouthernOceanCulturalConnections.php and https://measocc.teachingforchange.edu.au/mappable_items, the latter of which has ID numbers for reference to map.

AUTHOR CONTRIBUTIONS

AC, LR, KP, and JM-T did the facilitation and oversight. CK did the interactive map. LR, TB, AC, PF, DF, EJ, CK, JM-T, KP, MS, and ST did the round table conversation. LR, TB, AC, DF, EJ, CK, JMT, KP, MS, and VF did the text. PF and ST did the music. LR and PF did the animation. KP and LR did the **Figure 1**/Graphical abstract artwork. JM-T, LR, and KP did **Figure 2**. Interactive map with stories: (http://www.livingdata.net.au/content/collaborations/2020collaborations/2020-collaborations.php). All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.616089/full#supplementary-material

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REVIEW
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Local Drivers of Change in Southern Ocean Ecosystems: Human Activities and Policy Implications

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Local drivers are human activities or processes that occur in specific locations, and cause physical or ecological change at the local or regional scale. Here, we consider marine and land-derived pollution, non-indigenous species, tourism and other human visits, exploitation of marine resources, recovery of marine mammals, and coastal change as a result of ice loss, in terms of their historic and current extent, and their interactions with the Southern Ocean environment. We summarise projected increases or decreases in the influence of local drivers, and projected changes to their geographic range, concluding that the influence of non-indigenous species, fishing, and the recovery of marine mammals are predicted to increase in the future across the Southern Ocean. Local drivers can be managed regionally, and we identify existing governance frameworks as part of the Antarctic Treaty System and other instruments which may be employed to mitigate or limit their impacts on Southern Ocean ecosystems.

Keywords: Southern Ocean, climate change, fishing, pollution, non-indigenous species, tourism, Antarctic Treaty System, CCAMLR

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INTRODUCTION

The environment and ecosystems of the Southern Ocean are influenced by phenomena such as atmospheric and oceanic circulation acting at a global scale, as well as by human activities or processes that cause physical or ecological change in specific locations. These influences, or drivers of ecosystem change, may act in distinct ways in different regions, operate at different spatial scales and rates of change, and often interact with each other (Millennium Ecosystem Assessment, 2005). In the context of the Marine Ecosystem Assessment of the Southern Ocean (MEASO), local drivers are defined as those that influence ecosystems at a particular location or series of locations within the Southern Ocean, that can often be managed regionally. In contrast, global drivers have an influence over the whole of the Southern Ocean, and need to be managed through global initiatives (Morley et al., 2020).

The local drivers considered here are: pollution (both marine and land-derived), non-indigenous species (NIS), tourism and other human visits, recovery of previously exploited marine mammals, fishing, and coastal change as a result of ice loss and iceberg scour (**Figure 1**). This paper focuses on the ten Antarctic and sub-Antarctic MEASO areas which broadly cover (but do not align precisely with) the area managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (**Figure 2**). These sectors encompass the coastlines

of the Antarctic continent and its outlying islands and the sub-Antarctic islands, where the majority of scientific research stations and tourist landing sites are located (**Figure 3**). The areas most visited by humans tend to be the best studied, where the trends and impacts are best known.

Even in one of the least impacted oceans on Earth (Halpern et al., 2008), local drivers have at times been greater than can be sustained by the environment, and whilst drivers such as the presence of non-indigenous species and iceberg scour may be projected to increase in particular locations, others, such as the exploitation of marine mammals, and land-derived pollution, have passed their historic peak and have either ceased altogether or are declining (Duarte et al., 2020). The specific effects of local drivers on Southern Ocean species and ecosystems are dealt with in other papers published in this research topic (e.g., Bestley et al., 2020; Brasier et al., 2021; Caccavo et al., in press; Johnston et al., in review; McCormack et al., in review). Cavanagh et al. (2021) also considers the risk of climate change acting together with local human activities, and future impacts on the capacity of the ecosystem to deliver services such as fisheries.

The nature and scale of local drivers have differing consequences and magnitude at locations around continental Antarctica and the sub-Antarctic islands. Here, we assess the status of local drivers in the main regions of human activity of the Southern Ocean. As far as possible, given that records are limited prior to the 1980s, we assess the status and trends of drivers in the past. In doing so, we seek to establish a baseline of information on historical local drivers for use in ecological assessments of how Southern Ocean ecosystems have changed and may be changing in the future.

Monitoring the magnitude of some local drivers (such as fishing effort), and their impacts in specific locations (e.g., point source pollution at some research stations) provides a medium to high level of certainty on recent trends. However, the absence of monitoring of local drivers and related biological and environmental parameters across much of the Southern Ocean means that levels of certainty about the nature and extent of impacts and projected trends are generally low for those remote areas. No single driver acts in isolation and there is a high level of certainty that cumulative impacts will result from the interaction of local drivers with global drivers, despite a lack of understanding of the specific effects and projections of such interactions.

All human activities in the Southern Ocean, other than whaling, are regulated under the instruments of the Antarctic Treaty System (ATS). While this management aims to minimise impacts to the environment (Hughes et al., 2018), and to assess the cumulative impacts and interactions of both local and global drivers and their projected trends, this has not yet been fully achieved in practice. This is due in part to the separate consideration of different human activities by different components of the ATS (Grant et al., 2013), as well as a lack of integrated consideration of the effects of global drivers such as temperature, ocean circulation or sea ice extent within management frameworks (CCAMLR, 2017).

Since the first humans arrived in the region during the late 18th century and began to exploit its living resources, local drivers have had an impact on Southern Ocean ecosystems. The initially uncontrolled harvesting of marine mammals (firstly of fur seals, followed later by elephant seals and whales), as well as penguins hunted for oil, resulted in sharp declines of local and regional populations, and the assumed local extinction of some species, such as Antarctic fur seals at South Georgia (Hoffman et al., 2011). Harvesting of finfish was first undertaken in the Southern Ocean in the 1960s, contributing to the collapse of fish stocks that have yet to recover (e.g., notothenioids in the Scotia Sea region, Kock et al., 2007). This was followed by the start of krill fishing in the 1970s, and fishing remained unregulated until the establishment of CCAMLR in 1982, but even then controls on fisheries took some years to develop (Constable et al., 2000). The near extirpation of many large cetaceans over a sustained period during the peak of whaling activities during the first half of the 20th century may have further consequences as these species continue to recover (Roman et al., 2014). Whilst CCAMLR's current management measures aim to uphold the precautionary approach of ensuring that activities should have a low risk of causing long-term adverse effects, fishing activities still have the potential to drive change in populations of harvested species, as well as those of associated and dependent species, such as the decline of albatross populations as a result of incidental mortality in the toothfish fishery (Michael et al., 2017; Pardo et al., 2017; Bestley et al., 2020). Local drivers, including the activities of single fishing vessels, can therefore contribute to regional, long-term change.

With no Indigenous population on the Antarctic continent, or on most sub-Antarctic islands (with the exception of Polynesians thought to have visited and occupied some of the New Zealand sub-Antarctic islands as early as the 12th century), human activities on land have only had an impact since the first visits of sealers and explorers in the early 19th century. It was not until the second half of the 20th century that the footprint of land-based human activity began to expand, with scientific research and subsequently tourism both increasing in recent decades, in terms of numbers and geographical scope, as well as a diversification of activities (Pertierra et al., 2017; Brooks S.T. et al., 2019). The numbers of people visiting the Antarctic continent and sub-Antarctic islands remain very low, with the vast majority of the coastline and the interior rarely or never visited. Nevertheless, localised human activities on land have the potential to change or disrupt marine species and ecosystems at a local or even regional scale, especially where multiple drivers interact to generate cumulative impacts, where they are exacerbated by the effects of global drivers such as warming temperatures, or where they are the result of accidents or unforeseen events.

Here, we discuss specific local drivers in terms of their known current spatial and temporal extent, and their interactions with the Southern Ocean environment. We also reflect on how these local drivers may be positively or negatively affected by others, including global drivers. We summarise projected increases or decreases in the influence of local drivers, and projected changes to their geographic range, based on evidence from the scientific literature. Where appropriate, the level of confidence in a conclusion is given according to the approach of the IPCC (Mastrandrea et al., 2011). When not supported by a reference

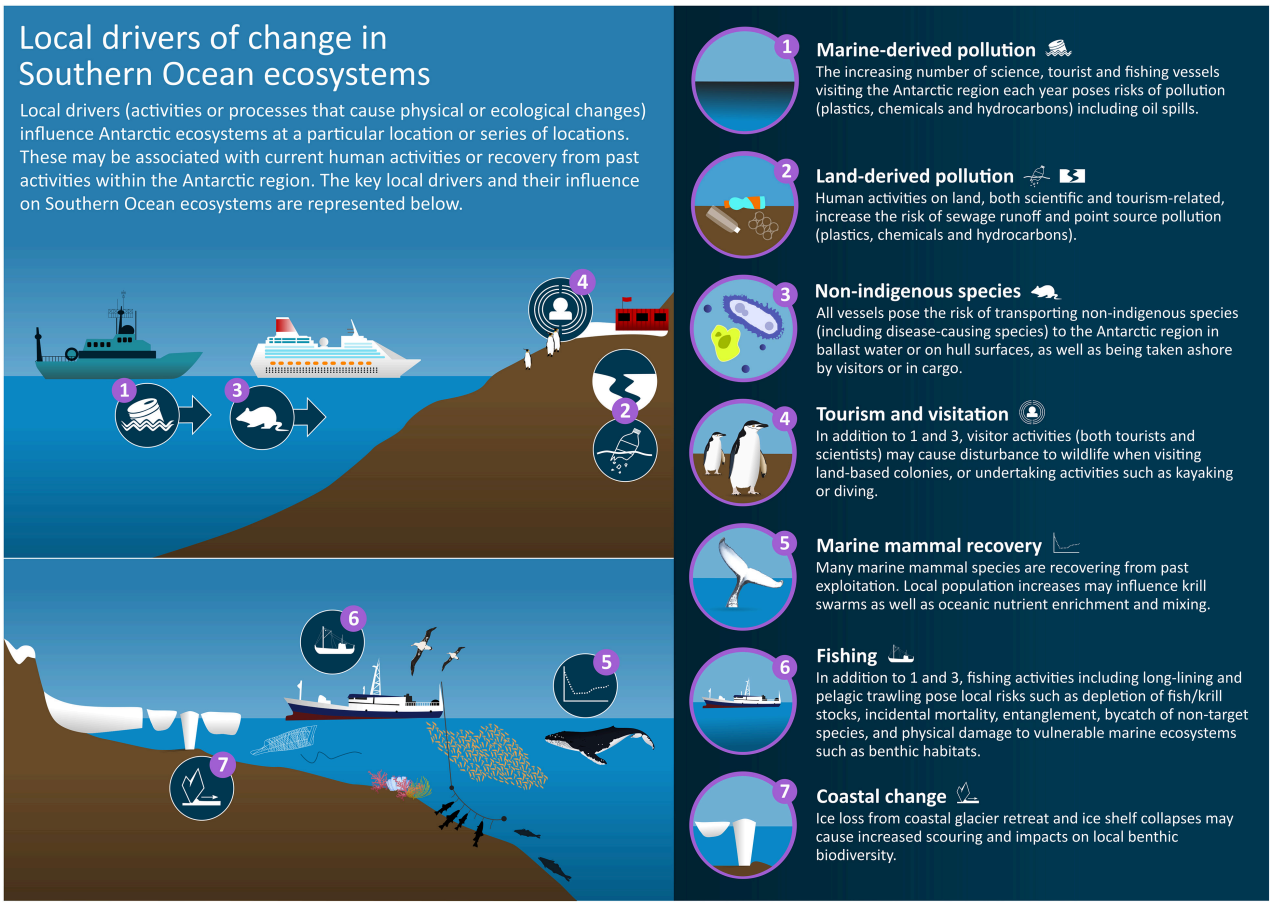

FIGURE 1 | Summary of local drivers of change influencing Southern Ocean ecosystems.

cited in the text, we judged confidence from the levels of agreement we observe in the scientific literature and the amount of evidence presented to support the conclusion, including consideration of any contrary evidence. The levels of confidence are not to be used as the inverse of confidence for alternative hypotheses, as those alternatives may not be addressed in the literature. Finally, we identify existing governance frameworks as part of the ATS and other instruments that have specific relevance to local drivers, and which may be employed to mitigate or limit their impacts on Southern Ocean ecosystems (Lee and Chown, 2007).

LOCAL DRIVERS

Marine-Derived Pollution

The Southern Ocean has relatively few direct sources of human-derived marine waste, so the input of pollutants is primarily from local shipping, fisheries, research station resupply activities or transported from further afield (Slip and Burton, 1991; Walker et al., 1997; Barnes et al., 2010; Waller et al., 2017; Ryan et al., 2019). Despite its remote location and distance from human habitation, the impact of marine debris on Southern Ocean wildlife has been reported since the 1970s. This includes entanglement of marine mammals (Payne, 1979; Bonner and McCann, 1982; Arnould and Croxall, 1995; Waluda and Staniland, 2013), and the ingestion and entanglement of debris by seabirds (Van Franeker and Bell, 1988; Huin and Croxall, 1996; Nel and Nel, 1999; Ryan et al., 2016; Phillips and Waluda, 2020). Beached marine debris has been reported from various oceanic shores in the Southern Ocean (Gregory et al., 1984; Ryan, 1987; Slip and Burton, 1991; Torres and Jorquera, 1995; Gregory and Ryan, 1997; Walker et al., 1997; Convey et al., 2002; Barnes and Fraser, 2003; Monteiro et al., 2018; Waluda et al., 2020). Floating debris such as fishing buoys and packaging bands have also been observed as far south as 73°S, in the Bellingshausen Sea (Barnes et al., 2010). In addition to this "macro-debris" (i.e., items >5 mm), recent work has suggested that microplastics (items <5 mm; Thompson et al., 2004), from both primary sources and the breakdown of larger items, are an emerging area of concern in the Southern Ocean. To date, microplastics have been found in pelagic waters (Isobe et al., 2017; Lacerda et al., 2019; Suaria et al., 2020), shallow marine sediments (Waller et al., 2017; Reed et al., 2018), benthic invertebrates (Sfriso et al., 2020), pelagic invertebrates (Jones-Williams et al., 2020), seals (Eriksson and Burton, 2003),

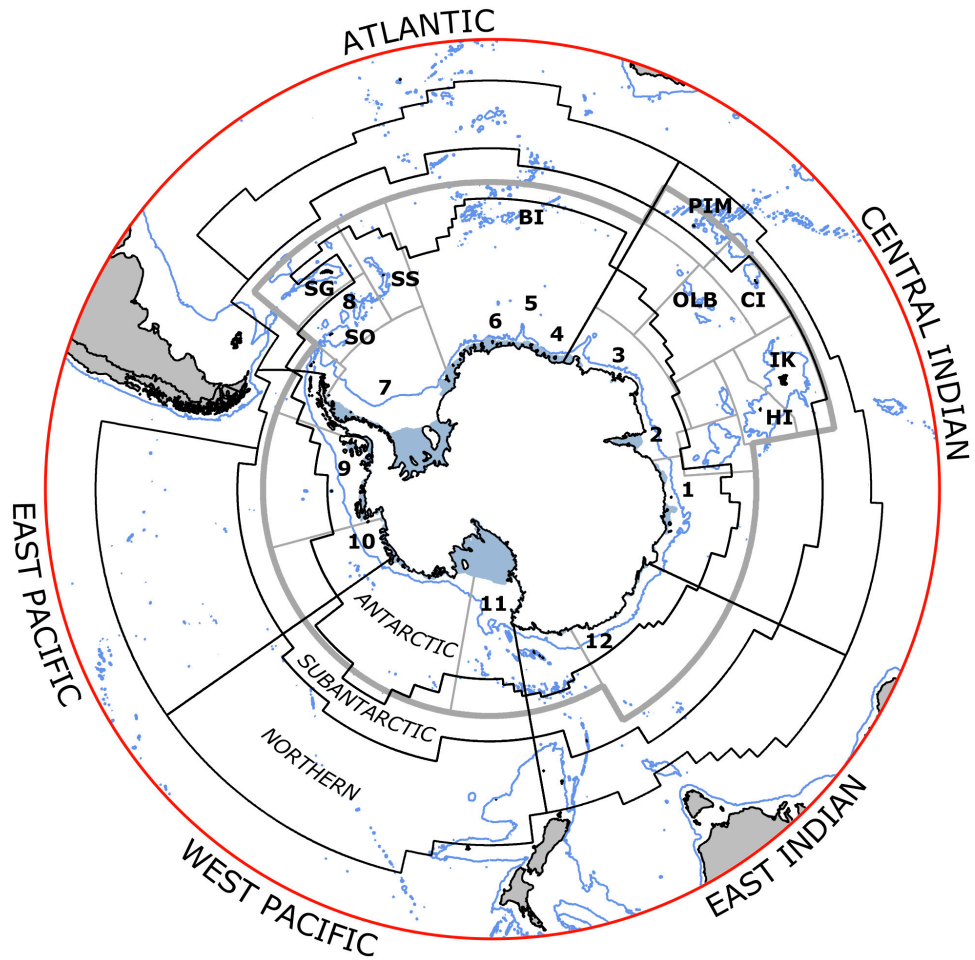

FIGURE 2 | Areas for assessing status and trends of local drivers in the Marine Ecosystem Assessment for the Southern Ocean (black lines). Sectors are divided meridionally: corresponding names of sectors are outside the circle. Zones extend from the coast to the Southern Antarctic Circumpolar Front (Antarctic), to the Subantarctic Front (Subantarctic) and to the Subtropical Front (Northern). Seas are marked in the Antarctic Zone as (1) Davis, (2) Cooperation, (3) Cosmonaut, (4) Riiser-Larsen, (5) Haakon VII, (6) Lazarev, (7) Weddell, (8) Scotia, (9) Bellingshausen, (10) Amundsen, (11) Ross, (12) Dumont D'Urville. Islands in the CCAMLR area include Heard (HI), Isle Kerguelen (IK), Crozet (CI), Prince Edward-Marion (PEM), Bouvet (BI), South Sandwich (SS), South Georgia (SG), South Orkney (SO), Ob and Lena Banks (OLB), and South Shetlands (not initialled but found on the north-western side of Antarctic Peninsula). Grey lines indicate the CCAMLR reporting areas (Subareas and Divisions).

and penguins (Bessa et al., 2019; Le Guen et al., 2020). While current concentrations of microplastics may be negligible on the Southern Ocean scale, they can be high at local scales if concentrated at point sources (Waller et al., 2017). The seafloor is often a final resting place for marine debris and microplastics, even in the Southern Ocean (Cunningham et al., 2020), although the impact on benthic species or foodwebs remains largely unknown (Horton and Barnes, 2020; Brasier et al., 2021).

The risk from point sources of pollution is highest on the northwest Antarctic Peninsula as this area has the highest human footfall including 35 coastal research stations (46% of the total number of research stations across the Antarctic continent) (COMNAP, 2017), and all of the top twenty most visited Antarctic tourist sites, which accounted for 68% of all landings in the 2017/18 season (IAATO, 2018) (see **Figure 3**).

Although they occur rarely, oil spills can have a greater significance in Antarctica then elsewhere in the world (Clarke and Harris, 2003), with substantial impacts on sediment meiofauna (Stark et al., 2017), littoral species (Kennicutt, 1990) and seabirds (Reid, 1995). The largest reported spills have been due to the sinking of vessels, including the *ARA Bahia Paraiso* (1989, 600,000 L diesel released near the US Palmer Station, Antarctic Peninsula), *MV Nella Dan* (1987, 270,000 L light marine diesel released near Macquarie Island, sub-Antarctic) and MV Explorer (2007, 185,000 L diesel released near King George Island, South Shetland Islands), which resulted in impacts including the mortality of marine and intertidal invertebrates, oiling of penguins, and reproductive failures and declines observed in local bird populations (Eppley and Rubega, 1990; Kennicutt, 1990; Kennicutt et al., 1991; Smith and Simpson, 1995; Chile, 2008).

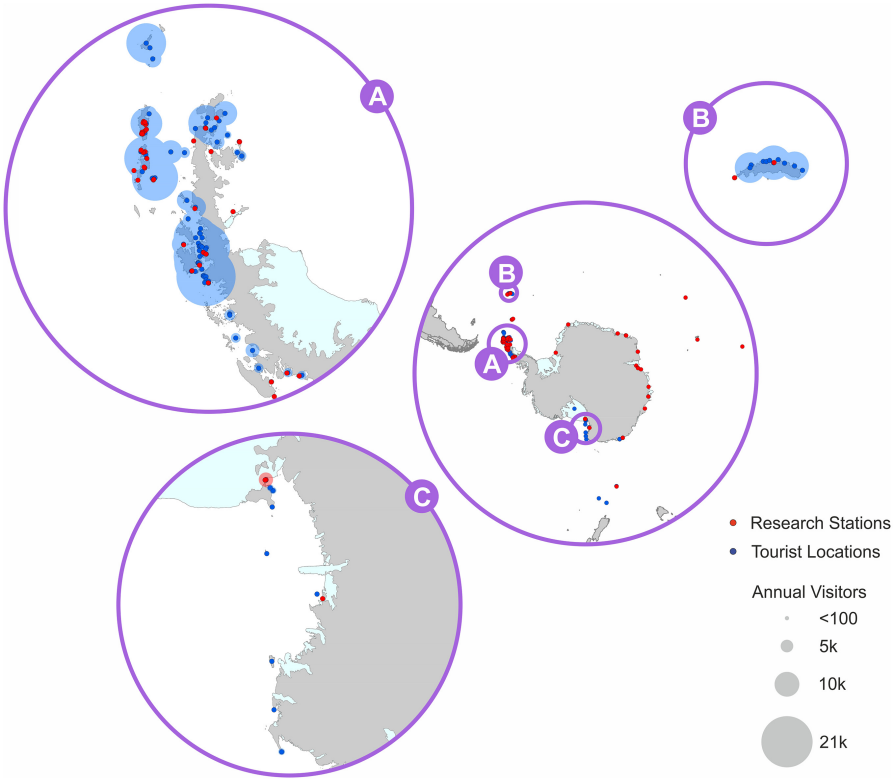

FIGURE 3 | Regions of highest land-based human activity (scientific research stations and tourist visits). Maximum occupancy of coastal Antarctic research stations (www.comnap.aq) and mean annual visitor numbers (2003/4-2014/15 seasons – IAATO) for Antarctica and the 2014/2015 season for South Georgia (www.gov.gs).

Most microplastics and other pollutants are global in origin and transported into the Southern Ocean through atmospheric and oceanic teleconnections. The transport of plastics, heavy metals and other pollutants in the Southern Ocean via the atmosphere, cryosphere and ocean currents is further considered in Morley et al. (2020). The impacts of persistent organic pollutants (POPs) originating from outside the Southern Ocean on higher predators are also discussed in Bestley et al. (2020).

Land-Derived Pollution

Across Antarctica, research stations and land-based scientific activities can act as local sources of land-derived pollution, hydrocarbons, POPs, wastewater effluent, and macro- and micro-plastics (Munari et al., 2017; Reed et al., 2018; Absher et al., 2019), with impacts observed predominantly at a local scale (Tin et al., 2009). Operation of ships, aircraft, research stations and field camps in Antarctica relies upon the combustion of hydrocarbons as a fuel source. Currently 58% of coastal research stations use a combination of fossil fuels and renewable energy. Logistical support for these stations also represents a potential pollutant load with ∼555 ship visits and 547 flights annually (data from COMNAP, 2017). Potential negative environmental consequences of spills are made all the more serious due to the typical lack of capacity within national Antarctic programmes to mount effective clean-up operations in the event of an incident.

Under the Protocol on Environmental Protection to the Antarctic Treaty (agreed 1991, entered into force 1998[1]), the disposal of most wastes within the Antarctic Treaty area (the area south of latitude 60°S) is prohibited. This includes the discharge of oil, noxious liquid substances and garbage from ships, but disposal of food waste and sewage is permitted within 12 nautical miles of the coast. National Antarctic programmes are encouraged to remove sewage and domestic liquid waste generated at research stations; however, due to the logistical difficulties of removing sewage waste from Antarctica, coastal research stations may dispose of sewage into the near-shore environment, provided there is capacity for initial dilution and rapid dispersal. No treatment of the sewage waste is required under the Protocol, except for maceration in cases where the number of personnel on station exceeds c. 30 individuals. Sewage can contain non-native microorganisms, pathogens, genetic fragments and a wide range of pollutants including heavy metals, hydrocarbons, detergents, microplastics and flame-retardant chemicals (for reviews see: Tin et al., 2009; Waller et al., 2017; Stark et al., 2019). Viable sewage-associated bacteria have been detected in high concentrations around outfalls and up to 2 km away, along with above-background concentrations of heavy metals, persistent organic pollutants (Hale et al., 2008; Wild et al., 2015; Stark et al., 2016), and other organic contaminants

[1]https://www.ats.aq/e/protocol.html

(Emnet et al., 2015), hydrocarbons, nutrients and faecal sterols in marine sediments (Lenihan and Oliver, 1995; Hughes, 2004; Hughes and Nobbs, 2004; Hughes and Thompson, 2004; Leeming et al., 2015; Stark et al., 2016).

The impacts of long-term sewage release to near-shore environments is not well understood, but sewage release from research stations has caused local changes in benthic biodiversity and abundance and may have implications for wildlife health (Conlan et al., 2004; Stark et al., 2016). In light of developments in sewage treatment technologies, the minimum standards set out in the Protocol may no longer be considered acceptable by some Parties, and increasing numbers of sewage treatment plants are being installed, particularly at larger Antarctic research stations (Hughes, 2003; Gröndahl et al., 2008; Brasier et al., 2021).

Other sources of Antarctic marine pollution from research stations may include macroplastics that are blown into the ocean, due to poor waste management, or historical waste that was discarded prior to the entry into force of the Protocol (Crockett and White, 2003). Historic waste dumps located on ice sheets or ice shelves may also emerge at the ice front to be released into the marine environment, for example, the buried and abandoned Halley III Research Station calved off the Brunt Ice Shelf into the Weddell Sea in 1993 (Aronson et al., 2011). Following deployment, scientific instrumentation may also be inadvertently or knowingly lost to the marine environment. Examples include meteorological radiosondes and balloons, expendable bathythermographs (XBTs), seabed experimental apparatus damaged by iceberg collisions, lost Argo floats or autonomous underwater vehicles and unrecoverable weights to which scientific devices are attached.

With a more comprehensive understanding and implementation of the Protocol, including improving waste management practices, levels of environmental pollution may decline, particularly as alternative technologies for power generation are employed (e.g., the Belgian Princess Elisabeth Station[2]). Nevertheless, as more research stations continue to be established in previously little impacted locations (e.g., the Turkish station on Horseshoe Island, Antarctica Peninsula, and new Chinese Station on Inexpressible Island, Ross Sea Region) and the human footprint across the continent expands, minimising environmental impacts becomes ever more important if SO marine environments are to remain close to pristine (Brooks S.T. et al., 2019). Locations with concentrations of research station infrastructure may be particularly vulnerable to marine pollution, particularly where aging infrastructure has led to chronic or catastrophic fuel spills that have affected the marine environment (Wilkness, 1990; Peter et al., 2008).

Tourism and Visitation

Antarctic tourism began in the 1950s and today is one of the three most significant human activities undertaken in the region, alongside scientific research and commercial fishing. In general, the impacts caused by national governmental operators in their delivery of science and other strategic priorities through the construction of research stations and other infrastructure may be locally greater than the impacts caused by Antarctic tourism (Tin et al., 2009). However, the growth of the tourism industry, and increasing diversity of activities it provides, will contribute to increasing human footprint in Antarctica, with a resulting loss of wilderness and increase in local human impact (Eijgelaar et al., 2010; Liggett et al., 2011; Pertierra et al., 2017). Since its establishment in 1991 the majority of Antarctic tour operators are members of the industry body IAATO (International Association of Antarctica Tour Operators), which coordinates tourism shipping activities and represents the industry at the normally annual Antarctic Treaty Consultative Meeting.

While the Antarctic tourist industry is driven by global demand, tourist activities influence sites at a local scale. The majority (>95%) of tourism activity occurs in the Antarctic Peninsula region, but visitors also travel in smaller numbers to the Ross Sea, and sites along the coast of East Antarctica (**Figure 3**). Most tourists visit Antarctica on cruise vessels that call at a number of coastal sites for brief shore-based activities, after which they return to the vessel. Around 50 yachts travel to the Antarctic each year, which can be commercial operations as well as private exploration (United Kingdom, Argentina, Chile in conjunction with the International Association of Antarctica Tour Operators, 2018). In recent years the tourist season has been extended to more than 150 days (November to April) due to the use of ice-strengthened passenger vessels, with an associated steep rise in tourist numbers. The 2018–2019 season recorded an increase of 8% from the previous year, with a total of 56,186 tourists visiting. Numbers increased again by 32% to 74,401 for the 2019/2020 season (IAATO, 2019), although this was curtailed in early 2020 due to the effects of COVID-19. The 2020/2021 season saw a near cessation of Antarctic tourism due to the pandemic, and it is not known how long it will take for the cruise industry to recover (Hughes and Convey, 2020).

Tourism has occurred at c. 250 locations in Antarctica, with the great majority concentrated at a small number of sites located on the northern Antarctic Peninsula and offshore islands (e.g., Neko Harbour, Goudier Island, Half Moon Island and Cuverville Island). Bender et al. (2016) reported that in the 2013/2014 season, just 15 of the Antarctic Peninsula sites made up 68% of all passenger landings. The level of human impact at these sites will depend upon their resilience, however, few sites have been assessed and monitored in this regard (see Tejedo et al., 2012, 2020; Russell et al., 2013).

Impacts caused by increasing visitation and the potential establishment of permanent infrastructure (noting that these are not exclusive to tourism) could include: a loss of wilderness and aesthetic values (Summerson and Tin, 2018), increased risk of the introduction of non-indigenous species (Chown et al., 2012), increased risk of pollution events at both small (e.g., dropping of litter) and large scale [e.g., fuel spill from a ship (Aronson et al., 2011)], disturbance of wildlife by humans (Burger and Gochfeld, 2007; Tejedo et al., 2016; Dunn et al., 2019) or aircraft (Hughes et al., 2008), increased atmospheric emissions from vessels, aircrafts and land vehicles (Amelung and Lamers, 2007; Eijgelaar et al., 2010) and increasing cumulative impacts at ice-free locations where scientific, logistic and tourism activities coincide (e.g., Deception Island) (Pertierra et al., 2014).

[2]http://www.antarcticstation.org/station/renewable_energies

Predicted climate change impacts such as increases in the area of ice-free ground (Lee et al., 2017), reductions in sea ice extent, and shifts in the distribution ranges of wildlife, are likely to affect the tourism industry by potentially changing access to established visitor sites, facilitating access to new locations and affecting the wildlife present at established landing sites.

An increasingly diverse range of activities are available to tourists including overnight camping, mountain climbing, visits to penguin colonies (including emperor penguins), whale watching, trips on small boats, swimming, SCUBA and submersible diving, underwater Remotely Operated Vehicles (ROVs), Remotely Piloted Autonomous Systems (RPAS), stand-up paddle boarding, photography, helicopter flights, kayaking, skiing/snowboarding, research station visits, as well as more extreme activities such as marathon running, long distance treks (e.g., by ski or using kites), paragliding, heli-skiing and base jumping. Many of these activities may have direct impacts upon marine species, either through disturbance of a range of biological groups [e.g., from the disturbance of benthic sediment population by the now prohibited practice of digging geothermally-heated bathing pits at the shoreline on Deception Island, to disturbance resulting from visitation of penguin colonies (Dunn et al., 2019)], generation of underwater noise (ROVs, large and small boat operations) and potential dispersal of non-native species [i.e., through repeated use of equipment at a series of locations without adequate cleaning during intervening periods (McCarthy et al., 2019)]. As ship traffic has continued to increase, the risk of ship strikes of whales has also increased, with nine whale strikes reported by IAATO to the International Whaling Commission (IWC) since 2001. Recognising this, IAATO has introduced new procedures for operations in the vicinity of whales, including limiting vessel speed to 10 knots at two marine sites to the west of the Antarctic Peninsula (IAATO, 2019).

Non-indigenous Species (NIS)

Antarctica and the outlying islands within the Polar Front typically have the highest proportion of native species of any global localities. For example of the > 1,200 species recorded from the South Orkney archipelago, only two (0.2%) are considered to be non-indigenous (Barnes et al., 2009) and some southern polar islands such as McDonald and Bouvetoya may even have none (Frenot et al., 2005). It is now clear that the Polar Front has more porosity than once thought (Barnes et al., 2006), yet still presents a considerable obstacle isolating the Southern Ocean from much species transport from elsewhere (Clarke et al., 2005). However, ships, aircraft and even plastic now cross the Southern Ocean, potentially carrying non-indigenous species (Lewis et al., 2003; Morley et al., 2020), although the risk is geographically uneven given the distribution of stations and tourist sites (**Figure 3**), and more risk is borne by the more visited Scotia Arc and northern Antarctic Peninsula. Only a small proportion of species which travel such a journey, survive and remain viable, and an even smaller proportion are able to recruit and establish. Environmental conditions are most similar to cool temperate continental shelves around the western Antarctic Peninsula and Scotia Arc, which may increase the risk in these areas. Furthermore, regional warming and sea ice losses have been highest within those areas, and this risk distribution is borne out by establishments of non-indigenous species recorded to date (Frenot et al., 2005; Barnes et al., 2006; Avila et al., 2020; Cárdenas et al., 2020; Hughes et al., 2020). With more research stations, of which several maintain year-round SCUBA activities, this region is also better monitored than elsewhere, although still far from adequate.

Over the last few decades there have been reports of single life stages of several marine species reported from various locations around the Scotia Sea and northern Antarctic Peninsula (for a recent overview see McCarthy et al., 2019). Considerable scientific and public discussion has occurred over the potential changing distributions of native fauna (most obviously stone crabs – Lithodidae) and the possible vulnerability of life on Antarctica's sea beds (Thatje and Fuentes, 2003; Griffiths et al., 2013). A single Mytilid mussel was found at Grytviken, South Georgia (Ralph et al., 1976), and Mytilids have also been reported from King George Island (Cárdenas et al., 2020), but establishment was not recorded in either case. However, new records of macro algae within the caldera at Deception Island may represent new discoveries of indigenous or non-indigenous species, detected due to increased sampling effort (Clayton et al., 1997). An invasive and potentially ecologically harmful bryozoan (*Membranipora membranacea*) has also been discovered on non-native kelp rafts at Deception Island (Avila et al., 2020). These kelp rafts, usually *Durvillaea antarctica* or *Macrocystis pyrifera,* have been demonstrated to be able to cross the Polar Front with evidence from genomics and oceanographic models (Fraser et al., 2018). Recently the polychaete worm *Chaetopterus variopedatus* has established and started spreading in the shallows at South Georgia (see Hughes et al., 2020). Once established, marine invasions have proved virtually impossible to reverse. There has been considerable concern that non-indigenous species establishments around Antarctica might prove to be particularly devastating because of the long Southern Ocean semi-isolation from biota elsewhere, but also due to the intensity of climate change there (Brasier et al., 2021).

Exploitation of Marine Species

The long history of human exploitation of marine species in the Southern Ocean developed in a progressive sequence of seals and penguins, whales, finfish, then krill. In terms of methods of exploitation, it went from capturing and killing individual marine mammals, to the use of industrial demersal and pelagic trawls and more recently to the use of demersal longlines to capture toothfish. Illegal, unreported and unregulated (IUU) fishing began in the mid-1990s using longlines but evolved to use indiscriminate gill netting from 2008. Detailed reporting of species caught, along with the geolocation of catches, only began in the 1990s. Most biomass was extracted from the Southern Ocean prior to this time. Here we present the time series of exploitation as best we can from available records to date. These time series indicate the pressures that local exploitation may have had on the species involved, but also the relative difference in food web effects in different MEASO areas. We also report on

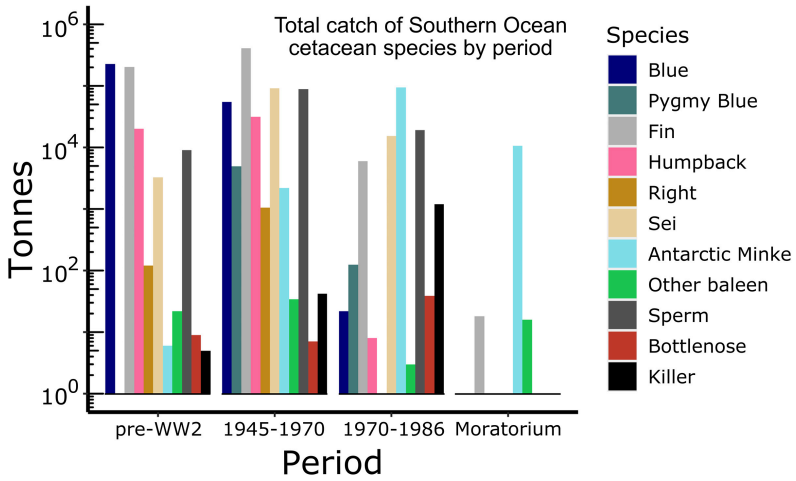

FIGURE 4 | Total catch (tonnes) of Southern Ocean cetacean species (right legend) in four different periods of whaling. Data from IWC Catch Records. *Y*-axis is on a $\log_{10}$ scale.

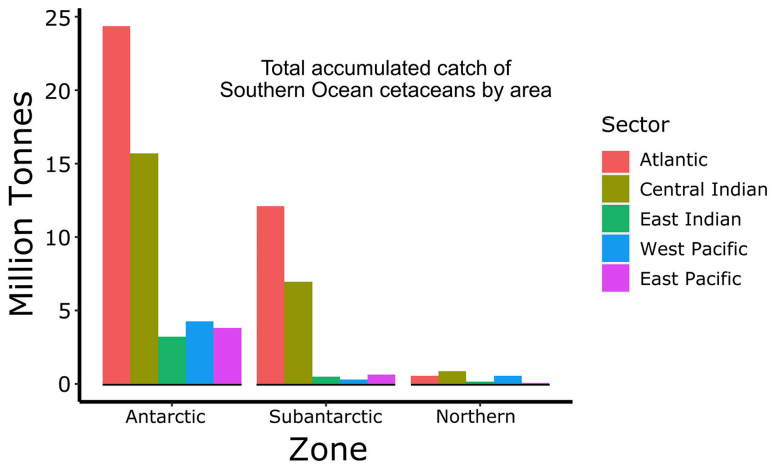

FIGURE 5 | Total accumulated catch (million tonnes) of Southern Ocean cetaceans in each sector (right legend) from each zone of MEASO areas as shown in **Figure 2**. Data from IWC Catch Records.

'incidental mortality' which is the unintentional capture or death of species not targeted by the fishery.

Marine Mammals

Exploitation of seals began in the eighteenth century with harvesting mostly occurring in the early 19th century when seal populations were decimated across many of the subantarctic islands. Reconstruction of the catch of seals has been difficult, requiring the interpretation of log books from vessels exploiting seals on subantarctic islands and from trade figures (Foley and Lynch, 2020). For many areas such as in the Indian Ocean sector, few records exist but the reported timeline is similar with the greater part of sealing finishing by the mid-19th century (King, 1959). A reconstruction of the Antarctic fur seal population at South Georgia has estimated annual takes of Antarctic fur seals of up to 150,000 animals on that island alone (Foley and Lynch, 2020). Similar takes are reported for seals and sea lions south of Australia and New Zealand (Ling, 1999).

Pelagic whaling caused the near extirpation of large whale species prior to the moratorium on commercial whaling in 1986 (Rocha et al., 2014). Reconstruction of whale catches has come from log books and records from shore stations and factory vessels during this time. Records are available from the Secretariat of the IWC. The available data on the numbers of different species caught were aggregated into four main periods of whaling – prior to the Second World War (WW2), a period of active whaling from 1945 to 1970, a period where depletions of the larger whales were obvious in the catch records from 1970 to 1986, and the period since the moratorium came into effect (**Figure 4**).

The potential impacts on the ecosystem of such removals in the different MEASO areas is shown by multiplying the catch in numbers by an approximate average mass of an adult male

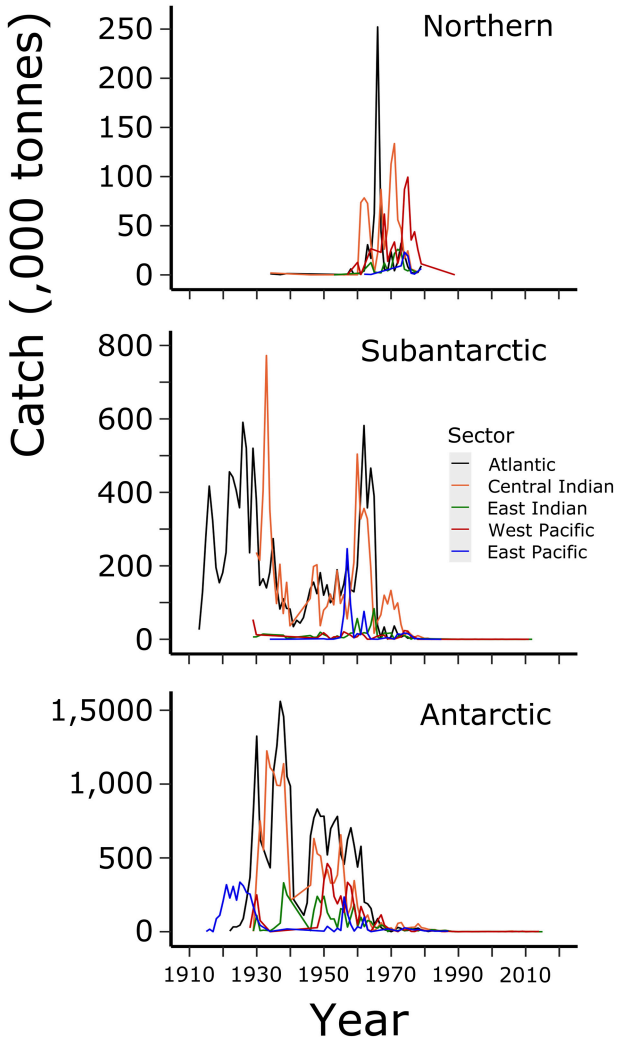

FIGURE 6 | Time series of catches (tonnes) of all Southern Ocean cetaceans in each sector (central right legend) from each zone (labelled panels) of MEASO areas as shown in **Figure 2**. Data from IWC Catch Records.

whale of each species. We note that these species migrate to lower latitudes of the Southern Hemisphere in winter and many were also hunted there, so these estimates represent a minimum value in terms of biomass removed. Even though this is approximate, the results presented in **Figure 5** show that most biomass was removed from the Antarctic Zone followed by the Subantarctic Zone and most direct removals of whales occurred in the Atlantic and Central Indian Sectors.

The time series of biomass removals is shown in **Figure 6**. The earliest whaling in the 20th century resulted in similar removals from the subantarctic zone in the Atlantic Sector, around South Georgia, and around the Antarctic Peninsula in the East Pacific Sector, as land stations were established in these locations for processing. After that and prior to WW2, the use of factory ships enabled more offshore hunting, with onboard processing eliminating the need to use land stations. Substantial biomass was removed from Antarctic Zone in the Atlantic Sector (Weddell Sea) and from the East Antarctic area of the Central Indian Sector. After WW2, catches were more widespread, including the Ross Sea in the West Pacific Sector in the 1950s and 1960s. By 1970, Southern Ocean areas were considered fished out, and the main fishery had moved north. Hence biomass taken from the Antarctic Zone was negligible compared to steady catches of mostly sei and fin whales in the Subantarctic and Northern Zones of the Central Indian and West Pacific Sectors.

Finfish and Krill

The dominant fisheries in the Southern Ocean began with groundfish fishing by predominantly the Soviet Union over the 1970s and 1980s (**Figures 7**, **8**). During this time, *Notothenia rossii* was fished close to extinction throughout the island shelf areas in the Antarctic and Subantarctic Zones of the Southern Ocean (Kock, 1992). Other groundfish species also became depleted throughout the Subantarctic Zone prior to the coming into force of CCAMLR in 1982 (Kock et al., 2007) and ended by 1990. Two bentho-pelagic species from this period remain targeted in the Southern Ocean. The mackerel icefish, *Champsocephalus gunnari*, is targeted in the Subantarctic Zone at South Georgia (Atlantic Sector) and Heard Island (Central Indian Sector) using trawls. Toothfish, *Dissostichus* species, are targeted throughout the Southern Ocean using longlines, although the catch for *Dissostichus eleginoides* (Patagonian toothfish) in the Subantarctic Zone far outweighs the catch of *Dissostichus mawsoni* (Antarctic toothfish) in the Antarctic Zone. Fishing for Antarctic krill (*Euphausia superba*) began in the 1970s and increased substantially in the 1980s, only to decline again in the 1990s following the collapse of the Soviet Union. Catches of krill are increasing again but are not yet at the levels of the 1980s. Other fisheries that have been explored include squid, mesopelagic fish (mainly myctophids), Antarctic silverfish (*Pleuragramma antarctica*) and lithodid crabs.

The spatial distributions and time series of catches of target species within each MEASO area were assessed using catch records from the CCAMLR Statistical Bulletin (hereafter referred to as the Bulletin, CCAMLR, 2019) (see outcomes in **Figures 9**, **10**). Rules for distributing catch from CCAMLR's large-scale reporting areas (Subareas and Divisions) into MEASO areas were developed based on the reports of the Scientific Committee and fishery reports published on the CCAMLR website[3] as well as Kock (1992). Each record in the Bulletin has the reporting area, flag state, year, target species and, in most cases, fishing method. Geographic locations and depth ranges were available in the descriptions of different methods and locations where target species were caught. For CCAMLR reporting areas that overlapped with MEASO areas, catches were partitioned by the proportions of seabed area in the different MEASO areas relative to these locations.

Fisheries for Patagonian toothfish are well established, with integrated assessments using estimated parameters for their stock dynamics along with estimates of abundance are available for the fishery at South Georgia in the Atlantic Sector and Heard

[3]www.ccamlr.org

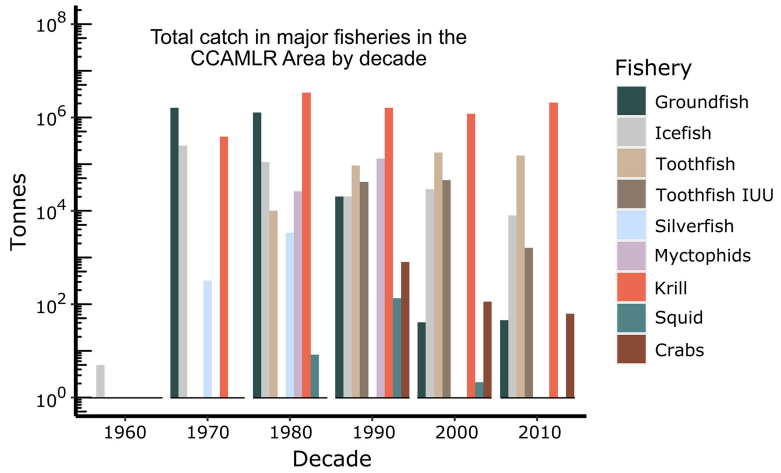

FIGURE 7 | Total catch (tonnes, all taxa) in each major fishery (legend) in the CCAMLR Area in each decade from the 1960s to the present. Data from the CCAMLR Statistical Bulletin 2019.

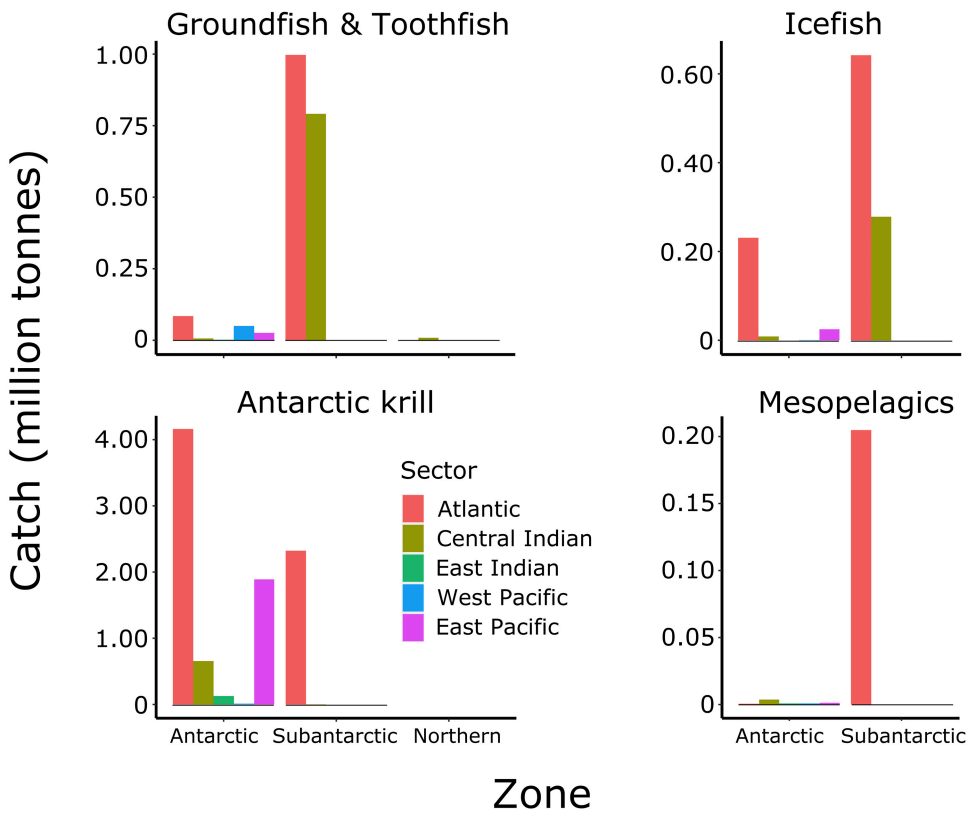

FIGURE 8 | Total accumulated catches (tonnes) of four major groups of target species in each sector (legend) from each zone for MEASO areas as shown in **Figure 2**. Groundfish are primarily *Notothenia rossii*, *Gobionotothen gibberifrons*, *Patagonotothen guntheri*, and *Lepidonotothen squamifrons*. Toothfish are *Dissotichus eleginoides* and *D. mawsoni*. Icefish are primarily *Champsocephalus gunnari* in the Subantarctic and *Chaenodraco wilsoni* in the Antarctic. Antarctic krill are *Euphausia superba*. Mesopelagics consist of myctophids (primarily *Electrona carlsbergi*) and silverfish (*Pleuragramma antarctica*). Data from the CCAMLR Statistical Bulletin 2019.

Island in the Central Indian Sector on the Kerguelen Plateau. These fisheries have regular stock assessments and biannual setting of catch limits, based on the use of the CCAMLR decision rule (Constable et al., 2000; Hillary et al., 2006; Candy and Constable, 2008). Also on the Kerguelen Plateau is the largest toothfish fishery around Isles Kerguelen. The Antarctic

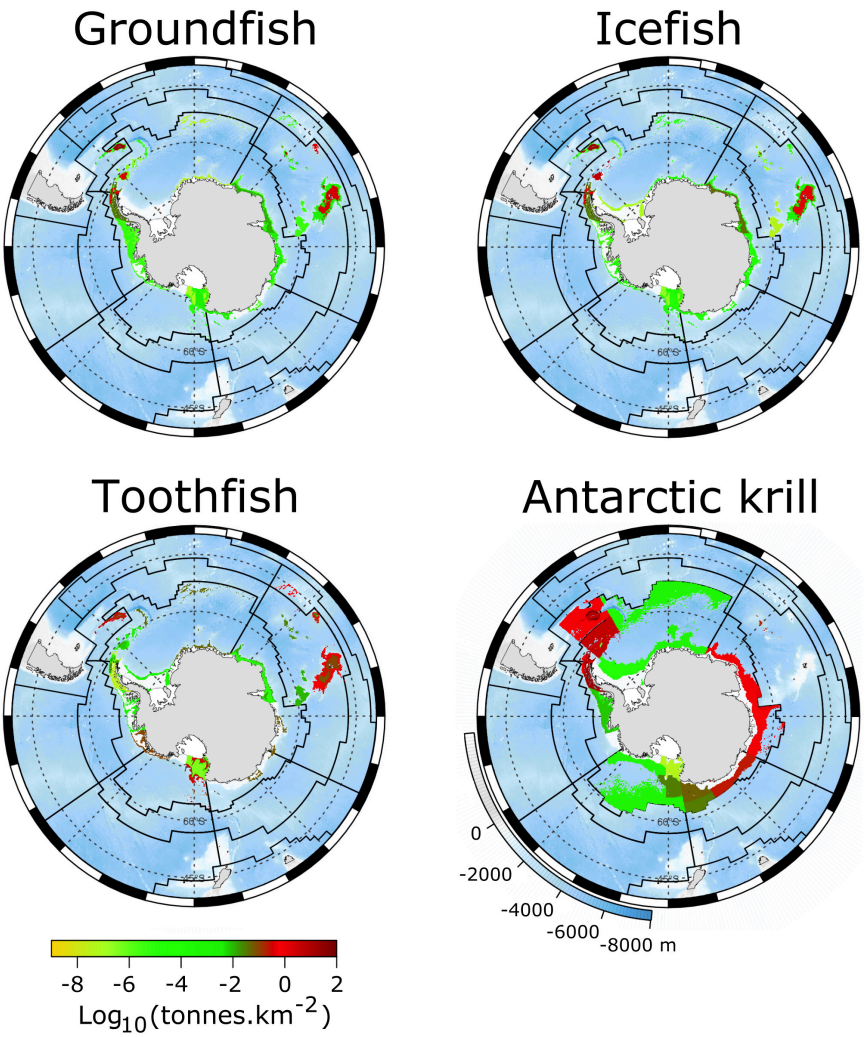

FIGURE 9 | Accumulated catch for groundfish, icefish, toothfish and Antarctic krill from 1970 to 2018 plotted against ocean depth (legend at bottom left of Antarctic krill panel) as catch density (tonnes per square kilometre) on a $\log_{10}$ scale (bottom left legend). Species are those listed in **Figure 8**. Source data: CCAMLR Statistical Bulletin 2019. Grey lines show a graticule, and black lines show the boundaries of the 15 MEASO areas in **Figure 2**.

toothfish fisheries around continental Antarctica are classified as exploratory fisheries with the need to have active research programmes to support the development of the fishery. The most advanced of these is the fishery in the Ross Sea, which began in 1998 and also has an integrated assessment (Mormede et al., 2014). The other Antarctic toothfish fisheries remain in early research phases, despite being present for over a decade. Combined, these fisheries are considered to be sustainable (Croxall and Nicol, 2004; Constable, 2011), although the effects of climate change will need to be considered in their management (Nicol et al., 2007; Larsen et al., 2014; Abrams et al., 2016; Constable et al., 2016c, 2017; Trebilco et al., 2020; Cavanagh et al., 2021).

A threat to the sustainability of the toothfish fisheries was the rise of illegal, unreported and unregulated (IUU) fishing by longliners in the 1990s (Österblom et al., 2015). The catch from IUU fishing was estimated by CCAMLR according to catch rates of the legal fishery, the number of observed IUU longlining vessels and the expected time fishing. Concerted effort amongst CCAMLR Members to combat IUU fishing led to a substantial decline in the IUU fleet and in estimated total illegal catch by 2008 (**Figure 7**). IUU fishing still occurs at a low level but mainly using gillnets. The loss of fish to gill nets is difficult to measure, because observations of vessels cannot be readily translated to the amount of fishing effort and catch rates are difficult to assess. As a result, estimates of IUU catch have not been made since 2008.

A further threat to the toothfish fishery is the depredation of toothfish from longlines (Söffker et al., 2015; Tixier et al., 2016). This can impact the viability of the fishery but also affect the mortality of fish from the fishery; estimates of depredation are needed in order to correctly estimate how many fish have been removed from the stock.

The fishery for Antarctic krill was undertaken in the Atlantic, Central Indian and East Pacific Sectors in its first decade.

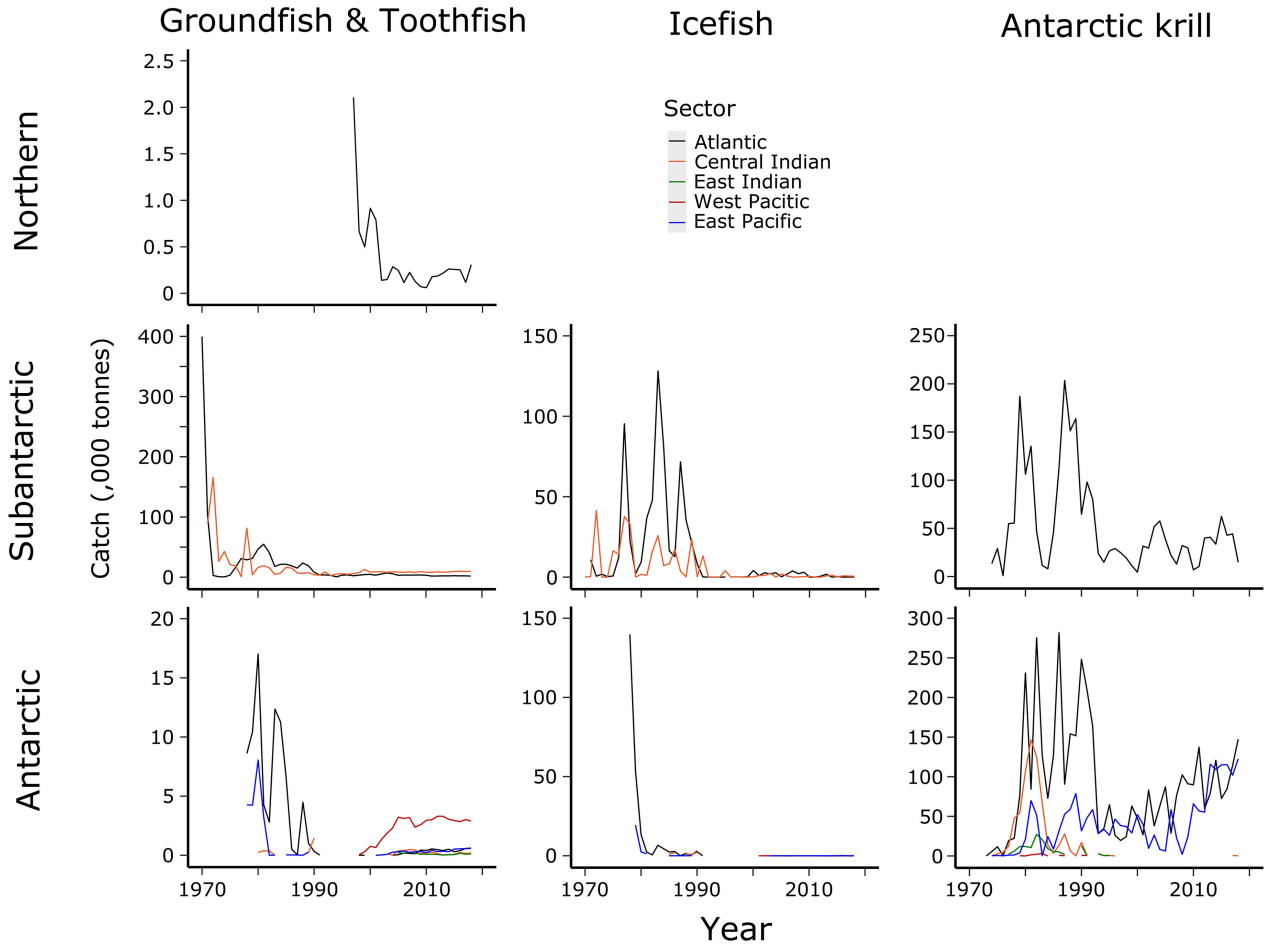

FIGURE 10 | Time Series of catches for target species in each sector (legend in centre top row) for each zone (rows) of MEASO areas (as shown in **Figure 2**). Groundfish and toothfish can be separated at 1991, with groundfish trawling occurring prior to that time and toothfish fisheries (primarily longlining) continuing after that time. Species are those listed in **Figure 8**.

Since then, the fishery has concentrated on the west Antarctic Peninsula (South Shetland Islands and, more recently, Bransfield Strait) in the Antarctic Zone of the East Pacific Sector, and the South Orkney Islands in the Antarctic Zone and South Georgia in the Subantarctic Zone of the Atlantic Sector. After a decline in the krill fishery in 1991, the catch around South Georgia has remained relatively constant, while catches have steadily increased around the South Orkneys (Nicol and Foster, 2016). With increasing open water conditions extending the fishing season into winter, the Bransfield Strait has become a very important location for the fishery (Kawaguchi et al., 2009; Nicol and Foster, 2016). While the krill catch limits are considered sustainable for the krill population as a whole (Constable, 2011), there remains great potential for localised effects of krill harvesting on krill predators (Constable, 2002; Constable et al., 2017), even at the current levels of harvest (Watters et al., 2013, 2020) and particularly under scenarios of climate change (Klein et al., 2018). Recent developments to distribute catch inversely to localised risks to predators has advanced the regulatory approach for krill and could be used to help manage for climate change impacts on the ecosystem (Constable et al., 2016b).

Scope for new fisheries in the Southern Ocean remains primarily in relation to mesopelagic fish and Antarctic silverfish, both of which are important prey species in pelagic and coastal waters, respectively (Koubbi et al., 2017; McCarthy et al., 2019; Saunders et al., 2019).

Incidental Mortality From Fisheries

Incidental mortality from fisheries includes the unintentional catch or entanglement of other fish, seabirds and seals. It can also arise from impacts of fishing gears without capture, such as might occur through the impacts of bottom fishing gears on benthos.

CCAMLR has successfully developed measures to reduce seabird mortality in fishing to only an occasional event. Croxall (2008) describes the measures and strategies put in place from the early 1990s to eliminate systemic incidental mortality from CCAMLR fisheries. Soon after the start of longlining for toothfish began in the late 1980s (**Figure 11**), concern for the capture of seabirds in this fishery led to the development of methods

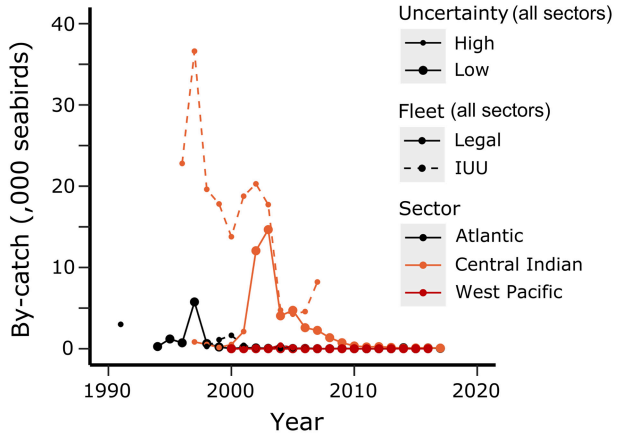

FIGURE 11 | Incidental mortality of seabirds estimated for trawl and longline fisheries (legal fleet; solid lines) and for illegal, unreported and unregulated fishing fisheries (IUU fleet; dashed lines) for each sector of the Southern Ocean (see **Figure 2**). Few birds are caught in the Antarctic Zone. Most are caught near to subantarctic islands. Data obtained from reports of the Scientific Committee of CCAMLR from 1994 to the present. Size of circle reflects the uncertainty in the estimates. Small circles reflect greater uncertainty – in IUU estimates these were labelled by SC-CAMLR as medians. Time-series of IUU estimates end in 2008; IUU fishing was low and vessels used gill nets and catches could not be estimated.

to deter seabirds from attacking baits during deployment and for deterring birds from approaching the gear during hauling. These methods included weighting longlines as well as deploying streamer lines. Strategies included having requirements for scientific observers on fishing vessels to monitor bird interactions with fishing gear and by restricting fishing from seabird foraging areas during the bird breeding season. IUU longline fishing vessels were likely to have had a great impact on seabirds during the height of IUU fishing over the decade from 1997 to 2007 (**Figure 11**). While seabird mortality in CCAMLR fisheries remains low, incidental mortality of Southern Ocean seabirds in longline fisheries outside of the CCAMLR Area remains a great risk to the conservation of some of these species (Clay et al., 2019).

The potential for bottom fisheries, notably trawling, to have significant long-lasting effects on benthic habitats and communities came to the attention of CCAMLR in 2006 (SC-CAMLR, 2006) and measures were taken in 2007 to conserve vulnerable marine ecosystems (VMEs). While CCAMLR established a Conservation Measure to prohibit bottom trawling in high seas areas in CCAMLR it also established measures to protect VMEs from demersal longlining with provisions to move on from areas where high biomass (defined as two buckets) of habitat-forming taxa were observed as bycatch in an individual longline shot (CCAMLR, 2007, 2008). **Figure 12** shows the overall fishing effort as effort density for bottom trawling (hours) and longlining (hooks) given the available effort data from the CCAMLR Statistical Bulletin CCAMLR (2019).

Scaling the effort to the level of disturbance of the seafloor, also known as the fishing footprint, is best done using haul data, including the location of each haul and, in the case of trawls, the swept area of the net (width of the opening of the net combined with the distance towed) and, for longlines, the swept area of the line, which is the amount of sideways movement of the line during its deployment, fishing and retrieval. These data are not available in the Bulletin. In the absence of those data, we examine the effort density per km^2 and use information from Welsford et al. (2014) on the characteristics of trawl and longline hauls to consider the proportion of seabed that might have been affected. We note that the densities in **Figure 12** may be lower than as experienced in local areas because of the method of evenly distributing the effort throughout depth range of a fishery in an area. In addition, localised concentrations may also reduce the effects because of repeated disturbance of the same area.

Effort densities in both trawl and longline fisheries were highest in the Subantarctic Zone in both the Atlantic and Central Indian Sectors. Trawling also had high effort densities in the Antarctic Zone of the East Pacific and Atlantic sectors, from trawling prior to CCAMLR around the Antarctic Peninsula and the islands of the Scotia Sea. Longline effort in the Antarctic Zone has been greatest in the West Pacific Sector associated with the Ross Sea fishery. The only bottom trawl fishery now in operation is at Heard Island. This has been assessed to be localised and not significantly impacting the benthic environment, part of which is due to the presence of the nearby marine protected area (Constable and Welsford, 2011; Welsford et al., 2014; Brooks C.M. et al., 2019).

The greatest accumulated recorded effort for trawling has been a density of 3.1 h per km^2. (log10 = 0.491) (noting the absence of records for the very large catches). For longlining, the greatest accumulated density has been 11,000 hooks per km^2 (log10 = 4.04). Using the mean estimates of swept areas for trawl gear (20 m) and longlines (6.2 m) from Welsford et al. (2014) and assuming trawling was undertaken at a conservative speed of 2 knots, this equates to the proportion of seabed area affected as 23% and 6.8%, respectively.

A shortcoming of the current analysis is the lack of availability of geolocated haul data. Nevertheless, our analyses indicate that the magnitude of impact is unlikely to be trivial at a local scale, if the fisheries are concentrating in sensitive benthic areas. Welsford et al. (2014) provide methods for using geolocated haul data, along with camera deployments on fishing gear, for assessing the direct impacts of fisheries on benthic habitats.

At present, CCAMLR has a process for registering VME locations and providing interim protection to areas identified as possible VMEs, known as risk areas, during longline operations (CCAMLR VME registry[4]). At present (accessed October 25, 2020), it has 53 locations registered as VMEs across the west Antarctic Peninsula, South Orkneys, Ross Sea and East Antarctica. For risk areas identified during fishing, seventy seven areas have been identified in the Ross Sea and one in East Antarctica. There is yet to be a follow-up evaluation of the nature and extent of those sensitive areas, which may be larger than the circumscribed locations.

[4]https://www.ccamlr.org/en/document/data/ccamlr-vme-registry

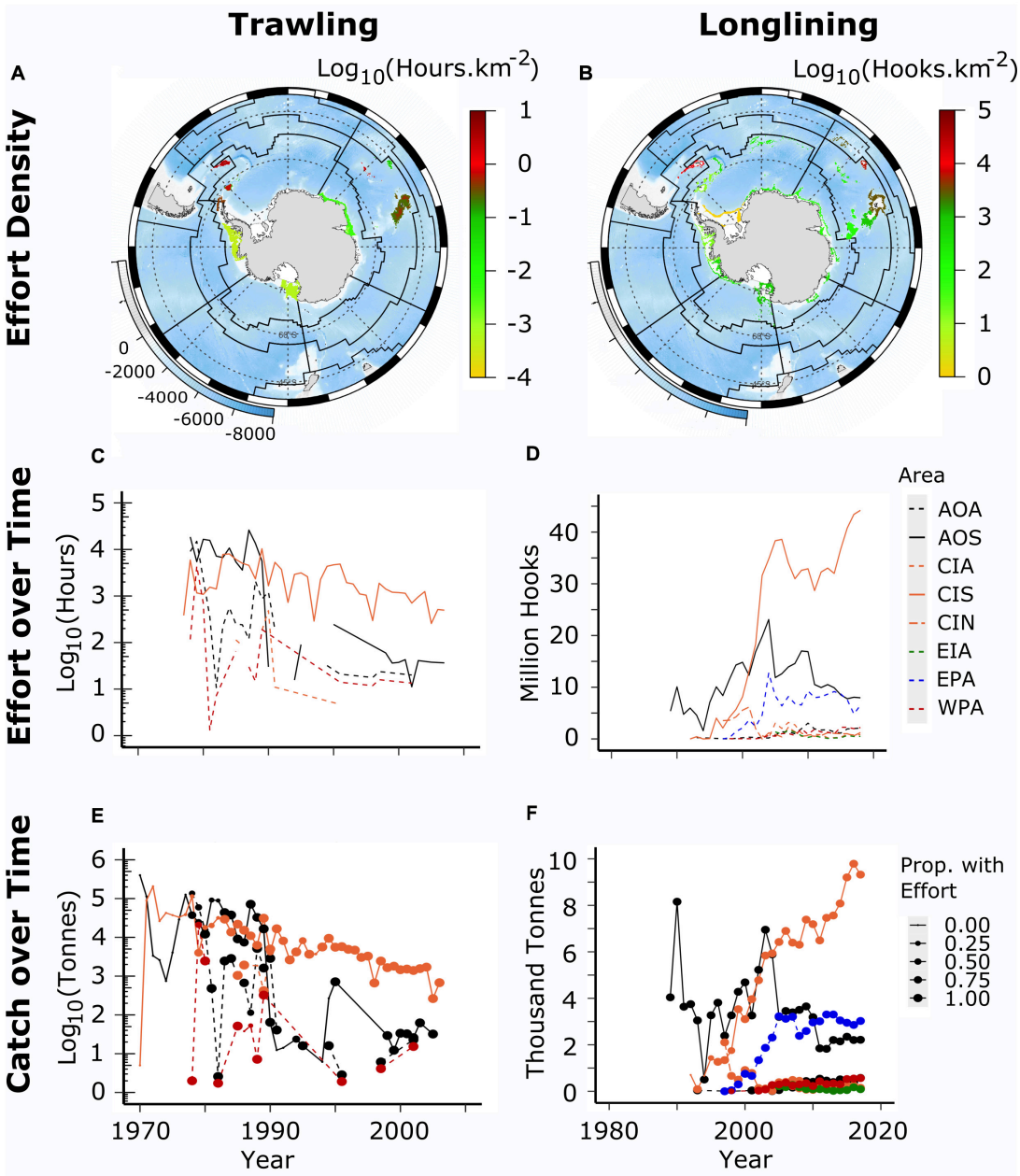

FIGURE 12 | Bottom fishing effort in MEASO areas for trawl and longline fisheries. Top row **(A,B)** shows effort density per km^2 – hours and hooks, respectively, on a log10 scale. Background is ocean depth (bottom left legend on each map). Black lines show boundaries of MEASO areas as depicted in **Figure 2**. Middle row **(C,D)** shows effort over time (split year) in each MEASO area according to the legend at right where labels indicate the sectors (first two letters) and zones (last letter) for each area. Sectors are Atlantic (AO), Central Indian (CI), East Indian (EI), West Pacific (WP), and East Pacific (EA). Zones are Antarctic (A), Subantarctic (S), and Northern (N). Bottom row **(E,F)** shows the time series of catches in each area – colour and line types according to the middle row legend. Catches are the total catch of targeted species in bottom fisheries (groundfish, icefish, and toothfish). Circle size indicates the proportion of the catch that had effort data associated with it.

Recovery of Marine Mammals

Exploitation and recovery of marine mammals has been widespread (Rocha et al., 2014). Here we focus on marine mammal recovery in the MEASO areas that have experienced most human impact; broader trends are reviewed by Bestley et al. (2020).

Following protection from exploitation, many marine mammal species are now recovering, with surveys showing growth, for example, in populations of humpback (Branch, 2011; Ward et al., 2011; Noad et al., 2019), southern right (Cooke et al., 2001; Carroll et al., 2013) and Antarctic blue whales (Branch et al., 2004), all of which seasonally feed in Southern Ocean

waters. As these whales, and some seal species such as fur and crabeater seals, are krill consumers; at a local scale increases in marine mammal abundance may be anticipated to influence krill swarms (Cox et al., 2009; Ducklow et al., 2013), and also influence oceanic nutrient enrichment and mixing (Lavery et al., 2014; Roman et al., 2014).

Krill swarms of different sizes and densities are differentially predated by different whale species (Cox et al., 2009; Santora et al., 2010, 2014; Friedlaender et al., 2014; Miller et al., 2019) due to their varying sizes, morphology and energetic requirements. Reductions in local krill abundance could reduce food available to more area-restricted central place foragers such as breeding penguins and seals. For example, a spatial study of multiple krill predators, using canyon waters near Livingstone Island, suggested an overlap between humpback whales and penguins which would support this idea (Santora and Reiss, 2011). Any reductions may be compounded by local krill fishing, particularly in the Antarctic Peninsula region where this activity is concentrated (Kawaguchi and Nicol, 2020) and partially coincident with the peak period when whales visit (Weinstein et al., 2017). However, prey competition is not necessarily the obvious outcome of whale presence, as whales are less spatially restricted than the central place foragers, may have differing krill swarm preferences (Friedlaender et al., 2009, 2016) and may even modify krill swarm behaviour (e.g., Cox et al., 2009). For example, it is most energetically efficient for whales to target the densest prey patches (Acevedo-Gutierrez et al., 2002; Goldbogen et al., 2011; Friedlaender et al., 2015), while smaller krill predators may be less restricted in their preference. The impact of whale foraging on krill swarm behaviour is also hard to predict; whale predation may, for example, change krill swarming behaviour in ways that make them more accessible to other predators, for example by dispersing high density krill swarms, or by bringing krill closer to the surface.

A second, widely discussed, possible impact of whale recovery concerns their role within the ecosystem as a biological pump, moving nutrients from deep waters to surface waters as they dive to forage, and enhancing surface water nitrogen and iron (and therefore primary productivity) in "pulses," through defecation in surface water (Lavery et al., 2014; Ratnarajah et al., 2014; Roman et al., 2014). Consequently, whales may initiate a positive feedback loop, where the productive places that they go to feed are then further enhanced in terms of primary productivity, because of their presence (Roman et al., 2014). This may be particularly pronounced in enclosed areas such as bays, where current flows are limited. There are widespread, strong and important biota-biogeochemistry interactions in Southern Ocean waters, near and offshore, from megabenthos through to microbes (Cavan et al., 2019; Henley et al., 2020).

In the western Antarctic Peninsula, high densities of humpback whales seasonally feed on krill in the Gerlache Strait and bays of the Peninsula (Nowacek et al., 2011; Johnston et al., 2012). There are no empirical abundance trends available for this population (which seasonally winters in the Pacific waters of central and south America). Model-based estimates using historical catch data suggest the population is close to carrying capacity (IWC, 2016), but high levels of female pregnancy detected within this population (63.5% of females, including mothers with calves, Pallin et al., 2018) suggest that it is still growing. Less is known about the abundance trajectories of other regionally important species; Antarctic blue whale numbers are thought to be increasing further offshore in the Peninsula region based on sighting surveys (Branch, 2007), but since they range widely (Branch et al., 2007), population changes may not be particularly concentrated in local waters. Antarctic minke whales can be locally abundant, but were not heavily exploited during the main commercial whaling period, and there is no evidence that their numbers are increasing locally; if anything, recent surveys suggest a 60% decline over the decade spanning the 1990s (IWC, 2013).

More than 170,000 whales were killed in South Georgia waters, indicating the historical importance of whales at a local scale within this ecosystem (Moore et al., 1999). Anecdotally-reported humpback sightings have risen rapidly in the last decade (Jackson et al., 2015, 2020), consistent with recent assessment that this humpback whale population is now close to recovery from whaling (Zerbini et al., 2019). Formal assessments are not available for other species, but southern right whales are regularly seen (Moore et al., 1999) and there has been steady 6–7% per annum population growth in the Argentine southern right whale calving ground seasonally associated with South Georgia (Cooke et al., 2001). There are also increasing reports of blue whales using South Georgia shelf waters, suggesting some regional recovery (Calderan et al., 2020). The impacts of these changes might mean increased competition for krill with other predators, but these may be balanced by positive benefits from the impact of whales on krill swarms, if whale predation makes them more available to smaller krill predators. Furthermore, as the South Georgia krill fishery operates only during winter, human impacts are minimal during the peak period of whale occurrence.

Coastal Change/Ice Loss and Iceberg Scour

Until recently, climate mediated-marine ice loss in the Southern Ocean was mostly restricted to West Antarctica, but this is now also rapidly occurring throughout East Antarctic seas (Turner and Comiso, 2017). One of the ways in which marine ice is being lost is increased iceberg calving (from ice shelf collapses and glacier retreat). Reduced seasonal freezing of the sea surface in space and time means that such icebergs are less likely to be locked into one location, so the potential of iceberg movement is also increasing (see Smale et al., 2008). Increased iceberg numbers and mobility drives a higher probability and frequency of collisions with the seabed and massive disruptions to benthic biodiversity (Gutt, 2001; Barnes and Souster, 2011). Monitoring of scouring in the productive shallows at Rothera (Barnes, 2017) and Carlini research stations (Deregibus et al., 2017) has shown that two thirds of life shallower than 25 m depth may be wiped out in some years at some locations.

Iceberg scouring decreases markedly with depth, but certain hotspots are regularly impacted even at several hundred meters depth. Large icebergs, tracked via earth observation satellites, have distinct geographic hotspots of grounding, including the East Amundsen Sea in West Antarctica, and the narrow shelf of the Davis and Cosmonaut Seas and Cape Norvegia (East Weddell sea) (see Barnes et al., 2018). Thus, although marine

ice losses are driven by global processes (warming) and have many similarly large influences (e.g., heat and gas exchange), the effect on biodiversity can be quite localised and predictable. Many local areas of iceberg production are likely to gain considerable biodiversity and ecosystem services, for example bays emerging from ice shelf collapses and fjords from glacier retreat (Cavanagh et al., 2021). In contrast, iceberg collision hotspots, such as in the Weddell Sea could lose biodiversity, but there seem to be more blue carbon winners than losers with marine ice loss so far (Barnes et al., 2018). However, it is harder to assess how well Southern Ocean biodiversity will be resilient to the breadth and complexity of stressors, many of which interact, especially on the seabed where we know least, yet most known species occur (Brasier et al., 2021; Zwerschke et al., 2021).

Other global drivers, such as strengthening of winds due to ozone loss, are likely to interact with sea ice changes, for example, in the generation and maintenance of polynyas, and thus influencing primary production (see Arrigo et al., 2008). Recent evidence suggests that moderate sea temperature increases in Antarctica's shallows may increase colonisation and growth in new pioneers (Ashton et al., 2017), thus promoting recovery from ice scour. However, new habitat emerging from glaciers and ice shelves, longer periods of food availability (plankton blooms) and fast growth rates (temperature) are balanced with more ice scour, freshwater input and sediment loading from retreating glaciers, with highly localised but substantial negative impacts (Sahade et al., 2015). The impacts of these many interacting climate-forced variables are difficult to predict with perhaps 'boom and bust cycles' in many nearshore locations, but at least initially there may be more winners than losers (Morley et al., 2019).

PROGNOSES AND PRIORITIES FOR THE FUTURE

In assessing the projected increase or decrease of the influence of local drivers within MEASO areas (summarised in **Table 1**), we identified that the influence on Southern Ocean ecosystems of non-indigenous species, fishing, and the recovery of marine mammals are predicted (*with medium to high confidence*) to increase in the future across all MEASO areas. Fishing and the recovery of marine mammals have the potential to cause ecosystem impacts at the regional or ocean basin scale, as a result of their influences on foodwebs and nutrient cycling. The impacts of these drivers particularly on other marine predators are uncertain given the potential additive effects of fishing, marine mammal recovery and climate change.

The establishment of marine non-indigenous species could have similarly extensive, although unpredictable, ecosystem impacts. While there are currently very few records of non-indigenous species becoming established in the Southern Ocean, increased influence of this driver is predicted (*high confidence*) in the Antarctic Peninsula region and at sub-Antarctic islands, because of the elevated risks from increasing ship traffic and visitation, regional warming and sea ice losses.

The impacts of local, land-derived pollution are currently low, and this is the only driver identified here which is projected (*low confidence*) to decrease in some locations where historical infrastructure has been removed or is no longer in use. However, there is potential for some increase in land-derived pollution (*medium confidence*) with the further development of research station infrastructure and human visits to Antarctica and sub-Antarctic islands, as well as expanded geographic reach following the exposure of more ice-free ground. With the exception of severe incidents such as large oil spills, most point-source pollution influences very small local areas (in comparison to other types of pollution originating from outside the Southern Ocean such as the atmospheric or oceanic transport of POPs), and the most vulnerable habitats are therefore likely to be those in the vicinity of research stations. Areas such as James Ross Island, the coast of East Antarctica and the Ross Sea have seen an increase in station numbers, and while improvements in technology and management have reduced the risk of pollution, the potential for inadvertent fuel spills or other unintended consequences increases with increased national operator activity.

Marine-derived pollution is predicted (*medium confidence*) to increase across most MEASO areas except for those with the lowest levels of ship traffic associated with fishing, research or tourism. Much of this is attributed to the increasing amounts of plastics discovered in marine ecosystems (although coverage of observers and observations has also increased), however, a large proportion is likely to originate from outside the Southern Ocean, given the relatively low numbers of vessels and potential sources (Waller et al., 2017; Horton and Barnes, 2020). The potential impact of marine-derived pollution will increase with additional shipping, particularly in areas of concentrated tourism or scientific research, and where these activities overlap.

Recent trends relating to tourism in the Southern Ocean indicate a projected increase in numbers and diversity of activities in the future (*high confidence*), although this has almost certainly been slowed in the short to medium term by the global impacts of the Covid-19 pandemic. Visitors to Antarctica also include scientific researchers and logistics operators, who may similarly visit wildlife colonies and undertake other activities with the potential to cause disturbance. In areas such as the Antarctic Peninsula where ship traffic is most concentrated, ship strikes and disturbance impact on recovering marine mammal populations are anticipated to increase (*medium confidence*).

Changes to coastal areas as a result of ice loss are also driven by global processes (particularly warming), but have local influences on biodiversity which can be predicted with a high level of confidence, particularly in areas experiencing most rapid warming such as the Antarctic Peninsula and South Georgia. Increased iceberg scour has a direct effect on seafloor communities, while marine and terrestrial areas that are exposed following glacial retreat or ice shelf collapse may provide new habitat for the establishment or spread of non-indigenous species.

The majority of the local drivers identified in **Table 1** are projected to increase or remain at similar levels of influence into the future, indicating that management of these drivers, particularly where they relate to local human activities, is critical. The interaction of all local drivers with each other or with global drivers also demonstrates the importance of such management being developed with integrated consideration of globally-driven

TABLE 1 | Assessment of the projected increase (+) or decrease (–) of the influence of local drivers within MEASO areas (based on information provided in the previous sections).

MEASO area *(defined in* Figure 3*)*	**DRIVER**						
	Marine-derived pollution	**Land-derived pollution *(scientific research stations shown in* Figure 2*)***	**Non-indigenous species**	**Tourism and visitation *(tourist landing sites and scientific research stations shown in* Figure 2*)***	**Marine mammal recovery**	**Fishing *(CCAMLR Subareas shown in* Figure 3*)***	**Coastal change**
AOA	+ ••	± •• (coastal research stations)	+ ••• (northeast Antarctic Peninsula, South Orkney Islands)	± •• (northeast Antarctic Peninsula, South Orkney Islands)	+ ••	+ ••• (CCAMLR Subarea 48.2)	+ ••• (Antarctic Peninsula, Weddell Sea coast)
AOS	+ ••	– •• (South Georgia)	+ ••• (South Georgia)	± •• (South Georgia)	+ •••	+ •• (CCAMLR Subarea 48.3)	+ ••• (South Georgia)
CIA	+ ••	± •• (coastal research stations)	+ •• (coastal research stations)	± •• (coastal research stations)	+ ••	+ •• (CCAMLR Subareas 58.4.1 and 58.4.2)	+ ••
CIS	+ ••	– •• (Crozet, Kerguelen, Heard Island and McDonald Island)	+ ••• (Crozet, Kerguelen, Heard Island and McDonald Island)	± •• (Crozet, Kerguelen, Heard Island and McDonald Island)	+ •••	+ •• (CCAMLR Subareas 58.4.3b, 58.4.4a, 58.4.4b, 58.5.1, 58.5.2, 58.6, 58.7)	n/a
EIA	+ ••	± •• (coastal research stations)	+ •• (coastal research stations – see **Figure 2**)	± •• (coastal research stations)	+ •••	+ •• (CCAMLR Subarea 58.4.1)	+ ••
EIS	± ••	– •• (Macquarie Island)	+ •• (Macquarie Island)	± •• (Macquarie Island)	+ •••	± •	n/a
WPA	+ ••	± •• (coastal research stations)	+ ••	+ •• (Ross Sea coast)	+ •••	+ ••	+ ••
WPS	± ••	n/a	?	n/a	+ ••	+ •• (CCAMLR Subareas 88.1 and 88.2)	n/a
EPA	+ ••	+ •• (coastal research stations)	+ •••	+ •• (western Antarctic Peninsula, South Orkney Islands)	+ •••	+ •• (CCAMLR Subareas 48.1 and 88.3)	+ •••
EPS	+ ••	n/a	?	n/a	+ •••	+ •• (CCAMLR Subareas 48.1 and 88.3)	n/a

± indicates no change; ? indicates no information, and n/a indicates that the driver is not relevant in that area. Black dots indicate the level of confidence (low confidence, medium confidence, high confidence). Local drivers may not have an influence across all of a given area; where this is the case, locations in brackets identify where the influence is greatest.

environmental change. Global human population growth will increase the demand for SO ecosystem services into the future, particularly provisioning services (fishing), but also tourism and the scientific or cultural value of marine biodiversity (Rogers et al., 2020; Cavanagh et al., 2021).

POLICY IMPLICATIONS

Local drivers can be controlled or mitigated, to varying degrees, by the implementation of conservation measures, regulations and guidelines under the instruments of the Antarctic Treaty System and other international governance organisations. In contrast, the regulation of global drivers such as increasing temperature, ocean acidification and sea ice change will require global policy action, such as the implementation of the United Nations Framework Convention on Climate Change (UNFCCC) Paris Agreement, and associated efforts to regulate human activities at national levels. Restrictions on human activities within the Southern Ocean (e.g., fisheries management, regulation of tourism, and establishing protected areas) are important in addressing local and regional drivers, and thus minimising cumulative impacts on Southern Ocean ecosystems, but will have little or no effect on the impacts of global drivers, which may be much more significant. Understanding the interactions between local drivers, and with global drivers, is therefore important for the design of effective policy responses. Management actions taken on individual drivers may affect other drivers, with potentially unintended consequences, therefore an ecosystem-based and integrated approach to management is critical (Millennium Ecosystem Assessment, 2005).

As far as possible, management actions should be informed by comprehensive and accessible information on the status and trends of marine biodiversity and human activities, and particularly the current and projected influence of local drivers. **Box 1** identifies some of the major research gaps and priorities that would help to enhance the information summarised in **Table 1**, and improve the foundations for management decision-making.

Table 2 identifies regulatory frameworks which have established conservation and management measures relevant to specific local drivers. The instruments of the ATS, including CCAMLR and the Protocol on Environmental Protection, form a comprehensive framework allowing for the regulation of fishing, tourism, and impacts associated with human activities including pollution and the introduction of non-indigenous species. Maintenance of the ATS is key to ensuring the ongoing limitation of negative impacts from local drivers on Southern Ocean ecosystems. However, continuing enhancement of its conservation and management approaches is also important, as current tools and frameworks may not be adequate to address future changes to local drivers, or to effectively consider the effects of multiple drivers in the context of climate change.

The Protocol provides general principles of environmental protection applicable to the Antarctic Treaty areas (the area south of latitude 60°S), notably through designation of the continent as a '*natural reserve, devoted to peace and science*.' However, the more detailed provisions described in

BOX 1 | Research gaps and priorities.

Projections of future changes in the influence and extent of local drivers in the Southern Ocean are heavily dependent on an improved understanding of how global drivers such as climate change will affect Southern Ocean ecosystems. The interaction between global and local drivers, such as the consequences of a changing climate for recovering marine mammal populations or for the potential establishment and spread of non-indigenous species, remains poorly understood. It is important to differentiate between trends that are the result of natural environmental variability and those that are anthropogenic or the result of climate change. Fishing and tourism are both ultimately controlled by global markets, and uncertainty about future economic constraints and demand for these services could also make their trajectories difficult to predict. Geopolitical uncertainty may be a further limitation on projections of future change, since changes to the Antarctic Treaty System could lead to the weakening of environmental and fishery regulations, and a corresponding increase in the negative impacts of human activities.

Key information requirements for identifying and managing risks to the Southern Ocean environment associated with local drivers include:

- Identification of local sources of pollutants (especially POPs and microplastics), and mechanisms of transport and accumulation.
- Assessment and monitoring of impacts associated with tourism and other visits.
- Conditions for establishment and rates of spread of marine non-indigenous species.
- Krill biomass and distribution in both fished and unfished areas.
- Vulnerability of marine species and habitats to the effects of all human activities (including local and global drivers).
- Projected responses of krill-dependent predators to fishing and climate change.
- Status of Southern Ocean cetacean populations and regional projections of recovery and consumption.
- Changes to the distribution of ice-free coastal areas and associated marine impacts. While local drivers are concentrated at sites visited by humans, these are also the sites that are most likely to be monitored, although comprehensive monitoring of any site has yet to be achieved. Information from other more remote sites will help to assess the extent to which these influences impact other areas within the MEASO region (although teleconnections to these remote locations, especially from populated areas to the north of the MEASO region, could cause unexpected influences). The coverage of *in situ* monitoring can be improved to some extent by remote observations, for example, satellite remote sensing to monitor coastal change and marine mammal abundance changes, time-lapse cameras to observe breeding success in wildlife colonies, and moorings or autonomous vehicles to obtain oceanographic and acoustic data. The establishment of longer time-series may be required in order to detect trends, and increasing data collection may also require increasing capacity for analysis. New mechanisms to integrate data, for example, using Essential Ocean Variables (EOVs), and to coordinate efforts and data sharing between existing programmes, such as through the Southern Ocean Observing System (SOOS), aim to provide ecosystem information that is accessible to decision-makers (Constable et al., 2016a; Benson et al., 2018; Newman et al., 2019). Ecosystem modelling may also facilitate better understanding of ecosystem processes such as predator-prey interactions and population dynamics, or considerations of how global and local drivers might affect species and foodwebs (Hill et al., 2006; Klein et al., 2018). Fishing vessels provide a large amount of information relevant for fisheries management, through the CCAMLR Scheme of International Scientific Observation (SISO), as well as direct involvement in the collection of data such as acoustic surveys and fish tagging. In recent years, the industry bodies ARK (Association of Responsible Krill harvesting companies) and COLTO (Coalition of Legal Toothfish Operators) have been increasingly engaged in discussions within CCAMLR on further developing fishing industry contributions to data collection. Continued efforts to utilise fishing vessels as scientific research platforms will be valuable in providing the data needed to improve fisheries management (Meyer et al., 2020). Efforts to improve the provision of information relating to local drivers would benefit from clear guidance on the specific information required by ATS bodies to inform management decisions.

(Continued)

BOX 1 | Continued
Improved practical co-operation between different groups involved in Southern Ocean management, primarily CCAMLR and the CEP, but also CCAMLR and the IWC, as well as ACAP, would also have significant benefits in terms of broadening the availability of relevant information, and facilitating the development of comprehensive and more strategic management approaches.

the five Annexes to the Protocol that have so far entered into force, are in most cases now almost 30 years old. Consequently, in most cases there is scope for revision and/or provision of additional guidance detailing potentially higher environmental standards and/or use of new technologies, as now common within many other regions of the planet. For example, impacts in the marine environment from sewage disposal could be reduced through the increased use of sewage treatment plants, including agreed minimum effluent quality standards. Policy development could include improvements in the Environmental Impact Assessment process, more stringent regulation of vessels to reduce the risk of introduction of marine species (particularly on vessel hulls), more comprehensive regulation of tourism activities, and more strategic planning for the implementation of the protected areas system including the adequate protection of vulnerable and/or representative near shore environments, as well as coastal locations accommodating concentrations of Antarctic wildlife. Nevertheless, there is a concern that the pace of change in Antarctic environments and of the level and scope of human activity in the region is not being matched by the pace of development of necessary environmental policy (Hughes et al., 2018).

Effective fisheries management requires an understanding of current and projected impacts from both local and global drivers on target species and associated and dependent species. Consideration of global drivers (climate change, as well as potential socio-economic drivers in terms of demand for ecosystem services, see Cavanagh et al., 2021) must be integrated into management decision-making. As a conservation-focussed body and an integral part of the ATS, CCAMLR differs from Regional Fisheries Management Organisations (RFMOs) in that it is able to address broader objectives of ecosystem conservation. CCAMLR's principles of conservation (Article II of the Convention) include preventing the decrease of harvested populations below levels that ensure their sustainable recruitment; maintenance of the ecological relationships between harvested, dependent and related populations of Antarctic marine living resources; and prevention of changes in the marine ecosystem which are not potentially reversible over two or three decades. Such precautionary approaches should include the spatial distribution of krill catch limits to prevent local impacts on predator populations, as part of the risk assessment and revised krill management strategy currently being developed by CCAMLR (Watters et al., 2013; Hill et al., 2016). Cooperation on data sharing, particularly between CCAMLR and the IWC on ecosystem modelling and consideration of cetacean population changes and krill consumption levels, would be a valuable contribution to this work.

TABLE 2 | Regulatory frameworks establishing measures relevant to specific local drivers.

Local driver	Regulatory framework	Existing measures to limit drivers or mitigate their impacts
Marine-derived pollution	Protocol on Environmental Protection to the Antarctic Treaty. CCAMLR. International Maritime Organisation (IMO).	Annex III (Waste disposal and waste management) and Annex IV (Prevention of marine pollution). Conservation Measure 26-01 on General environmental protection during fishing (including disposal of plastics). MARPOL Annex V on the Prevention of Pollution by Garbage from Ships. International Code for Ships Operating in Polar Waters.
Land-derived pollution	Protocol on Environmental Protection to the Antarctic Treaty.	Annex I (Environmental Impact Assessment) and Annex III (Waste disposal and waste management).
Tourism and visitation	Antarctic Treaty. Protocol on Environmental Protection to the Antarctic Treaty.	Resolution X (2011) on Guidelines for Visitors to the Antarctic. Visitor Site Guidelines (specific instructions on the conduct of activities at the most frequently visited Antarctic sites). Environmental Protocol Annex V (Area protection and management) – designation of Antarctic Specially Protected Areas (ASPAs) and Antarctic Specially Managed Areas (ASMAs).
Non-indigenous species	Antarctic Treaty. Protocol on Environmental Protection to the Antarctic Treaty. CCAMLR. IMO	Resolution X (2011) on Guidelines for Visitors to the Antarctic. Committee on Environmental Protection Non-Native Species Manual. Resolution 28/XXVII on Ballast water exchange in the Convention Area. International Code for Ships Operating in Polar Waters.
Fishing	CCAMLR. Regional Fisheries Management Organisations (RFMOs) adjacent to the CCAMLR Area. Agreement on the Conservation of Albatrosses and Petrels (ACAP).	Conservation Measures establishing: catch limits, open and closed areas, gear restrictions, reporting requirements, bycatch limits, minimisation of incidental mortality, open and closed seasons, and protected areas (including MPAs). Management of fish stocks adjacent to the CCAMLR Area, mitigation of bycatch and incidental mortality. Mitigation of incidental mortality of seabirds, including outside the CCAMLR Area.
Recovery of marine mammals	CCAMLR. IWC.	Krill fishery management strategy – inclusion of cetaceans in the risk assessment framework to inform spatial allocation of krill catch. Population assessments of whale recovery; formal review and validation of regional abundance and trend estimates.
Coastal change	CCAMLR	Conservation Measure 24-04 on establishing Special Areas for Scientific Study in newly-exposed marine areas following ice shelf retreat or collapse.

In addition to fishery-specific measures, CCAMLR also has a mandate to implement marine protected areas (MPAs) with objectives including the conservation of biodiversity, establishment of scientific reference areas, protection of areas vulnerable to the impacts of human activities, and of areas to maintain resilience to climate change (CCAMLR Conservation Measure 91-04). While progress toward CCAMLR's agreed objective to establish a representative system of MPAs has been limited to date, the adoption of a suite of additional areas currently under negotiation would substantially improve the representation of Southern Ocean biodiversity in protected areas (Brooks et al., 2020). Antarctic Specially Protected Areas (ASPAs) can also be implemented in marine areas under the Protocol on Environmental Protection, and could be nested within MPAs or established in complementary areas as part of a more strategic approach to the conservation of marine ecosystems across both CCAMLR and the CEP. Localised conservation and management actions such as MPAs, ASPAs or VME designations could also act as a driver of recovery for marine ecosystems, by reducing or removing other drivers that have previously resulted in negative impacts, for example, the recovery of locally impacted benthic habitats following closure to fishing (considered in Brasier et al., 2021).

The interaction between CCAMLR and the CEP also has an important role to play in identifying and progressing issues of common interest with regard to local drivers. For activities which affect the marine environment, cross-over responsibilities are established within the respective conventions, for example to ensure that all CCAMLR Members acknowledge the special obligations and responsibilities of the Antarctic Treaty Consultative Parties for the protection and preservation of the environment of the Antarctic Treaty area (CCAMLR Convention, Article V), and to provide for CCAMLR approval of marine Antarctic Specially Protected Areas (Environmental Protocol, Annex V). Joint workshops have also agreed customary practices establishing which body will 'lead' on topics such as non-native marine species (CEP) and marine spatial protection (CCAMLR) (ATCM, 2009), while cooperation on climate change and monitoring was the focus of the most recent joint CEP and CCAMLR Scientific Committee discussions (CCAMLR, 2016). Although not yet implemented to their full potential, the range of tools available across CCAMLR and the Environmental Protocol, particularly on spatial protection, should allow for comprehensive systems of marine protection and management to be established in the Southern Ocean, tailored to the specific requirements of different regions and human activities.

Additional global frameworks such as the International Maritime Organisation (IMO) provide additional measures that apply to all vessels in the Southern Ocean, particularly through the International Code for Ships Operating in Polar Waters. Adjacent RFMOs[5] can also implement measures that may reduce impacts on Southern Ocean species (for example bycatch mitigation measures to protect highly migratory seabirds, and controls on discarding fishing gear). However, cooperation between CCAMLR and neighbouring RFMOs would benefit from improved communication, and data-sharing to address changes in stock structure, by-catch and environmental and climate change impacts (CCAMLR Performance Review, CCAMLR, 2017).

Integrated management across the ATS and related instruments is needed to address the specific impacts of local drivers in the context of broader environmental conditions, particularly in relation to climate-related change. Such management will be most effective where it is informed by robust scientific information and projections of change, and new innovations (particularly in modelling and remote observations) will help to provide this. However, there is also a need for precautionary measures to ensure that risks are minimised, especially where data are limited or when confidence in projections of the nature and extent of the impacts of drivers on biota is low. Although heavily impacted by historic exploitation of marine species, the Southern Ocean remains less affected by current local drivers of change such as pollution and fishing than much of the rest of the global ocean. The unique governance frameworks of the Antarctic Treaty System provide the means to ensure that this status is maintained into the future.

AUTHOR CONTRIBUTIONS

SG and CLW outlined the manuscript and coordinated text contributions. SG, AC, DB, MB, MD, KH, JJ, and CMW contributed text on individual sections. SG and CLW designed **Figures 1**, **3** which were produced with assistance from HG, Stacey McCormack and the MEASO Support Group. AC produced **Figures 2**, **4**–**12**. SG and SM developed **Tables 1**, **2** with input from all authors. All authors contributed to development and revision of the manuscript.

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[5]RFMOs adjacent to the CCAMLR Area are: South-East Atlantic Fisheries Organisation (SEAFO), South Indian Ocean Fisheries Agreement (SIOFA), South Pacific Regional Fisheries Management Organisation (SPRFMO), Commission for the Conservation of Southern Bluefin Tuna (CCSBT).

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Productivity and Change in Fish and Squid in the Southern Ocean

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Southern Ocean ecosystems are globally important and vulnerable to global drivers of change, yet they remain challenging to study. Fish and squid make up a significant portion of the biomass within the Southern Ocean, filling key roles in food webs from forage to mid-trophic species and top predators. They comprise a diverse array of species uniquely adapted to the extreme habitats of the region. Adaptations such as antifreeze glycoproteins, lipid-retention, extended larval phases, delayed senescence, and energy-conserving life strategies equip Antarctic fish and squid to withstand the dark winters and yearlong subzero temperatures experienced in much of the Southern Ocean. In addition to krill exploitation, the comparatively high commercial value of Antarctic fish, particularly the lucrative toothfish, drives fisheries interests, which has included illegal fishing. Uncertainty about the population dynamics of target species and ecosystem structure and function more broadly has necessitated a precautionary, ecosystem approach to managing these stocks and enabling the recovery of depleted species. Fisheries currently remain the major local driver of change in Southern Ocean fish productivity, but global climate change presents an even greater challenge to assessing future changes. Parts of the Southern Ocean are experiencing ocean-warming, such as the West Antarctic Peninsula, while other areas, such as the Ross Sea shelf, have undergone cooling in recent years. These trends are expected to result in a redistribution of species based on their tolerances to different temperature regimes. Climate variability may impair the migratory response of these species to

environmental change, while imposing increased pressures on recruitment. Fisheries and climate change, coupled with related local and global drivers such as pollution and sea ice change, have the potential to produce synergistic impacts that compound the risks to Antarctic fish and squid species. The uncertainty surrounding how different species will respond to these challenges, given their varying life histories, environmental dependencies, and resiliencies, necessitates regular assessment to inform conservation and management decisions. Urgent attention is needed to determine whether the current management strategies are suitably precautionary to achieve conservation objectives in light of the impending changes to the ecosystem.

Keywords: marine ecosystem assessment, climate change, conservation management, Antarctic, fisheries, notothenioids, myctophids, squid

INTRODUCTION

The fish and squid species of the Southern Ocean are uniquely adapted to the extreme conditions of the waters surrounding Antarctica. These adaptations leave Southern Ocean fish and squid vulnerable to the environmental variability introduced by climate change and the potential for compounding impacts of existing drivers on diversity and biomass in the region. Hereafter, we collectively refer to these species as 'fish' unless there is a need to address species from other regions, or to explicitly differentiate between finfish and squid. In this paper, we assess the current state of knowledge for selected taxa, divided into seven groups by ecological function or habitat, as well as considering the utility of non-taxonomic groupings. We explore the interplay between hydrography and life history for their effects on population structures and health of species. We consider the ways in which data are collected on Antarctic fish, namely through the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) and from fisheries-independent sources. We assess challenges to the interpretation of these data with respect to observation bias and sampling. At its heart, this chapter presents an assessment of the impacts of drivers of change on Antarctic fish and squid abundance, considering the impacts of fisheries, climate change, pollution and pathogens. Finally, we outline prognoses for the future, including the identification of knowledge gaps and areas that will present challenges for researchers and managers.

TYPES OF FISH AND SQUID IN THE SOUTHERN OCEAN

Fish and squid of the Southern Ocean are often considered with respect to groupings corresponding to ecological function and/or habitat. A typical distinction is between benthic and pelagic fish species (**Table 1**). The pelagic habitat can be further subdivided by depth and its corresponding light regimes. The Southern Ocean has very few epipelagic fish taxa, i.e., those which occupy the upper 200 m of the water column. The limited diversity of epipelagic species relates to the nature of the notothenioid fishes, the dominant clade in high-Antarctic waters in terms of diversity and abundance (Eastman, 2005). The notothenioid fishes diversified in an adaptive radiation from a benthic ancestor (Eastman, 1993). Adaptations such as reduced ossification and lipid sacs facilitated pelagization of some notothenioids despite their lack of a swimbladder (Devries and Eastman, 1978; Eastman and DeVries, 1981; Klingenberg and Ekau, 1996). Still, only nine notothenioid species are categorized as pelagic, including the most prominent pelagic Antarctic fish, *Pleuragramma antarctica* (Duhamel et al., 2014). The same authors list a total of 156 pelagic species in the Southern Ocean, 72 of which are recorded only occasionally south of the Sub-Tropical Front (STF). Unlike *P. antarctica* and a few cryopelagic notothenioids, the majority of pelagic species can be described as meso- or bathypelagic, i.e., dwelling in the twilight zone (∼200–1,000 m) or deeper. The most speciose family in this domain are the lanternfish (Myctophidae), but several others are regularly recorded (e.g., Bathylagidae, Stomiidae, Paralepididae, and Zoarcidae). Other species are typical deep-sea inhabitants that live beyond the Antarctic continental shelf in the vast deep-sea basins of the Southern Ocean. A total of 206 species, 9 of which are occasionally recorded south of the STF, are categorized as deep-sea fish (Duhamel et al., 2014). Common deep-sea representatives are snailfishes (Liparidae), eelpouts (Zoarcidae), grenadiers (Macrouridae), and some notothenioids (e.g., *Bathydraco* spp.). The toothfish species (*Dissostichus eleginoides* and *Dissostichus mawsoni*) traverse the boundaries of such a habitat-based classification, as they forage in both benthic, neritic as well as pelagic and deep-sea habitats (Hanchet et al., 2015; Troccoli et al., 2020). In addition, many fish species change habitat occupancy with ontogeny, such as a shift from pelagic larvae and juveniles to benthic adults.

The neritic zone, comprising the shallow (<200 m) waters of the Antarctic continental shelf as well as peri-insular subantarctic shelves and oceanic seamounts, is inhabited by 120 species, 3 of which have only occasionally been recorded south of the STF (Duhamel et al., 2014). Various notothenioids, mostly with benthic or epibenthic lifestyles, occur throughout the depth range of the neritic habitat (Eastman, 2017). Rays (Rajidae) and eel cods (Muraenolepididae) are abundant in some neritic habitats of the Southern Ocean as well. The ecology of neritic species has been investigated in diverse regions of the Southern Ocean. On the Antarctic shelf, species assemblages are related to the topography and disturbance of the environment. Projects from the Census of

TABLE 1 | Common taxa of fish and squid in the Southern Ocean, the types of habitats in which they reside, and the functional groupings to which they are often assigned.

Taxon	Common term for group to which it belongs	Trophic group	Habitat	Commercially targeted	Specific mention in conservation measures of CCAMLR
Myctophidae	Lanternfish	Mid	Mesopelagic, bathypelagic	Historical	*Electrona carlsbergi*
Macrouridae	Grenadiers	Mid	Benthopelagic	Bycatch	*Macrorus* spp.
Notothenioidae	Silverfish	Mid	Cryopelagic, epipelagic	NA	NA
	Marbled rockcod	Mid	Benthic	Historical	*Notothenia rossii*
	Toothfish	Top	Benthopelagic	Current	*Dissostichus eleginoides, Dissostichus mawsoni*
Channichthyidae	Icefish	Mid	Epipelagic, benthopelagic	Historical	*Champsocephalus gunnari*
				Current	*Champsocephalus gunnari*
Cephalopoda	Antarctic squid	Mid/top	Epipelagic, mesopelagic, bathypelagic, benthopelagic	NA	NA

Antarctic Marine Life (Schiaparelli et al., 2013) revealed that there are clear differences between assemblages on banks, shelf breaks, inner shelf depressions, and outer shelf canyons (Causse et al., 2011). This has helped to draw fish ecoregions (Koubbi et al., 2010) that are probably explained by the capacity of neritic fish to deal with stressors in their environment, particularly habitat disturbance from iceberg scouring. Neritic fish assemblages in subantarctic areas are influenced by the geography of islands. Bays and fjords such as in South Georgia or Kerguelen are important spawning or nursery grounds for some species. The geography and island mass also influence the velocity of the Antarctic Circumpolar Current, creating retention areas which are very productive and essential for the early life stages of fishes (Koubbi et al., 2009). More details on the biogeographic and depth-related groupings of Southern Ocean fish can be found, e.g., in Duhamel et al. (2014) and Eastman (2017).

Regarding ecological function, or more specifically position in the food web, most Southern Ocean fish can be considered forage species that occupy a mid-trophic level. Plankton feeders like myctophids and Antarctic silverfish occur in vast numbers and are key food sources for various higher trophic level predators, including larger fishes, penguins, flying seabirds, and marine mammals (Vacchi et al., 2017). Many notothenioids and squid are mid-level consumers of other fish, crustaceans, and various other invertebrates, including cnidarians, salps, polychaetes, echiurans, sipunculids, priapulids, and molluscs (DeWitt et al., 1990; Xavier et al., 2018). Some notothenids form large aggregations as well, at least historically, such as the marbled rockcod *Notothenia rossii* (Kock, 1992). While toothfishes (*Dissostichus* spp.) are preyed upon by seals and sperm and killer whales, they arguably are top predators of the marine realm themselves, with a role similar to that of sharks in other oceans, feeding on a variety of fish and squid (Fenaughty et al., 2003; Hanchet et al., 2015). Here, we review the productivity and change for selected groups of both forage species and top predators.

Research has focused mostly on the notothenioids because of their commercial relevance and fascinating evolutionary history (Kock, 2007; Matschiner et al., 2015). Recently, the importance of mesopelagic fish, particularly myctophids, has become widely-appreciated and attracted increased scientific attention (Hill et al., 2012; Taillebois et al., 2017; McCormack et al., 2020; Woods et al., 2020). Given the overall diversity of Southern Ocean fish, it seems clear that much remains to be learned about other species in addition to notothenioids and myctophids, but comparatively few studies have investigated these so far (see e.g., Todgham et al., 2007; Duhamel et al., 2010; Dettai et al., 2011; Moteki et al., 2011; McMillan et al., 2012; Pinkerton et al., 2013; Prirodina and Balushkin, 2015; Christiansen et al., 2018).

Life Histories, Functional Relationships and Population Ecology

Understanding life histories and geographical connectivity are essential to assess and model population and stock structure (Jones et al., 2007). The term 'stock' is typically used in fisheries contexts to refer to an independent, self-recruiting population (Reiss et al., 2009). Hereafter, we use the term population when discussing life histories and ecologies of fish. Population health is defined as the robustness of a population to variation in its environment, i.e., its ability to withstand die-off events, poor recruitment years, and climate change impacts (Young et al., 2018). Understanding population structure is key in assessing population health. Many approaches exist to ascertain population structure, including genetics, otolith analyses, parasitology, tagging, and age/growth analysis; integration of multiple techniques yields the most informative results (Paris et al., 2018).

We consider here three important aspects of life history and connectivity: (1) ontogenetic dispersal, (2) water column occupation, and (3) reproduction patterns and longevity. While many Antarctic fish occupy benthic niches as adults and are thus more restricted spatially, most have pelagic or cryopelagic larval phases that enable dispersal (Eastman, 2005). Inhabiting the water column provides these larvae with the opportunity to be transported over large distances depending on their exposure to prevailing current systems (Loeb et al., 1993; Matschiner et al., 2009; La Mesa et al., 2016). Furthermore, many fish and squid species, particularly those that account for large proportions of biomass within the Southern Ocean (e.g., Antarctic silverfish, myctophids), have wholly pelagic or mesopelagic life histories, and thus their life histories are necessarily more convoluted (Duhamel et al., 2014).

The prevailing hydrography in the Southern Ocean informs current hypotheses regarding population structure of many species of Antarctic fish (Ashford et al., 2017b). Driven by the westerlies, the ACC is the largest current system in the world, hovering around 60°S with varying widths and extents as it makes its way around the Antarctic continent (Rintoul and da Silva, 2019). The ACC has the potential to transport shelf species where it approaches the continental slope along the western Antarctic Peninsula and East Antarctica (Orsi et al., 1995). It forms portions of the Ross and Weddell Gyres, where it can transport fish from offshore seamounts toward the continental shelf (Rintoul and da Silva, 2019; Vernet et al., 2019). The Antarctic Slope Current (ASC) is measured from the Amundsen Sea to the tip of the Antarctic Peninsula, traveling in an anti-clockwise direction along the continental slope (Thompson et al., 2018). The ASC can promote regional transport between trough systems at the edge of the continental shelf, as well as facilitating circumpolar transport for shelf species (Ashford et al., 2017b; Caccavo et al., 2018). Finally, the buoyancy-forced Antarctic Coastal Current (AACC) hugs the coast, and is detected along all parts of the Antarctic continent to varying degrees depending on the season, given its relationship to meltwater runoff and wind stress (Moffat et al., 2008; Núñez-Riboni and Fahrbach, 2009; Kim et al., 2016). The AACC moves in an anti-clockwise direction and promotes local transport and inshore connectivity between trough heads (Ashford et al., 2017b; Caccavo et al., 2018).

Given the life history of Antarctic fish and the hydrography of the Southern Ocean, the null hypothesis for population structure for Antarctic fish is one of panmixia (Matschiner et al., 2009; Damerau et al., 2012). In many species, however, evidence for the contrary has been found. Recent work on the myctophid *Electrona antarctica* revealed a complex population structure influenced by the ACC and the ASC in East Antarctica characterized by divergent otolith nucleus chemistry, which reflects exposure to distinct early life environments (Zhu, 2018). Antarctic silverfish were found to have a largely contiguous population with evidence for high levels of gene flow between the Ross and Weddell Seas, as well as the Antarctic Peninsula (Zane et al., 2006; Caccavo et al., 2018, 2019). This connectivity was hypothesized to be supported by the ASC, as exceptions to this finding coincided with areas not reached by the near-circumpolar slope current (the western Antarctic Peninsula and the South Orkney Islands) (Agostini et al., 2015; Caccavo et al., 2018). Importantly, connectivity was found to vary over time in Antarctic silverfish, a phenomenon referred to as chaotic genetic patchiness (Agostini et al., 2015; Caccavo et al., 2018). Chaotic genetic patchiness has also been observed in icefish populations of *Chaenocephalus aceratus* at the South Shetland Islands (Papetti et al., 2007). Complex patterns of genetic connectivity were observed between populations at the South Shetland and South Orkney Islands related to the ACC in *C. aceratus* and *Chionodraco rastrospinosus* (Papetti et al., 2007, 2012). Work on Patagonian and Antarctic toothfish found mixed evidence of population heterogeneity on a circumpolar scale. Populations between the Indian, Pacific and Atlantic sectors of the Southern Ocean were significantly different using nuclear markers, while mitochondrial markers only differentiated the Pacific population (Toomey et al., 2016). Early genetics work in Antarctic toothfish with a small number of markers indicated conflicting results (Parker et al., 2002; Kuhn and Gaffney, 2008; Mugue et al., 2014), while otolith chemistry supported distinct populations between the Ross Sea and the Antarctic Peninsula (Ashford et al., 2012). Such variability in connectivity over time emphasizes stochasticity as an important aspect of population structure.

Forage Species

Myctophids

Myctophids (Family Myctophidae) are the most abundant and biomass dominant family of Southern Ocean ichthyofauna inhabiting the mesopelagic (200–1,000 m) and bathypelagic (>1,000 m) zones (Gjøsæter and Kawaguchi, 1980). Biomass estimates are likely to be an order of magnitude higher than the previously reported estimate of 212–396 million tonnes (Lubimova et al., 1987; Kaartvedt et al., 2012), with highest abundances at frontal zones (Pakhomov et al., 1996; Van de Putte et al., 2010; Collins et al., 2012). These small fish (<20 cm in length, **Table 2**) are relatively diverse, with 68 species recorded south of the Sub-Tropical Front (STF; Duhamel et al., 2014). Community composition is influenced by meso- and sub-mesoscale oceanographic features with a sharp transition in assemblages at the major frontal zones, the Polar Front, the Subantarctic Front and the Sub-Tropical Front (Koubbi et al., 2011b; Duhamel et al., 2014). The high association of lanternfish with certain pelagic ecoregions exposes them to impacts from major environmental changes in the subantarctic and subtropical zones, where a southward shift in frontal regions has been observed (Constable et al., 2014).

Most myctophid species migrate vertically on a diel basis, feeding in surface waters at night and descending to mesopelagic depths during the daylight hours (Brierley, 2014; Duhamel et al., 2014). This behavior has implications for carbon sequestration and climate regulation, as organic carbon is actively transported from the surface to the deep ocean (Brierley, 2014; Irigoien et al., 2014). Myctophids are important mid-trophic level components of the pelagic food web, comprising a key link for the transfer of energy from primary consumers and omnivorous macro-zooplankton to a range of top predators (Murphy et al., 2012; Schaafsma et al., 2018). Importantly, their central position in the food web means that they exert considerable control on the ecosystem by top-down control on lower trophic levels, and on higher trophic levels via variations in their biomass (Griffiths et al., 2013).

In some regions and seasons, the energy pathway through myctophids is the most important in sustaining top-predator biomass (McCormack et al., 2020). It has been suggested that this pathway may become increasingly important and provide a potential buffer against reductions in Antarctic krill biomass (Murphy et al., 2007a; McCormack et al., 2020). Extensive study of the Scotia Sea ecosystem has allowed for the characterization of these alternative energy pathways in this region. Bioregionalization studies have identified a transition from a krill-dominated to a fish-dominated community in the Scotia Sea broadly partitioned by the Southern Antarctic

TABLE 2 | Summary data for common taxa of fish and squid in the Southern Ocean on their life histories, population ecology, and stock structure.

Taxon	Common term for group to which it belongs	Lifespan (years)	Age at maturity (years)	Size (cm)	Preys	Predators	Ontogenic movements
Myctophidae	Lanternfish	2 – 7	2 – 3	5 – 20	Plankton	Penguins, flying seabirds, seals, larger fish	Association with pelagic ecoregions, geographically distributed along latitudinal gradients, evidence for seasonal migration
Nototheniidae	Silverfish	12 – 14	4 – 7	10 – 20	Plankton	Penguins, flying seabirds, seals, whales, larger fish	Early life at sea ice edge, ontogenic migration toward the continental slope, followed by retention in local trough systems
	Marbled rockcod	13 – 20	6 – 8	50	Plankton	NA	Inshore migrations associated with reproduction
	Toothfish	25 – 40	12 – 17	100 – 200	Fish, cephalopods, crustaceans	Seals, whales	Spawning on offshore seamounts followed by transport inshore by gyre systems to the shelf where juveniles develop
Champsocephalus gunnari	Icefish	4 – 5	2	44	Krill	Penguins, flying sea birds, seals, larger fish	Northern peninsula and subantarctic shelf and slope areas
Cephalopoda	Antarctic squid	1 – 2	Semelparous	NA	Fish, crustaceans, smaller squid	Toothfish, penguins, flying sea birds, seals, whales, skates, sharks	NA

NA, unknown.

Circumpolar Current Front (SACCF) (Stowasser et al., 2012; Ward et al., 2012). North of the SACCF, myctophids are key to the conversion of secondary productivity to King penguins (Bost et al., 1997, 2002; Olsson and North, 1997; Raclot et al., 1998; Cherel et al., 2010), Gentoo penguins (Xavier et al., 2017), albatrosses (Xavier et al., 2003), Antarctic fur seals (Croxall et al., 1999), and cephalopods (Rodhouse et al., 1992); while krill trophic pathways dominate in the south (Stowasser et al., 2012; Ward et al., 2012).

Similar trophic pathways have been identified in the southern Kerguelen Axis region in East Antarctica. In this region, myctophids are important prey items for Emperor penguins, Weddell seals, and southern elephant seals (McCormack et al., 2020). Here, the ecological role of myctophids varies latitudinally (McCormack et al., 2020). Latitudinal variation in diet and relative trophic position has been demonstrated for key myctophid species (Riaz et al., 2020; Woods et al., 2020). Euphausiids are the main prey item for myctophids residing in the pelagic zone south of the Southern Boundary of the Antarctic Circumpolar Current (SB-ACC). In contrast, myctophids residing north of the SACCF consume a more diverse range of prey items, including copepods, amphipods, fish, and gelatinous prey (Clarke et al., 2018; Riaz et al., 2020). Northern myctophids also occupy higher trophic levels compared to those in the south (Woods et al., 2020), indicating a more diverse range of trophic linkages.

Further north near the Kerguelen Islands, the pelagic ecosystem in the Polar Frontal Zone (PFZ) is void of Antarctic krill (Koubbi et al., 2011a). A high abundance and diversity of myctophids is characteristic of this ecosystem, in which 14 species coexist (Cherel et al., 2010). Their high abundance and availability in the water column emphasizes their importance to predators in the area, such as King penguins (Cherel et al., 2010; Duhamel et al., 2010) and breeding female southern elephant seals (Cherel et al., 2008). The isotopic signatures of the myctophid assemblage provides evidence of trophic partitioning, indicative of the coexistence of a concentrated number and diversity of species (Cherel et al., 2010). Species showed differences in either habitat usage or trophic level, which indicated latitudinal movements and a size-based trophic structure, with larger-sized species occupying higher trophic levels compared to smaller-sized species (Cherel et al., 2010). Studies undertaken in the Scotia Sea and in the Indian Ocean (Kerguelen Axis and Kerguelen Islands) have demonstrated the spatially variable trophic role of myctophids in the Southern Ocean ecosystem.

Antarctic Silverfish

The Antarctic silverfish (*Pleuragramma antarctica*) is a key species in the continental shelf ecosystems of the Southern Ocean (Vacchi et al., 2017). Although devoid of a swimbladder, silverfish are pelagic throughout their life history (Eastman and DeVries, 1989). Embryos develop under the solid fast ice in coastal areas among ice platelets (Vacchi et al., 2012; Guidetti et al., 2015). Larvae are found from 0 to 100 m and descend to deeper layers at the post-larval phase; post-larvae and juveniles up to 2+ years are found at depths up to 400 m (La Mesa et al., 2010) and adults are typically found at depths from 400 to 700 m (La Mesa and Eastman, 2012). There is also horizontal segregation of the early life stages (Koubbi et al., 2011b). Silverfish exhibit diel vertical migrations, moving to shallower depths at night and deeper during the day (Plötz et al., 2001; Fuiman et al., 2002; Robison, 2003; Lancraft et al., 2004) to avoid visual predators and to profit from the congregation of prey species such as *Euphausia superba*, which are nearer to the surface at night (Hopkins and Torres, 1988; Robison, 2003; Lancraft et al., 2004).

Antarctic silverfish are generalist feeders relying on various food items depending on life stage, location, and availability. Larvae feed on diatoms and small copepods (Koubbi et al., 2007; Granata et al., 2009). Other life stages predominantly feed on euphausiids, *Euphausia crystallorophias* in the continental shelf waters and *E. superba* near the continental slope and over deeper waters, and copepods, including *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, *Metridia gerlachei,* and *Euchaeta antarctica*, though other invertebrates and fish are also suitable prey items (Pinkerton, 2017; Tavernier and Giraldo, 2017; Carlig et al., 2019). Changes in habitat occupancy correlate with ontogenetic shifts in diet composition, such that silverfish occupy several trophic levels throughout their 12–14-year lifespan (**Table 2**) (Kellermann, 1987; Giraldo et al., 2011, 2015; Tavernier and Giraldo, 2017). Involved in the energy transfer from primary producers to large fish predators (Mintenbeck et al., 2012), in areas where krill is less abundant, the Antarctic silverfish is the main prey item for krill-dependent species, such as Adélie penguins (La Mesa et al., 2004).

Early life dependence on coastal fast ice, and later movement into deeper waters expose silverfish to hydrographic features along the continental shelf resulting in a complex life history which generates the conditions for a dynamic population structure and underlying patterns of connectivity (Ashford et al., 2017b). The silverfish life-history hypothesis incorporates these physical–biological interactions, predicting that cross-shelf circulation mediates retention within populations and exposure to along-shelf transport pathways (Agostini et al., 2015; Ashford et al., 2017b; Brooks et al., 2018b; Caccavo et al., 2018, 2019). Schools of adult silverfish have been observed moving inshore along the Antarctic Peninsula (Daniels and Lipps, 1982), and aggregations attributed to adult silverfish have been detected using bio-acoustic tools in the Ross Sea, supporting the hypothesis that silverfish are moving into Terra Nova Bay during winter to spawn (O'Driscoll et al., 2018b). Large amounts of eggs develop within the platelet ice layer under the fast ice in the western Ross Sea (Vacchi et al., 2012). Assemblages of silverfish larvae have been found in the summer polynya of the eastern Weddell Sea (Hubold, 1984), in waters along the Antarctic Peninsula (Kellermann, 1986), and in the Dumont d'Urville Sea (Koubbi et al., 2011b). Such observations suggest homing behavior in silverfish, wherein spawning migrations occur from open waters to coastal ice shelves where environmental conditions resemble those experienced during larval stages (Koubbi et al., 2011b; Ghigliotti et al., 2017). Such a migration is facilitated by the circulation within glacial trough systems across the continental shelf. Outflows aid in the dispersal of developing fish away from hatching sites, while inflows function to retain adults by transporting them back to spawning areas. The discovery of newly hatched larvae in trough systems along the Weddell Sea, Ross Sea, and Antarctic Peninsula (Hubold, 1984; Guidetti et al., 2015; La Mesa et al., 2015; Ashford et al., 2017b) implies this cycle of dispersion and retention occurs in multiple areas around Antarctica.

Icefishes

Icefishes, or Channichthyidae, are unique among vertebrates for their 'white blood' lacking hemoglobin. Icefishes are endemic to the Southern Ocean except for the pike icefish *Champsocephalus esox*, which occurs in southern Patagonia and around the Falkland Islands (Duhamel et al., 2014). Only a few icefish species were targeted by commercial fisheries starting in the 1970s, but following concerns of overexploitation and depletion of stocks, most fisheries were closed within a couple of decades (Kock, 1992; Kock and Jones, 2005). Today, only the mackerel icefish *Champsocephalus gunnari* fishery is still open (**Table 1**) and concentrates around South Georgia (CCAMLR Subarea 48.3) and Heard Island (CCAMLR Division 58.5.2) where the 2019/2020 catch limits were 3,225 and 527 tonnes, respectively (**Table 3**) (CCAMLR, 2019).

Icefish biology varies greatly across species (**Table 2**). Most icefishes are benthic and distributed on the continental shelf and slope from shallow depths down to 2,000 m (Duhamel et al., 2014; Eastman, 2017). There are a few species, however, that are benthopelagic and undertake diel migrations from the ocean floor to the water column for feeding (Kock, 2005a). Icefish reproduction does not differ from other notothenioids and is characterized by late sexual maturity, long gametogenesis time, high reproductive effort with large eggs, relatively low fecundity, and reproductive events occurring from late summer to early winter (Kock, 2005a,b; Militelli et al., 2015; Riginella et al., 2016; Le François et al., 2017; Mintenbeck, 2017; Novillo et al., 2019). Many icefishes display elaborate reproductive behavior involving nesting and egg guarding (Desvignes et al., 2019 for review), similar to many other notothenioid species (Jones and Near, 2012; La Mesa et al., 2021). In contrast, *C. gunnari* displays higher fecundity and smaller egg size than other icefishes, potentially compensating for a broadcast spawning strategy (Militelli et al., 2015).

Due to their unique phenotypic traits (Kock, 2005a,b; Braasch et al., 2015) icefishes have been extensively studied. Analysis of icefish skeletons has revealed the existence of developmental heterochronies (alterations in the timing and rate of bone development) that reflect paedomorphic characteristics (Voskoboinikova, 1997; Albertson et al., 2010; Eastman et al., 2014; Postlethwait et al., 2016). Studies of the population structure and connectivity for several icefish species inhabiting different parts of the Southern Ocean have investigated the hybridization potential between species (Papetti et al., 2009; Damerau et al., 2012; Young et al., 2015, 2018; Desvignes et al., 2019; Schiavon et al., 2021). Finally, the response of icefishes to environmental stressors such as temperature continues to be an active area of research (**Table 3**) (Beers and Sidell, 2011; Mueller et al., 2012; Joyce et al., 2018; O'Brien et al., 2018). Icefishes are also genetically and physiologically studied for being 'evolutionary mutant models' in regard to the absence of hemoglobin in their blood and the lack of cardiac myoglobin in some species (Near et al., 2006; Albertson et al., 2009; Desvignes et al., 2016; Harter et al., 2018; Bargelloni et al., 2019; Kim et al., 2019).

Notothenia rossii

Historically, one of the most important commercial fish species was the marbled notothen or marbled rockcod (*N. rossii* Richardson, 1844). This abundant demersal species reaches more than 50 cm in length and often occurs in dense shoals

TABLE 3 | Summary of impact drivers and future impacts by taxa.

Taxon	Common term for group to which it belongs	MEASO area	Historical impact	Drivers of historical impact	Future impacts	Drivers of future impacts
Myctophidae	Lanternfish	Subantarctic (all zones) Antarctic (all zones)	No data No data	No data No data	Positive Negative	
Nototheniidae	Silverfish	Antarctic (all zones)	No data	No data	Negative	
	Marbled rockcod	Subantarctic (AOS, CIS)	Negative		Mixed	
	Toothfish	Subantarctic, Antarctic (all zones)	Negative		Mixed	
Channichthyidae	Icefish	Subantarctic (AOS and CIS) Antarctic (AOA)	Negative		Negative	
Cephalopoda	Antarctic squid	All zones	No data	No data	Positive	

Climate change; *pollution;* *sea ice loss;* *fisheries.*

in subantarctic fjords and shelf waters (DeWitt et al., 1990; Kock and Jones, 2005). The adults spawn in specific areas at depths of 120–350 m, and the larvae and juveniles spend at least 6–8 months in the water column before settling in nearshore macroalgae habitats (DeWitt et al., 1990; Barrera-Oro et al., 2014). The biology of *N. rossii* has been widely studied, with recent research on diet (Barrera-Oro and Winter, 2008; Moreira et al., 2014; Barrera-Oro et al., 2019), reproduction and growth (Calì et al., 2017; Ferreira et al., 2017), buoyancy (Eastman et al., 2011), and population recovery and connectivity (Kock and Belchier, 2004; Marschoff et al., 2012; Young et al., 2012, 2015). In addition, the species is often used as a model for physiological changes under increasing temperature and/or acidification (Mark et al., 2012; Strobel et al., 2012, 2013; Machado et al., 2014; Miya et al., 2014; Forgati et al., 2017; Kandalski et al., 2018). Gaps in our knowledge of *N. rossii* remain regarding the impacts of climate change, current population status and dynamics, and their recovery from overfishing (but see Barrera-Oro et al., 2017; Young et al., 2018; Duhamel et al., 2019).

Squid

The abundance, biomass, ecology, and life history of Antarctic squid is still poorly known, though information is increasing. Squid are known to play an important role in the Southern Ocean as both prey and predators, with their distribution and trophic role in Antarctic marine ecosystems reviewed recently (Xavier et al., 2016, 2018). For example, the colossal squid *Mesonychoteuthis hamiltoni* is the world's largest (heaviest) invertebrate and can prey on large fish (Rosa et al., 2017), and *Moroteuthopsis longimana* is a large squid that is highly abundant in the diet of numerous top predators in the Southern Ocean (Xavier and Cherel, 2021). Of the 54 cephalopod species found in Antarctic waters south of the Polar Front (PF), 20 species are from oegopsid squid (Xavier et al., 2018). Loliginid squid are absent in the region. The lifespan of Antarctic squid species is likely to be 1–2 years, exhibiting slightly slower growth and a longer life cycle than lower latitude squid. These adaptations allow Antarctic squid to withstand the low temperatures and highly seasonal primary and secondary production characteristic of the Southern Ocean (**Table 2**) (Collins and Rodhouse, 2006). The southern Kerguelen plateau region was recently suggested to be an important spawning area and nursery for several Antarctic squid species, such as *M. longimana* (Cherel and Weimerskirch, 1999; Lin et al., 2020). Antarctic squid are semelparous, i.e., they reproduce only once in their life (Collins and Rodhouse, 2006).

Currently, there are no commercial fisheries targeting squid species in the Southern Ocean. Historically, there was a fishery for the sevenstar flying squid *Martialia hyadesi* around South Georgia. This fishery was initiated during the 1996/1997 season, and had a catch limit of 2,500 tonnes in accordance with CCAMLR Conservation Measure 99/XV (CCAMLR, 1996) and subsequent annual measures. After a few years of relatively limited landings, the squid fishery closed during the 2009/2010 fishing season. Whether there is future interest in re-opening this fishery remains to be seen.

Most scientific information on Antarctic squid still comes from studies on the diet of their predators. Indeed, the importance of the squid *M. hyadesi* and *Galiteuthis glacialis* in the diet of albatrosses is directly related to their reproductive performance (Xavier et al., 2003; Mills et al., 2020). There are large data gaps for most species of Antarctic and subantarctic squid (areas not sampled from nets and where higher predator data are scarce or absent), so conclusions about their distribution remain tentative (Rodhouse et al., 2014a). Critically, data on large specimens and on the biology of species during the winter months remain underrepresented in observations, limiting our ability to determine seasonal changes in distribution patterns and spawning strategies (Lin et al., 2020). As a result, knowledge of

the abundance, physiology, biology, ecology, and diet of Antarctic squid remain rather limited.

Top Predators

Toothfish

Antarctic toothfish

The Antarctic toothfish (*Dissostichus mawsoni* Norman, 1937) is a large predatory fish endemic to the Southern Ocean, and an important target of commercial fisheries. The species has a circumpolar distribution along the continental shelf and slope (Hanchet et al., 2015; Yates et al., 2019). Genetic studies indicate that habitat discontinuities, such as canyons and abyssal plains, may contribute to the development of genetically distinct populations at the circumpolar scale (Kuhn and Gaffney, 2008). Antarctic toothfish primarily lives in the frigid high Antarctic waters and have a suite of adaptations (e.g., Ciardiello et al., 1995; Metcalf et al., 1999; Kiss et al., 2004; Pointer et al., 2005), including high concentrations of antifreeze glycoproteins (AFGPs) in their blood (Haschemeyer et al., 1977).

Ontogenetic changes have been reported in the buoyancy of this species (Near et al., 2003), leading to the spatial segregation of length classes. Pelagic larval stages are found near the surface, while large adults are caught typically from 1,000 to 1,600 m, down to a maximum depth of 2,210 m (Hanchet et al., 2015). The occurrence of recently consumed large adult *D. mawsoni* in sperm whale stomachs collected over abyssal depth supports the hypothesis that *D. mawsoni* spend considerable time off the bottom in the pelagic zone (Yukhov, 1971). Data collected in tagging programs suggest that *D. mawsoni* are relatively sedentary, with most individuals exhibiting strong site fidelity and dispersing only short distances (less than 20–50 km) (Hanchet et al., 2008). Nevertheless, a small proportion of fish have been shown to move northward for long distances (between 200 and 2,300 km), possibly in association with reproduction (Parker and Mormede, 2015).

An opportunistic carnivore, Antarctic toothfish feeds primarily on fish, cephalopods and crustaceans; differences in diet have been found among size classes and geographical areas (Fenaughty et al., 2003; Stevens et al., 2014). While *D. mawsoni* are among the top fish predators in the Southern Ocean, they are also prey for large sea mammals, including sperm whales (Yukhov, 1971), Weddell seals (Kooyman, 1967; Calhaem and Christoffel, 1969; Testa et al., 1985; Castellini et al., 1992; Davis et al., 1999; Fuiman et al., 2002; Ainley and Siniff, 2009), and killer whales (Pitman and Ensor, 2003; Ainley and Ballard, 2012; Eisert et al., 2014). Despite this, the trophic level of *D. mawsoni*, derived from stable isotopes analyses is similar to that of killer whales and Weddell seals (Pinkerton and Bradford-Grieve, 2014).

Despite a reasonable understanding of the Antarctic toothfish biology and ecology, aspects of its life history are still a matter of debate and uncertainty (Yukhov, 1982; Hanchet et al., 2008; Ashford et al., 2012; Hanchet et al., 2015; Ainley et al., 2016). The number of populations of Antarctic toothfish remain unknown (Hanchet et al., 2015). *Dissostichus mawsoni* can live almost 40 years, grow relatively slowly (Hanchet et al., 2015), and come into maturity at 13 and 17 years of age for males and females, respectively (**Table 2**) (Parker and Grimes, 2010). However, the frequency of *D. mawsoni* spawning remains unknown, and the timing and location of spawning activity has only recently been documented in the northern Ross Sea region during the austral winter (Stevens et al., 2014; Parker et al., 2019). The effect of physical–biological interactions between life history and oceanographic features has been considered, but requires further research to better understand these dynamics (Ashford et al., 2017a).

Patagonian toothfish

The Patagonian toothfish (*D. eleginoides* Smitt, 1898) is a large, deep-water, slow-growing predator and scavenger of the family Nototheniidae, and an important commercially targeted species in the southern Atlantic, Indian, and Pacific Oceans, as well as in the Southern Ocean, where it has been found as far south as 75°S (Hanchet et al., 2004; Collins et al., 2010; Duhamel et al., 2014). Patagonian toothfish occur over a depth range from 50 to 2,500 m (Collins et al., 2010), with a circumpolar distribution spanning the Polar Front (PF) north to 35°S on the Patagonian Shelf (within the Atlantic), to 30°S off Chile (within the Pacific), and to 40°S within the SW Indian Ocean (López-Abellán, 2005; Collins et al., 2010).

Ontogenetic segregation has been observed in *D. eleginoides*, with specimens' length strongly correlating with increasing depth. Juveniles and sub-adults are found in shallow water (150–400 m) until 7–8 years old (Laptikhovsky and Brickle, 2005), before moving down the slope to deeper water (Laptikhovsky et al., 2006; Collins et al., 2010). Off South Georgia, mature female *D. eleginoides* were found deeper on the slope than smaller, mature, male toothfish; both sexes converge at intermediate depths to spawn (Heaps et al., 1999). The species shows strong site fidelity, with a mean annual movement rate of 10 km (Agnew and Clark, 2006). Population genetics studies have shown that oceanographic and geographic discontinuities drive population differentiation in this species (Smith and McVeagh, 2000; Appleyard et al., 2004; Rogers et al., 2006; Toomey et al., 2016). The existence of a large population along the South American continental shelf is hypothesized, driven by the continuity of the deep-sea habitat and the biological features of the species (Canales-Aguirre et al., 2018). The Patagonian toothfish is an opportunistic carnivore, showing ontogenetic shifts in diet associated with down-slope migration and a general switch to scavenging as size increases (Collins et al., 2010; Roberts et al., 2011). Juvenile populations inhabiting shelf areas mainly prey on small demersal notothenioid fish, supplemented with krill, squid or pelagic fish depending on availability; adults on the slope prey on large fishes such as macrourids, morids, and rajids; in deeper waters, specimens consume mainly shrimps, squid, and scavenged prey (Pilling et al., 2001; Roberts et al., 2011).

Patagonian toothfish can live more than 50 years (Horn, 2002) and mature between the ages of 6 and 10 for males and 10 and 13 for females (**Table 2**) (Everson and Murray, 1999). However, gaps remain in the knowledge of the life cycle of Patagonian toothfish, specifically regarding their reproductive biology (Heaps et al., 1999; Arana, 2009). On the Patagonian shelf, toothfish are known to spawn on the Burdwood Bank in two

spawning peaks, a first small peak in May and a second main peak in August (Laptikhovsky et al., 2006). At South Georgia, the spawning period has historically broadly been recognized as April to September; however, long-term assessment of spawning dynamics, spanning almost two decades, showed a progressive shift of peak spawning in females toward the end of July (Brigden et al., 2017). Current knowledge suggests that not all mature females spawn every year, and skip spawning has been hypothesized for the species (Everson and Murray, 1999; Arana, 2009; Boucher, 2018), leading to uncertainties in the estimation of spawning biomass and other population indicators.

DATA

Inherent biases exist in Southern Ocean sampling and fisheries-dependent data for most Antarctic fish and squid species. The remote and extreme nature of the Southern Ocean makes it a difficult place to conduct systematic research on abundance, biomass, and productivity. Most data collected and used in management is fisheries-dependent, coming from fisheries observers who report data from commercial fishing vessels[1]. Fisheries are limited by gear and the environment, e.g., they can only fish as deep as their gear allows, and will be constrained by ice. Gear selectivity can bias the sample catch by selecting for specific age groups, e.g., longline gear tends to select larger individuals (Ashford et al., 2005). The CCAMLR observer program demands 100% observer coverage on toothfish fishing vessels, which ensures consistent observation; however, the observers do not always follow a rigorous (e.g., random) sampling design, instead favoring opportunistic sampling[2]. In some regions, such as the subantarctic waters around the Heard and McDonald Islands, the fishing industry works with the Australian government to perform an annual random stratified survey, which provides valuable fisheries-independent data (Constable and Welsford, 2011; Brooks et al., 2019). However, in more remote areas like the Ross Sea, fishery-dependent data are the most readily-available data source and can still be used to draw important conclusions regarding Antarctic toothfish life history and management.

With the exception of some localized nearshore work focused on toothfish, icefish and Antarctic silverfish (e.g., Fuiman et al., 2002; O'Driscoll et al., 2018a,b; Parker et al., 2019), sampling is conducted almost exclusively in the summertime and in ice-free areas. Vessels tend to avoid areas where summer sea ice concentration remains too high, and instead aggregate mostly around research stations and along the logistical routes toward them (Griffiths et al., 2014). Benthic sampling is focused on the shelf zone and rarely goes deeper than 1,000 m. Pelagic sampling often focuses on the pelagic zone (<200 m) and neglects the mesopelagic and deeper zones. This can be understood in a context of optimization of ship time and the use of specific sampling protocols (Griffiths et al., 2014).

Data on fish and squid in the Southern Ocean are therefore both patchy and spatially and temporally biased, limited mainly to small-scale studies. Nonetheless, computational methods allow extrapolation to less well-sampled areas (Koubbi et al., 2011a; Xavier et al., 2016). For example, species distribution modeling was used to couple fishery catch and effort data with environmental factors to develop a distribution model for Antarctic toothfish (Yates et al., 2019).

Fisheries Data

CCAMLR makes catch and fishing effort statistics from 1970 to the present for all fisheries in CCAMLR's Convention Area publicly available in an annual Statistical Bulletin[3]. These statistics are reported as green weight (i.e., weight before processing) in tonnes, and based on monthly catch and effort data for reporting areas of CCAMLR Subarea and Division (**Figure 1**). These are derived from haul-by-haul catch and effort data reported to the CCAMLR Secretariat by Member countries, although the first two decades of fisheries were mostly reported in the aggregate form by reporting areas. The Statistical Bulletin also includes trade statistics (landings and exports) of toothfish and planimetric seabed areas by selected depth intervals in the Convention Area. In addition to fisheries data published in the Statistical Bulletin, CCAMLR receives data from scientific observers onboard fishing vessels, research survey data, and from the CCAMLR Ecosystem Monitoring Program (CEMP) on dependent and related species, as well as receiving information on compliance activities.

All high-resolution fishery and research data not in the Statistical Bulletin are not available to those outside of CCAMLR due to commercial confidentiality concerns by fishing Members. These data may only be released with permission from CCAMLR Members, according to the Rules for Access and Use of CCAMLR Data[4].

Active Acoustic Data

Studying fish ecology in the ocean's mesopelagic realm is challenging because rapid light attenuation limits visual observations, and net sampling can only ever sample a small portion of the community (Warren, 2012). In contrast, active acoustics facilitate the collection of relatively large spatial and temporal data sets, which at frequencies of 38 kHz and below can sample throughout the mesopelagic zone (Kloser et al., 2009). While acoustic data can be collected from a range of platforms (see Benoit-Bird and Lawson, 2016), hull-mounted echosounders are the platform most regularly deployed in the Southern Ocean, and hold the potential to build a comprehensive region-wide spatial data set.

Active acoustics are widely used to monitor commercially important fish stocks, including Antarctic krill. However, there has been a recent increase in the use of active acoustics to study mesopelagic fish globally and in the Southern Ocean, where acoustic backscatter is used as a proxy for fish biomass

[1]https://www.ccamlr.org/en/fisheries/fisheries

[2]https://www.ccamlr.org/en/science/observer-sampling-requirements-dissostichus-spp

[3]https://www.ccamlr.org/en/publications/statistical-bulletin

[4]https://www.ccamlr.org/en/document/publications/rules-access-and-use-ccamlr-data

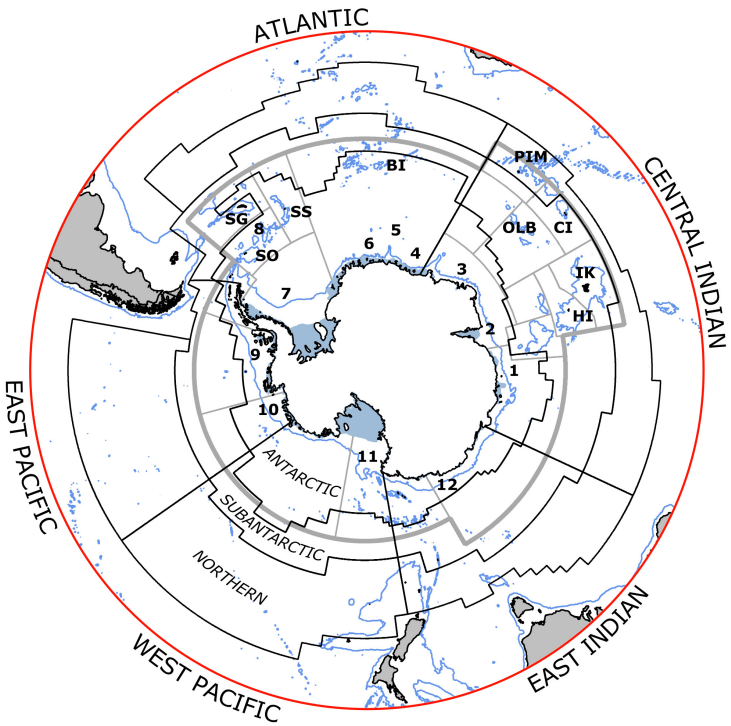

FIGURE 1 | Areas for assessing status and trends of fish and squid in the Marine Ecosystem Assessment for the Southern Ocean (black lines). Labels indicate the sectors (first two letters) and zones (last letter) for each area. Sectors are Atlantic (AO), Central Indian (CI), East Indian (EI), West Pacific (WP), East Pacific (EA). Zones are Antarctic (A), Subantarctic (S), Northern (N) (zonal boundaries are the Southern ACC Front between A and S, and Subantarctic Front between S and N, and Sub-Tropical Front in the North). Seas are marked in the Antarctic Zone as (1) Davis, (2) Cooperation, (3) Cosmonaut, (4) Riiser-Larsen, (5) Haakon VII, (6) Lazarev, (7) Weddell, (8) Scotia, (9) Bellingshausen, (10) Amundsen, (11) Ross, (12) Dumont D'Urville. Islands in the CCAMLR area include Heard (HI), Isle Kerguelen (IK), Crozet (CI), Prince Edward-Marion (PEM), Bouvet (BI), South Sandwich (SS), South Georgia (SG), South Orkney (SO), South Shetland (SSh); and Ob and Lena Banks (OLB). Gray lines indicate the CCAMLR reporting areas (Subareas and Divisions).

(Saunders et al., 2013; Irigoien et al., 2014; Moteki et al., 2017; Proud et al., 2017). Acoustic data have provided insight into diel vertical migration behavior, and the relationships between environmental variables and the horizontal and vertical distribution of acoustic scattering layers (Béhagle et al., 2016; Escobar-Flores et al., 2018). Multi-frequency acoustic data have also been used to investigate the schooling behavior of mesopelagic fish around South Georgia (Fielding et al., 2012; Saunders et al., 2013).

While all notothenoids lack a swimbladder, making them weak acoustic targets, there have been investigations into the potential use of marine acoustics to study the notothenioids Antarctic silverfish and Antarctic toothfish. Due to their biological features, lack of swimbladder, and occurrence of few dense structures, the Antarctic silverfish are poor reflectors of sound. A reliable calculation of the species target strength has been obtained by *ex situ* experiments and *in situ* analyses (reviewed in O'Driscoll et al., 2017), paving the way for the use of marine acoustics to estimate abundances of this key mid-trophic species. Estimates of the acoustic target strength of the Antarctic toothfish has been performed from *in situ* observations (O'Driscoll et al., 2018a). Compared to conventional fishery-based methods, acoustics can be operated from a diverse range of platforms, representing a promising means to obtain high spatial and temporal resolution data at an affordable cost. Moorings, normally deployed for the study of currents and environmental conditions, might represent suitable platforms for acoustic instrumentation, allowing observations also in periods of the year when vessels cannot operate due to the sea-ice cover. At Terra Nova Bay, echosounder deployment on moorings allowed the observation of reflections consistent with adult silverfish in September, providing complementary information in support of the hypothesis of coastal migration of fish for spawning during that period (O'Driscoll et al., 2018b).

However, to meaningfully interpret patterns in acoustic data and estimate fish abundance and biomass, we require knowledge of the taxa present and their unique scattering properties or 'target strength' (Simmonds and MacLennan, 2005; Davison, 2011). Within the Southern Ocean there is a notable decline in acoustic backscatter toward the pole (Proud et al., 2017; Dornan et al., 2019), which parallels a change in the mesopelagic fish community (Escobar-Flores et al., 2018; Dornan et al., 2019). However, the biomass dominant mesopelagic fish species in colder polar waters tend to lose the highly reflective gas-component in their swimbladders, making them weak acoustic targets and potentially masking high polar fish biomass (Dornan et al., 2019). Another confounding factor is that of target identification (Demer, 2004). Net sampling is routinely used

to ground-truth acoustic data; however, net avoidance behavior (Kaartvedt et al., 2012) and backscatter from gas-bearing siphonophores, which are poorly sampled by nets, have the potential to bias biomass estimates if they are not accounted for (Kloser et al., 2016; Proud et al., 2019).

Because of the uncertainties associated with net and acoustic sampling, and the lack of target strength models, estimates of mesopelagic fish biomass have large uncertainties. However, the international community is increasingly recognizing the value of standardizing methods of acoustic data collection and processing, and investing in the development of new tools and approaches to enable robust estimation of mesopelagic biomass (Newman et al., 2019). This was evidenced by the recent MEsopelagic Southern Ocean Prey and Predators (MESOPP) project (2016–2019; Lehodey, 2019). As highlighted by MESOPP and the Southern Ocean Observing System (SOOS) (Lehodey, 2019; Newman et al., 2019), better coupling of observational data and ecosystem models has strong potential for helping resolve uncertainties in acoustic and net observations. Similarly, combining acoustic and net observation data with observations from new platforms such as optical profilers and animal-borne sensors is likely to lead to a greatly improved ability to estimate mesopelagic biomass in the near future (Kloser et al., 2016; Newman et al., 2019).

Groundfish Trawl Surveys

Bottom trawl surveys for groundfish (demersal finfish) have been undertaken in the Southern Ocean since the mid-1960s (Shust, 1998), though results of these early surveys have only appeared in published literature since the late 1970s (Kock, 1992). Most Antarctic demersal fish surveys are undertaken on shelf areas <500 m, and the results are used to characterize abundance, distribution, and demography of fish stocks, as well as to assess changes in the composition and abundance of fish populations over time. In addition, trawl surveys have been used to collect specimens for a variety of purposes, including genetic, physiological, ecological, and process studies.

Net avoidance has been reported for a number of mesopelagic fish species (Collins et al., 2012; Kaartvedt et al., 2012), and is likely common in other fish and squid species as well. The implications of this avoidance are difficult to quantify with traditional methods, and it is likely that better resolved biomass estimates of mesopelagic fishes and squid will depend upon emerging technologies such as codend-less nets towed at higher speeds and equipped with high-speed cameras, optical profiling, and animal-borne acoustic tags (Newman et al., 2019).

Data collected from trawl surveys is primarily used to generate scientific advice for fishery management and conservation under the auspices of CCAMLR. Most surveys are fishery independent, and have been conducted across most archipelagoes of the Southern Ocean. Most trawl surveys are multi-species, though the objective is usually to provide information on currently harvested species (e.g., *C. gunnari* and *Dissostichus* spp.) for stock assessments. The primary regions of the Southern Ocean regularly or periodically surveyed are South Georgia (Reid et al., 2007; Clarke et al., 2008), Kerguelen (Duhamel et al., 2019), Heard and MacDonald Islands (Constable and Welsford, 2011; Ziegler and Welsford, 2019), the South Shetland Islands, and the South Orkney Islands (Kock and Jones, 2005; Arana et al., 2020).

Mark-Recapture (Tagging) Programs

There has been an ongoing fish tagging program for toothfish (*Dissostichus* spp.) in the Southern Ocean administered by the CCAMLR Secretariat for almost two decades. This tagging program is primarily fisheries-based and uses tag and recapture data to estimate abundance of toothfish, which is then directly incorporated into stock assessment models (Hillary et al., 2006; Candy and Constable, 2008; Mormede et al., 2014). Additionally, this information has been used to characterize movement and growth of fish (Williams and Tuck, 2002; Marlow and Agnew, 2003).

Toothfish tagging and reporting of recaptures is compulsory by all fishing vessels targeting toothfish or undertaking research fishing for toothfish in the Southern Ocean. As of the 2019/2020 fishing season, approximately 285,000 toothfish have been tagged, and 29,000 have been recaptured across all regions of the Southern Ocean. More information on the CCAMLR tagging program can be found at https://www.ccamlr.org/en/science/ccamlr-tagging-programme.

DRIVERS OF CHANGE AND THEIR IMPACTS

The Southern Ocean has experienced rapid climate-related change over recent decades including increases in sea surface temperatures and regional reductions in sea ice extent (**Table 3**) (William, 1997; Curran et al., 2003; Meredith and King, 2005; Morley et al., 2020 this volume). Climate models suggest that further warming and sea ice loss is likely during the current century (Hill et al., 2013; Cavanagh et al., 2017), which may have a negative impact on oceanic biota and the local ecosystems (Murphy et al., 2007a; Flores et al., 2012; Constable et al., 2014; Atkinson et al., 2019). In this section, we first consider the major environmental impacts of climate change on different fish and squid groups, followed by an exploration of other types of drivers of change (fisheries, pollution, and pathogens), and their potential impacts.

Effects of Climate Change

The effects of climate change on fish are not well studied. Fishes of the Southern Ocean are expected to be affected by increasing temperatures because of their special adaptations to colder temperatures (e.g., the presence of antifreeze proteins in their blood) (Constable et al., 2014). In this respect, any life stage of fish inhabiting shallower waters could become vulnerable. Icefish in the Subantarctic Zone may be especially vulnerable in the shallow waters adjacent to islands (Constable et al., 2014; Reid, 2019). For deeper water species, such as toothfish, the prognosis is less clear. One study indicated the potential for Antarctic toothfish to become extinct, due to its restricted range and affinity for below freezing temperatures (Cheung et al., 2008).

However, that study did not include data for *D. mawsoni* from the Ross Sea, where it has large abundances.

Recently, productivity of Patagonian toothfish on the Kerguelen Plateau has been related to oceanographic conditions, where prey availability may decrease because of increased variability in these conditions in coming years (Subramaniam et al., 2020). This has also been suggested for icefish populations that prey on krill (Reid, 2019), for which the area of greatest productivity is expected to move south (Johnston et al., under review).

In contrast to these results, climate change may favor the relative importance of the energy pathway through fish, possibly resulting in increased productivities of fish predators, such as toothfish (Trebilco et al., 2020). This is predicated on changes in productivity (see Pinkerton et al., 2021 this volume) increasing the relative importance of zooplankton that preyed on by mesopelagic fish. Productivity of mesopelagic fish may also be altered by changing sea ice conditions affecting the life cycles of mesopelagic fish in the Antarctic Zone (Moteki et al., 2017). These hypotheses need to be tested in stock dynamic models embedded in food web models coupled to biogeochemical and Earth system models.

Myctophids

Changes to the Southern Ocean are expected to impact the ecology and behavior of Southern Ocean myctophids, but there is presently insufficient baseline information to detect, monitor, or predict the consequences of this change on these fish. However, there is evidence to suggest that sustained ocean-warming will impact the broad-scale distribution patterns and abundance of myctophids in the region.

A recent study has predicted that most species will undergo a major poleward shift in their distribution patterns under realistic scenarios of ocean-warming in the Southern Ocean (Freer et al., 2019). As the ocean warms in the coming decades, predominantly temperate and subantarctic species are predicted to gain suitable habitat as they extend to higher latitudes, whilst more high-latitude Antarctic species with restricted thermal ranges are likely to lose habitat, and are thus the group most vulnerable to climate change. Saunders and Tarling (2018) further reported evidence for a major biogeographic shift in body size patterns under sustained ocean-warming, with smaller sized myctophid species and life stages increasing their southernmost ranges to waters at higher latitudes, possibly displacing those that reside in these regions ordinarily. Increases in ocean temperature are also likely to alter the vertical distribution and behavior patterns of Southern Ocean myctophids, as the vertical distribution patterns of several myctophid species, particularly the more temperate and subantarctic types, appear to be temperature dependent (Kozlov et al., 1991; Duhamel et al., 2000; Collins et al., 2008, 2012). However, the exact vertical migration behavior of all myctophid species currently remains unresolved, so it remains unclear how they will be impacted and what will be the implications for food web and ecosystem dynamics. The overall effects of such shifts in distribution patterns and community structure would be a reduction in the size spectra of myctophids in the Southern Ocean and a reduction in myctophid fish biomass (Dornan et al., 2019), which could have implications for trophic interactions and thus the wider Southern Ocean ecosystem (Murphy et al., 2007b; Saunders et al., 2019; Trebilco et al., 2020).

A further plausible consequence of ocean-warming on Southern Ocean myctophids is that their abundance may be negatively impacted by changes in food web structure (Murphy et al., 2007b). Although the Southern Ocean food web is predominantly centered on Antarctic krill (Murphy et al., 2007b), myctophids are an integral part of the system, being both prey for many higher predators and major consumers of zooplankton and krill (Saunders et al., 2019). Under realistic scenarios of regional ocean-warming and projected redistribution and/or declines in krill biomass (Atkinson et al., 2004, 2019; Flores et al., 2012), the role of myctophids in Southern Ocean food webs may become increasingly important as higher predators turn more to myctophids as alternative food sources (Murphy et al., 2007b; Trebilco et al., 2020). Increased predation pressure on myctophids is therefore likely to lead to substantial reductions in the abundance of all species in the region, as well as possible adverse impacts on their population dynamics and changes in their behavior. Populations of the larger, krill-consuming myctophids, may also be impacted concurrently by sustained reductions of krill in their diet (Saunders et al., 2019). The extent to which myctophids can prevail and support the Southern Ocean ecosystem against such change is currently unknown and is a critical knowledge gap that requires urgent attention.

Squid

Antarctic squid are likely to be influenced by climate change, including by changes in mesoscale oceanography, position of the oceanic fronts (and associated productivity), sea ice extent, and ocean acidification (Rodhouse, 2013; Xavier et al., 2018). A recent long-term study showed that the habitat of *Taonius notalia*, *Gonatus antarcticus*, *G. glacialis*, and *Histioteuthis atlantica* had changed over the last 50 years despite their trophic levels remaining similar (Abreu et al., 2020).

As with squid and other cephalopods elsewhere, Antarctic squid have a unique set of biological traits, including rapid growth, short lifespans (in comparison with other marine organisms, such as fish), and life-history plasticity, which may allow them to adapt well to climate change (Rodhouse, 2013; Rodhouse et al., 2014b; Doubleday et al., 2016). Indeed, increasing temperature is thought to accelerate the life cycles of squid (and other cephalopods), particularly those species with high thermal ranges (e.g., species distributed in more than one water mass), improving their reproductive success (Doubleday et al., 2016; Xavier et al., 2016; Queirós et al., 2020). Moreover, as there are no fisheries established for Antarctic squid, they do not experience pressure from fishing, while their natural predators, such as the Antarctic and Patagonian toothfish, do.

Species Targeted by Fisheries

History of Finfish Fisheries

The first commercial fishing for Antarctic fish commenced during the 1969 – 1970 austral summer around South Georgia, followed by Kerguelen in 1970 – 1971 by Soviet trawlers (Kock et al., 1985; Kock, 1992). These catches were primarily groundfish,

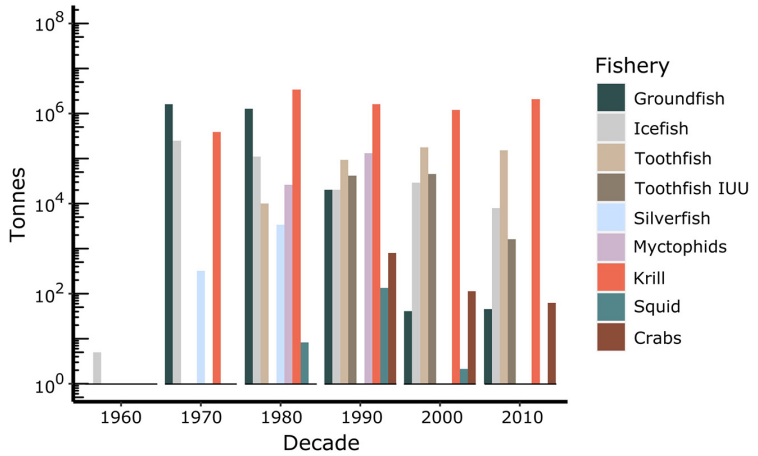

FIGURE 2 | Total biomass (tonnes) caught in the different fisheries undertaken in the CCAMLR Area from 1969 to 2019. Source: CCAMLR Statistical Bulletin 2019 (https://www.ccamlr.org/en/publications/statistical-bulletin), except for catches of toothfish taken in illegal, unregulated or unreported (IUU) activities, which were derived from the CCAMLR Fishery Reports for toothfish (http://fisheryreports.ccamlr.org/).

dominated in the early years by *Notothenia rossii* (**Figure 2**). Commercial fishing expanded to the southern Scotia Arc region and Antarctic Peninsula in 1977 – 1978, targeting *N. rossii* and *Champsocephalus gunnari* (Kock and Jones, 2005), as well as at Ob and Lena Banks in 1978 – 1979. This coincided with an expansion to high-Antarctic coastal areas when Polish and East German vessels fished for *Chaenodraco wilsoni* off the Antarctic Peninsula. A short-lived pelagic fishery for the myctophid *Electrona carlsbergi* was initiated in 1987 – 1988 off South Georgia. The first commercial fishing trials for Patagonian toothfish *D. eleginoides* in the Southern Ocean took place off South Georgia in 1978 – 1979, followed by Kerguelen in 1983 – 1984, and a further expansion at South Georgia in 1988 – 1989. The fishery for Antarctic toothfish *D. mawsoni* was initiated in the Ross Sea in 1997 – 1998.

To date, there have been seven species of Antarctic fish specifically targeted by fishing vessels at various times and in various locations around the Southern Ocean: *C. gunnari*, *C. wilsoni*, *D. eleginoides*, *E. carlsbergi*, *Lepidonotothen squamifrons*, *N. rossii*, *Patagonotothen guntheri* (Kock, 1992), and *D. mawsoni*. *C. gunnari, L. squamifrons,* and *N.rossii* were heavily depleted in the subantarctic, and some have yet to recover (e.g., *N. rossii*) (Kock, 2007; Marschoff et al., 2012). Antarctic finfish fisheries are now dominated by *D. eleginoides* and *D. mawsoni*, along with small fisheries for *C. gunnari* exclusively on shelf areas of CCAMLR Subarea 48.3 and Division 58.5.1.

CCAMLR first met in 1982 and inherited a number of depleted fisheries from the activities in the 1970s. Its precautionary approach was established in 1991 for krill and later applied to toothfish and icefish fisheries, including exploratory fisheries (Constable et al., 2000). This approach is intended to take account of parameter uncertainty and environmental stochasticity, although the degree to which this has been achieved has been debated (e.g., Abrams et al., 2016). A challenge to the sustainability of toothfish fisheries was the emergence of illegal, unregulated and unreported (IUU) fishing in the CCAMLR Area in the 1990s and 2000s, though levels of IUU fishing have decreased over the past decade (**Figure 2**) (Miller, 2004; Österblom et al., 2015).

Toothfish fisheries are now present in CCAMLR Subareas 48.3, Divisions 58.5.1 and 58.5.2 (*D. eleginoides*), and Subareas 88.1 and 88.2 (*D. mawsoni*), along with smaller established fisheries for *D. eleginoides* in Subarea 48.4 (South Sandwich Islands), Subarea 58.6 (Prince Edward and Marion Islands), and Subarea 58.7 (Crozet Island). There are also small exploratory fisheries for *D. eleginoides* in parts of Subarea 48.6 (near Bouvet), Division 58.4.4 (Ob and Lena banks) and 58.4.3a (Elan Bank). Additional to the fisheries in the Ross Sea, exploratory fisheries for *D. mawsoni* are currently undertaken in the southern regions of Subarea 48.6, as well as the coastal and seamount high Antarctic regions of Subarea 88.2 (western Amundsen Sea), and Divisions 58.4.1 and 58.4.2 (coastal East Antarctica). In recent years, purported research fishing for *D. mawsoni* has been undertaken in Subarea 48.1 (Antarctic Peninsula), and Subarea 88.3 (southern Antarctic Peninsula/eastern Amundsen Sea).

Pressures on Stocks From Fishing

Pressures on stocks from fishing in MEASO areas were determined using catch data from the CCAMLR Statistical Bulletin 2019 (see Grant et al., under review, for more). These data were allocated to MEASO areas according to evidence for fishing depths and locations in reports of the Scientific Committee, CCAMLR Conservation Measures, and descriptions in the scientific literature on the fishing operations, Kock (1992) in particular. Available fishing area in the depth ranges of the fisheries was used to spread the catch uniformly across the identified reporting area of operation. Seabed areas were calculated from the GEBCO 2014 grid at 4 km^2 resolution[5]. Catches were spread uniformly across the

[5]https://www.gebco.net/news_and_media/gebco_2014_grid.html

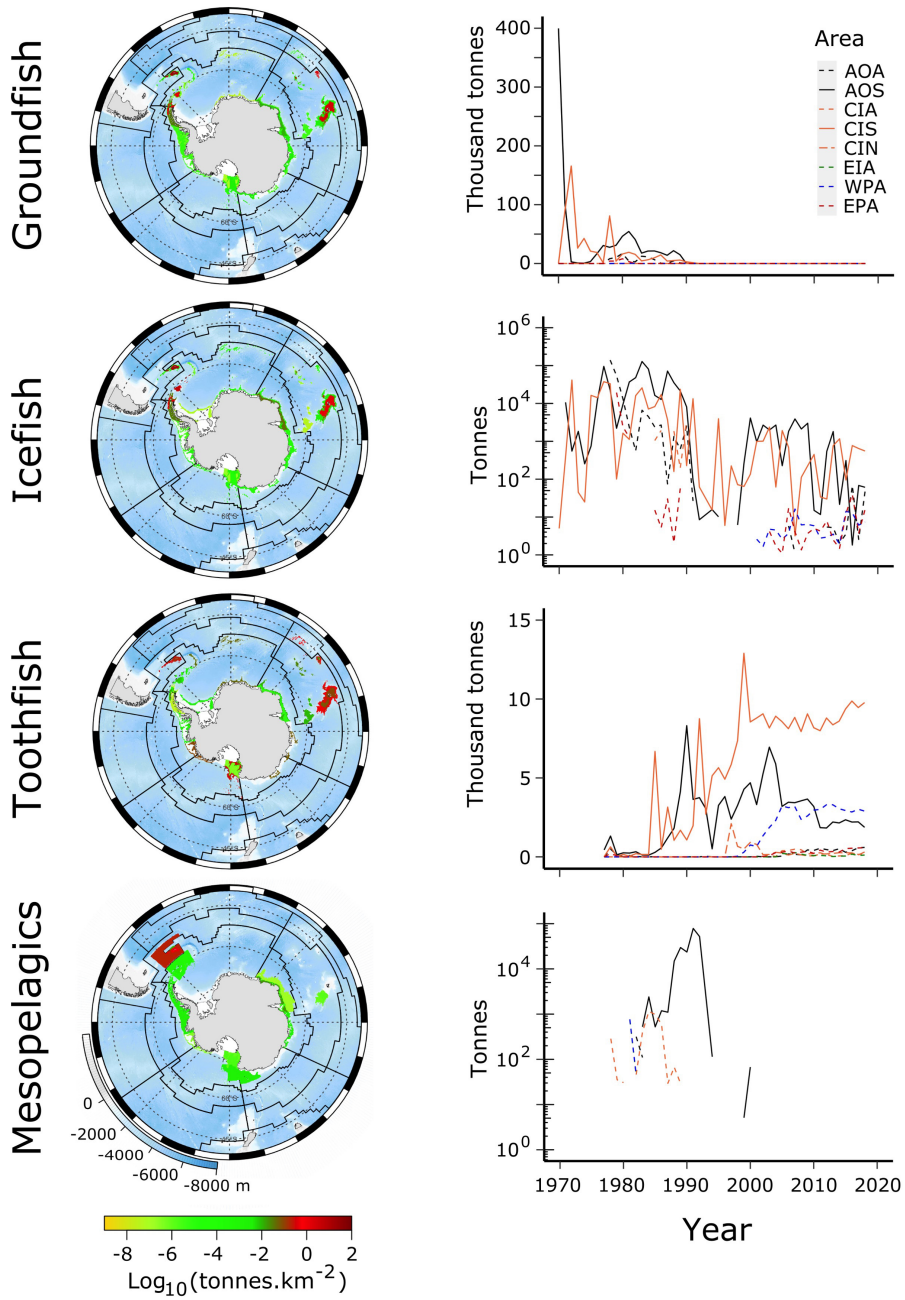

FIGURE 3 | Catches of groundfish, toothfish, icefish, and mesopelagic fish from 1970 to 2018, derived from the CCAMLR Statistical Bulletin 2019. **(Left column)** Total catch over this period as $\log_{10}$ (catch density in tonnes.km^{-2}) (see color ramp at bottom). Background is ocean depth in meters (bottom left legend on bottom map). Black lines show boundaries of MEASO areas as depicted in **Figure 1**. **(Right column)** Time-series of catches of the fish group in each of the MEASO areas according to the line types in the legend in the top right panel. Legend labels indicate the MEASO sectors (first two letters) and zones (last letter) for each area. Sectors are Atlantic (AO), Central Indian (CI), East Indian (EI), West Pacific (WP), East Pacific (EA). Zones are Antarctic (A), Subantarctic (S), Northern (N). Y-axis is $\log_{10}$ for Icefish and Mesopelagics but labeled with corresponding tonnes. Gray lines show a graticule (see Grant et al., under review).

area identified from those sources for an individual catch based on country, depth range for a given target fishery and gear type, and, where reports allowed it, year. **Figure 3** shows the total catches of target species in the CCAMLR area along with time-series of those catches in the MEASO assessment areas.

Until CCAMLR established limits to catches of target species, the annual catches in some areas were two orders of magnitude greater than what is now considered sustainable. Groundfish, including *N. rossii*, experienced the greatest catches and are yet to recover (Kock, 2007; Marschoff et al., 2012). The groundfish fishery had its highest catches in the Subantarctic Zone of the

Atlantic and Central Indian Sectors during the 1970s and 1980s, ending in the early 1990s.

Icefish were the next largest fishery to groundfish. The icefish fishery in the Subantarctic Zone (South Georgia in the Atlantic Sector and the northern Kerguelen Plateau in the Central Indian Sector) was concentrated on *C. gunnari*, a bentho-pelagic species that is important prey for seals. Annual catches are now less than two orders of magnitude than the fishery in the 1970s and 1980s. Although catches are now considered sustainable (Marine Stewardship Council[6, 7]), it is unknown whether stocks will ever reach the abundances observed in the early fishery.

In the Antarctic Zone, *C. gunnari* was exploited in the Atlantic Sector around the South Orkney and east of the South Shetland Islands for only a few years before stocks became depleted. Other icefishes were exploited in bottom trawl activities in the early decades but in much lower abundances.

The distribution of each species of toothfish, *D. mawsoni* and *D. eleginoides*, are mostly constrained to the Antarctic Zone and north of that zone, respectively. There is some crossover in range at the South Sandwich Islands and Bouvet Island in the Atlantic Sector and on the southern Kerguelen Plateau in the Central Indian Sector. The fisheries for *D. mawsoni* have all been longline fisheries. *Dissostichus eleginoides* has been exploited using trawl, longlines, and pots. Longline fisheries take older mature fish whereas trawl fisheries concentrate on juvenile fish in the shallower shelf areas (see Text Footnote 1).

Over the time-series of these fisheries, annual catches are considered sustainable using the CCAMLR Decision Rule for toothfish[8, 9, 10, 11, 12].

Some questions have been raised about the long-term sustainability of the fishery for *D. mawsoni*, particularly in relation to structural uncertainty in the model of the dynamics of this stock and in the role that this species may play as prey in the food web of the Ross Sea (Abrams et al., 2016; but see Pinkerton and Bradford-Grieve, 2014; Hanchet et al., 2015). Such evaluations would help resolve different perspectives on what is required to successfully manage the stocks under CCAMLR. Furthermore, the vast majority of analyses used in management are not available in the public domain (e.g., papers from CCAMLR working group meetings), despite this being a recommendation of the most recent CCAMLR performance review[13]. Thus, independent analyses of CCAMLR data and fisheries management have proved difficult (Abrams et al., 2016; Ainley et al., 2016).

Pelagic and mesopelagic fish have been of interest to commercial fishers since the 1980s. Myctophids were an important fishery in the late 1980s in the Subantarctic Zone of the Atlantic Sector. In the Antarctic Zone, there has been interest from time to time in the Antarctic silverfish *P. antarctica*. However, a fishery for this species has never developed. Should mesopelagic species be of interest in the future, it would be expected that such species will be managed in a similar manner to Antarctic krill.

Although krill fisheries are not assessed here (see Johnston et al., under review), they catch larval fish and may be contributing to the lack of recovery of some over-exploited stocks (Nicol and Foster, 2016).

Pollution

Climate change is expected to increase the levels of pollutants at the poles. Warming air temperatures increase the levels of persistent organic pollutants (POPs) available for atmospheric transport, while ocean-warming could lead to an increased release of POPs that have been trapped in the pack ice over time (Nash, 2011; Hellmer et al., 2012). Local anthropogenic activities such as industry, fishing, tourism, and research activities contribute to the progressive, point-source contamination of the Antarctic with POPs and microplastics (UNEP, 2011; Waller et al., 2017).

There is little information on plastics in the diet of fish and squid from Antarctic waters. To date, there have been no reports of plastic in the diet of Antarctic squid, however, two microplastic items (acrylic resin) were recovered from the gastrointestinal tract of a single Antarctic toothfish *D. mawsoni* from the Banzare Banks (Cannon et al., 2016). The same study also sampled *Gymnoscopelus nicholsi* from the Southern Ocean but found no evidence of plastic in the diet of this species. Similarly, Waluda (unpublished data) found no plastic in the gastrointestinal tract of eight species of fish (n = 142 individuals including *C. gunnari*, *E. carlsbergi*, *L. nudifrons*, *Lepidonotothen larseni*, *Parachaenichthys georgianus*, *Psilodraco breviceps,* and *Trematomus hansoni*) caught during a groundfish survey around South Georgia in 2011.

While no studies exist for the impact of pollutants on early life stages of Antarctic fish, there is growing evidence that environmental pollutants such as polychlorinated biphenyls (PCBs), polycyclic aromatic hydrocarbons (PAHs), and dioxins have adverse effects on embryonic and early larval development in fish (Nahrgang et al., 2016). The sensitivity of early life stages to environmental changes might be enhanced due to stressor interactions. Indeed, in the Antarctic dragonfish *Gymnodraco acuticeps*, combined exposure to ocean acidification and warming caused alterations in metabolism and developmental rate in embryonic stages (Flynn et al., 2015).

Mercury is considered to be one the most dangerous substances exhibiting toxicological characteristics, which raises environmental concerns. In marine ecosystems mercury can easily accumulate along food webs, ultimately concentrating in top predators in its different chemical forms (Wiener et al., 2007; Bargagli, 2008; Tavares et al., 2013). Some mercury uptake can occur from sea water through the gills, but mercury in prey is likely the main intake pathway (Lacoue-Labarthe et al., 2009). Squid, which link primary consumers and top predators, may play an important role as vectors of

[6] https://fisheries.msc.org/en/fisheries/south-georgia-icefish-pelagic-trawl/

[7] https://fisheries.msc.org/en/fisheries/australia-mackerel-icefish/

[8] https://fisheries.msc.org/en/fisheries/south-georgia-patagonian-toothfish-longline/@@view

[9] https://fisheries.msc.org/en/fisheries/australian-heard-island-and-mcdonald-islands-toothfish-icefish-fisheries/@@view

[10] https://fisheries.msc.org/en/fisheries/macquarie-island-mi-toothfish/@@view

[11] https://fisheries.msc.org/en/fisheries/sarpc-toothfish/@@view

[12] https://fisheries.msc.org/en/fisheries/ross-sea-toothfish-longline/@@view

[13] https://www.ccamlr.org/en/organisation/second-ccamlr-performance-review

mercury bioaccumulation. The main comprehensive source of information on Hg bioaccumulation in Southern Ocean squid is the recent work by Seco et al. (2020), which documents the concentrations of total, and proportions of organic, mercury in the tissues of 8 squid species caught around South Georgia between 2007 and 2017. While several studies have shown that Patagonian toothfish *D. eleginoides* have elevated mercury levels (Méndez et al., 2001; McArthur et al., 2003; Guynn and Peterson, 2008), Hanchet et al. (2012), Son et al. (2014), and Yoon et al. (2018) reported lower levels of mercury concentrations for the Antarctic toothfish *D. mawsoni*, usually not exceeding the 0.5 mg kg^{-1} food safety threshold.

Major gaps remain in our knowledge of the impacts of pollution on fish and squid in the Southern Ocean, and importantly, the extent to which these impacts may have population level effects (Seco et al., 2021). Studies that build on *in situ* work identifying the physiological mechanisms of pollution impacts will be critical to build hypotheses that identify vulnerable species and populations.

Pathogens

Many Antarctic fish species are heavily parasitized, especially in their liver and guts, by various helminth worms as well as other groups such as acanthocephalans, hirudinea, and copepods (Oguz et al., 2015; Gordeev and Sokolov, 2017; Klimpel et al., 2017; Münster et al., 2017; Kuhn et al., 2018; Muñoz and Rebolledo, 2019). Fish parasite community assemblages help to elucidate the ecology of their hosts, their role in the food web, and in the life cycle and transfer of parasites across species in the Southern Ocean (Kloser et al., 1992; Palm et al., 2007; Klimpel et al., 2010; Mattiucci et al., 2015; Kuhn et al., 2018). While all affected fish show various levels of chronic inflammation at infection sites, only Antarctic icefishes, which tend to be the most infected group, showed a significantly negative correlation between parasitic load and condition index (Santoro et al., 2013).

While no Antarctic fish diseases have been attributed to bacteria, X-cell disease caused by Alveolata protists (Freeman et al., 2017) and characterized by tumor-like growths (xenomas) on fish gills was reported in a few Antarctic notothenioid species (Franklin and Davison, 1988; Bucke, 1992; Davison, 1997; Evans and Tupmongkol, 2014). X-cell disease negatively affects condition index (Davison, 1997) and is likely to impair the capacity of the gills to extract oxygen from seawater. Affected fish displayed signs of chronic hypertension and extended recovery time from exercise, potentially altering their capacity to swim and thus forage (Davison and Franklin, 2003).

Viruses in Antarctic fish are poorly studied compared to other Antarctic animals (Smeele et al., 2018). There are only two reports on the identification of polyomaviruses (circular double stranded DNA viruses) in two fish species in the Ross Sea (Buck et al., 2016; Van Doorslaer et al., 2018).

Under global climate change, modifications in environmental conditions such as sea water temperature, acidity, salinity, ice coverage, and sediment input can have important consequences on pathogen abundance, distribution, and assemblage in the Southern Ocean (Danovaro et al., 2011; Klimpel and Palm, 2011; Palm, 2011). At the opposite end of the host-pathogen interaction, the same environmental stressors may push fish and squid past a point from which the parasitic load can start impacting the overall health of the host, making viral outbreaks more likely to occur. Both situations can potentially lead to dramatic effects on the fitness and the survival of the fish host.

CONCLUDING REMARKS

Globally, regions of the Antarctic are the fastest changing in the world, yet the impacts of these changes on marine ecosystems, including fish, remain unknown and highly complex. Circumpolar frontal systems seem to be in the process of changing their position, though the mechanisms behind these changes – and how they will impact fish and squid – remain uncertain. CCAMLR and its scientific community have recognized the critical need to manage for environmental uncertainty (an essential part of the CAMLR Convention mandate), including climate change (Rayfuse, 2018). For example, CCAMLR added climate change as an agenda item in 2008 (CCAMLR, 2007, 2008). In 2009, CCAMLR adopted resolution 30 on Climate Change, which recognizes "that global climate change is one of the greatest challenges facing the Southern Ocean. . ." and urged CCAMLR to consider climate change impacts in its management (CCAMLR, 2009). Yet, little progress in managing fish with climate change considerations has been made in the decade since the adoption of Resolution 30. The proposed Climate Change Response Work Plan proposed in 2017 will be important in adjusting fisheries to be sustainable in the changing Southern Ocean ecosystem (Brooks et al., 2018a).

What happens in Antarctica does not stay in Antarctica – water masses of the Southern Ocean and their dependent ecosystems are intricately connected to the global oceans (see Murphy et al., under review). Addressing the gaps in our knowledge of fish and squid ecology and adapting management strategies to an ever-changing Southern Ocean will require a global perspective: consideration of geopolitics, and collaboration with adjacent management bodies. In turn, understanding the impacts of climate change and fisheries on fish and squid ecology in the extreme environments of the Southern Ocean will ultimately inform how these same drivers will impact fish and squid globally.

AUTHOR CONTRIBUTIONS

JC, HC, AC, LG, and RT conceptualized the manuscript and developed the author team. JC managed the author team, including author recruitment, solicitation of contributions, as well as manuscript streamlining and editing. HC wrote the introduction to Section "Types of Fish and Squid in the Southern Ocean." JC wrote Section "Life Histories, Functional Relationships and Population Ecology." BW, CC, and AV wrote Section "Forage Species." LG wrote Section "Antarctic Silverfish." TDe wrote Sections "Icefishes" and "Pathogens." HC wrote Section "*Notothenia rossii*". JX wrote Sections "Forage Species" and "Drivers of Change and Their Impacts." CB

and LG wrote both parts of Section "Toothfish." CB, AV, RT, and AW wrote the introduction to Section "Data." CB and CJ wrote Section "Fisheries Data." TDo wrote Section "Active Acoustic Data." AC and CJ wrote Sections "Groundfish Trawl Surveys" and "Mark-Recapture (Tagging) Programs." JC and AC wrote the introduction to Section "Drivers of Change and Their Impacts." AC wrote Sections "Effects of Climate Change" and "Pressures on Stocks from Fishing." CC and RS wrote Section "Drivers of Change and Their Impacts." CB, CJ, and AC wrote Section "History of Finfish Fisheries." AS, MV, CW, and JX wrote Section "Pollution." CB, JC, and AC wrote Section "Concluding Remarks." JC and AC created **Tables 1–3**. AC created **Figures 1**–**3**. All authors reviewed and approved the final version of the manuscript.

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Global Connectivity of Southern Ocean Ecosystems

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Southern Ocean ecosystems are globally important. Processes in the Antarctic atmosphere, cryosphere, and the Southern Ocean directly influence global atmospheric and oceanic systems. Southern Ocean biogeochemistry has also been shown to have global importance. In contrast, ocean ecological processes are often seen as largely separate from the rest of the global system. In this paper, we consider the degree of ecological connectivity at different trophic levels, linking Southern Ocean ecosystems with the global ocean, and their importance not only for the regional ecosystem but also the wider Earth system. We also consider the human system connections, including the role of Southern Ocean ecosystems in supporting society, culture, and economy in many nations, influencing public and political views and hence policy. Rather than Southern Ocean ecosystems being defined by barriers at particular oceanic fronts, ecological changes are gradual due to cross-front exchanges involving oceanographic processes and organism movement. Millions of seabirds and hundreds of thousands of cetaceans move north out of polar waters in the austral autumn interacting in food webs across the Southern Hemisphere, and a few species cross the equator. A number of species migrate into the east and west ocean-basin boundary current and continental shelf regions of the major southern continents. Human travel in and out of the Southern Ocean region includes fisheries, tourism, and scientific vessels in all ocean sectors. These operations arise from many nations, particularly in the Northern Hemisphere, and are important in local communities as well as national economic, scientific, and political activities. As a result of the extensive connectivity, future changes in Southern Ocean ecosystems will have consequences throughout the Earth system, affecting ecosystem services with socio-economic impacts throughout the world. The high level

of connectivity also means that changes and policy decisions in marine ecosystems outside the Southern Ocean have consequences for ecosystems south of the Antarctic Polar Front. Knowledge of Southern Ocean ecosystems and their global connectivity is critical for interpreting current change, projecting future change impacts, and identifying integrated strategies for conserving and managing both the Southern Ocean and the broader Earth system.

Keywords: Southern Ocean, ecological connections, food webs, socio-economic, climate change, fisheries, global connectivity, scale

INTRODUCTION

Southern Ocean ecosystems were traditionally considered as largely distinct and separate from ecosystems in the rest of the world's oceans (Longhurst, 1998; Knox, 2007). This view of a unique isolated ecosystem contrasts with the view of the physical Southern Ocean as the center of the global thermohaline circulation that mediates the exchange of energy and heat between the oceans and influences patterns of circulation and sea level across the planet (Marshall and Speer, 2012; Talley, 2013; Chown et al., 2015). This almost paradoxical view of a highly connected ocean but an isolated ecosystem reflects, in part, the multi-front structure of the upper Southern Ocean. This structure restricts meridional (north-south) exchanges in surface waters, where most life occurs, while there is strong physical connectivity in intermediate and deeper waters through flow along density surfaces. Although the biological isolation of Antarctica has, to some extent, been qualified and its richness highlighted (Clarke and Johnston, 2003; Clarke et al., 2005; Barnes et al., 2006; Chown et al., 2015; Fraser et al., 2018; Chown and Brooks, 2019), the view of a "separate ecosystem" remains pervasive, which constrains approaches to analyses of the structure and function of Southern Ocean ecosystems and their role in the Earth system. This view also influences cultural and socio-economic perceptions, both of which affect the development of conservation and sustainable management measures and assessments of the impacts of change. Climate change is affecting Southern Hemisphere atmosphere and ocean circulation, with associated increases in ocean temperatures and reductions in sea ice, influencing Southern Ocean chemistry (e.g., reductions in pH), and biogeochemistry (e.g., carbon and nutrient budgets) (see Henley et al., 2020; Morley et al., 2020). Simultaneously, some previously exploited whale populations are increasing (Branch et al., 2004; Branch, 2011), and substantial commercial fisheries exist (Cavanagh et al., 2021a,b; Grant et al., 2021). Significant changes are already being observed in Southern Ocean ecosystems, and further perturbations are expected in the coming decades, making the development of an understanding of the impacts of climate change and direct human activities a key research priority (Murphy et al., 2008, 2012; Chown et al., 2012; Murphy and Hofmann, 2012; Constable et al., 2014; Rintoul et al., 2018).

Southern Ocean ecosystems support a range of globally essential ecosystem services, yet the underlying processes involved are poorly understood (Grant et al., 2013; Cavanagh et al., 2021a). The influence of Southern Ocean ecosystems on global ocean biogeochemical processes and carbon budgets is recognized (Sarmiento et al., 2004; Palter et al., 2010; Treguer et al., 2018; Henley et al., 2020), but the scale of influence and the ecological processes involved are less well known (Le Quéré et al., 2016; Treguer et al., 2018). There is evidence of biological exchanges across the Antarctic Polar Front (APF) at all trophic levels (plankton, fish, cephalopods, seabirds, and marine mammals), but the degree of connectivity of Southern Ocean and sub-Antarctic and wider Southern Hemisphere ecosystems has been relatively poorly characterized and quantified (Xavier et al., 1999; Barnes et al., 2006; Bernard et al., 2007; Moon et al., 2017). Views of Southern Ocean ecosystem processes and links with the wider global ocean have generally relied on the zonally (east–west) averaged perspective of Southern Ocean dynamics and north–south exchanges that have dominated analyses of physical dynamics for a number of decades (Turner et al., 2009). Although the importance of local and regional processes in maintaining ecosystem structure and functioning is known, the implications for understanding Southern Ocean scale dynamics and global connectivity (Rintoul, 2018) or implications for conservation and management of living resources (Reid, 2018) has received little consideration. The extent and importance of such ecological connectivity between oceanic ecosystems across the global oceans and the potential for feedback effects has also received little attention in analyses of the impacts of climate change or in the development of Earth system models (IPCC, 2019).

Current national and international bodies involved in fisheries management are generally unable to incorporate ocean scale connections in conservation and management measures. Activities in the Antarctic and the Southern Ocean are regulated under the Antarctic Treaty System (ATS). Development of measures for conservation and management of fisheries within the Southern Ocean is overseen at a circumpolar scale under the ATS by the Commission for Conservation of Antarctic Marine Living Resources (CCAMLR; Press et al., 2019; Reid, 2019). CCAMLR has developed activities with adjacent regional fisheries management bodies, but is yet to engage broadly to influence decisions outside the ATS on matters that affect the Southern Ocean (Anon, 2017). The International Whaling Commission (IWC) and the Agreement on the Conservation of Albatrosses and Petrels (ACAP) also consider Southern Ocean conservation issues within a global remit, while the Convention for the Conservation of Migratory Species (CMS) aims to provide coordinated legal frameworks for conservation of species throughout their migratory range, through the United Nations environmental treaty system. The spread of responsibility for

management of living resources in the Southern Ocean and across the Southern Hemisphere in disparate organizations with different remits limits the ability to incorporate ocean scale climate change and human activities as integral inputs to conservation and management.

The rapid changes being observed in Southern Ocean ecosystems and the major changes expected over the next few decades present a critical challenge to the ecosystem-based management approach and make the understanding of the impacts of change a priority (Murphy et al., 2012, 2016; Constable et al., 2014; Reid, 2018). This analysis, a contribution to the Marine Ecosystem Assessment for the Southern Ocean (MEASO), provides an assessment of how the Southern Ocean and associated human activities interact with and have reciprocal dependencies on global ecological and human systems. Here we examine the processes involved in biogeochemical and ecological exchanges between Southern Ocean ecosystems and the wider global ocean along with their importance at regional (circumpolar) and global scales. We note that although the sub-Antarctic Front (SAF) is an important physical structure and the APF an ecological boundary, marking the northern extent of ice-influenced surface waters, there is no fixed definition of the Southern Ocean (Longhurst, 1998; Boltovskoy, 1999; Chapman et al., 2020; Hindell et al., 2020; see Constable et al., this volume, for discussion on the areas being examined in MEASO). We first consider the Southern Ocean's physical and biogeochemical connectivity with the global ocean, which provides the basic framework for examining ecological connectivity. We then examine ecological connections that depend on the scales of biological movement, from microbes and plankton to highly mobile seabirds and marine mammals, and consider the extent to which these exchanges are important in maintaining populations and local and regional food webs. Lastly, we consider the interactions of human activities and associated impacts in the Southern Ocean, including both regionally-specific and global influences that will be important in conserving and managing the region in the future.

SOUTHERN OCEAN ECOSYSTEM CONNECTIONS

Processes Underpinning Connectivity

Two fundamental sets of processes determine the degree of natural ecological connectivity between oceanic ecosystems:

(i) *Physical advection processes–operating at different scales*, can transport dissolved nutrients and carbon, organic material, and organisms from one ecosystem to another (Mann and Lazier, 2005). This includes transport via ocean currents, eddies, and diffusion or associated with sea ice or in the atmosphere. Atmospheric processes are important in transporting elements into marine ecosystems (e.g., iron or mercury associated with dust deposition, Cossa et al., 2011; Moore et al., 2013) and some microorganisms (Mestre and Höfer, 2021) and in the movement patterns of some seabirds (Weimerskirch et al., 2012).

(ii) *Biological processes of movement–operating at different scales*, which utilize or can override physical processes over particular scales to allow an organism to achieve spatial displacement from one ecosystem to another or maintain position. Movement processes also transport elements (e.g., macro- and micronutrients), organic material, and organisms between ecosystems (Costa et al., 2012; Shepard et al., 2013; Walther et al., 2015; Hays, 2017).

Physical and Biogeochemical Connections

Physical Connectivity

The general perspective of Southern Ocean connectivity with the global ocean is a two-dimensional zonally-averaged view of meridional exchanges (**Figure 1A**; Turner et al., 2009). Increased observations and improvements in models over the last decade have enabled the spatial and temporal variability across multiple scales and three-dimensional nature of Southern Ocean connectivity to be better understood (**Figure 1** and **Supplementary Table 1**; Garzoli and Matano, 2011; Marshall and Speer, 2012; Talley, 2013; Frenger et al., 2015; Spence et al., 2017; Tamsitt et al., 2017, 2020; Tanhua et al., 2017; Rintoul, 2018; Foppert et al., 2019; Meijers et al., 2019b; Roach and Speer, 2019; Chapman et al., 2020).

The Southern Ocean is the central connection between the ocean basins in the global overturning circulation (Marshall and Speer, 2012; Talley, 2013), with the extent and intensity of northward or southward exchanges at particular depths being regionally variable around the Southern Ocean (Talley, 2013; Jones et al., 2016; Spence et al., 2017; Rintoul, 2018; Foppert et al., 2019; Meijers et al., 2019a; **Figures 1B,C** and **Supplementary Table 1**). There are differential inflows and outputs of Antarctic Bottom Water (AABW), deep water, and intermediate and mode waters in the Pacific, Atlantic and Indian Oceans and between the ocean basins in the Southern Ocean (Ferster et al., 2018; Tamsitt et al., 2020; Yamazaki et al., 2020). The eastern and western boundary regions in the major ocean basins appear to be particularly important in north-south exchange (Jones et al., 2016; Tamsitt et al., 2017). These circulation exchanges also vary inter-annually and seasonally, affecting the volume of water transported as well as heat and salt content (Cerovecki et al., 2019; Meijers et al., 2019a). In contrast to the eastward flowing Antarctic Circumpolar Current (ACC), regions near the continent are characterized by complex flows often dominated by westward flowing currents as part of the Antarctic Coastal Current. The polar gyre systems in the Weddell and Ross Sea regions provide locally complex mixing of water masses, which do not fit a simple two-dimensional zonally averaged view (Rintoul, 2018; MacGilchrist et al., 2019; Yamazaki et al., 2020). Frontal systems comprise a series of dynamic and variable zones (Chapman et al., 2020; **Figure 1D**). For example, the APF does not have a fixed location and instead varies within a broad zone. Associated with these dynamic frontal zones, there is extensive eddy activity that is most intense in areas of major bathymetric features and moves water across frontal systems in and out of the Southern Ocean (Frenger et al., 2015; Foppert et al., 2017;

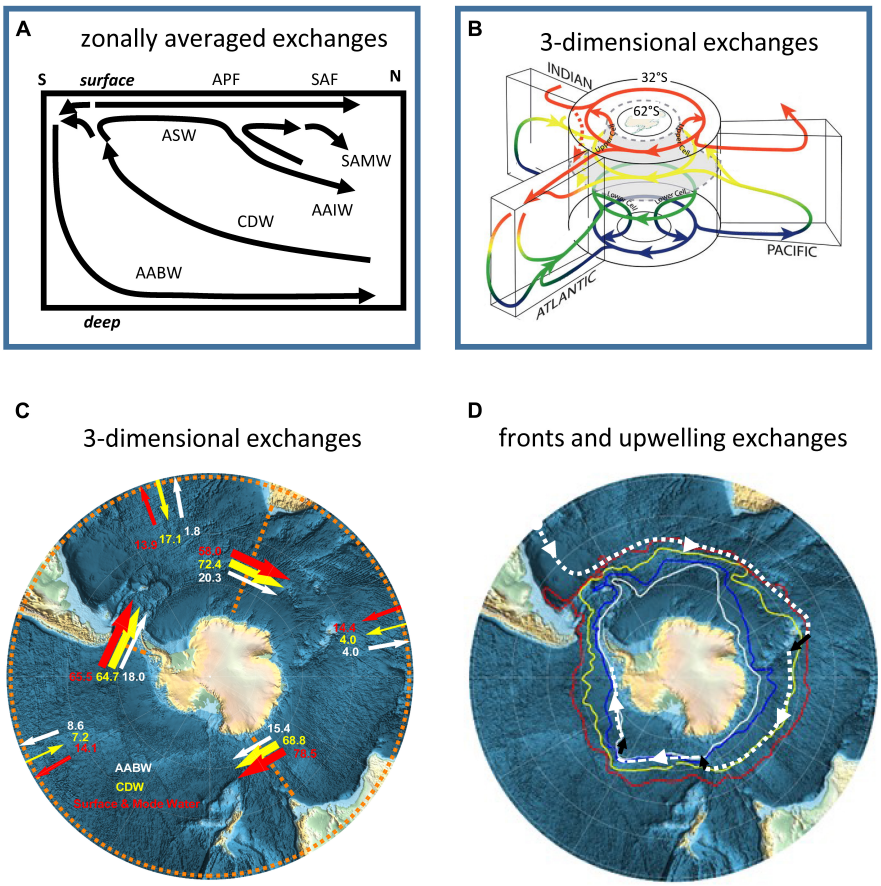

FIGURE 1 | Illustrations of physical connectivity of the Southern Ocean with the wider global ocean. **(A)** Zonally-averaged vertical view (surface to deep ocean) of the meridional flows of the major water masses into and out of the Southern Ocean (S, south; N, north; APF, Antarctic Polar Front; SAF, Sub-Antarctic Front; AASW, Antarctic Surface Water; CDW, Circumpolar Deep Water; AABW, Antarctic Bottom Water; AAIW, Antarctic Intermediate Water; SAMW, Subantarctic Mode Water). 3-dimensional perspectives of Southern Ocean connectivity: **(B)** global thermohaline schematic from Lumpkin and Speer (2007). Color indicates approximate density ranges. See their Figure 4 for details;© American Meteorological Society. Used with permission.), **(C)** model calculations of inter-basin exchanges (depth-integrated residual volume transports, (Sv, where 1 Sv = 10^6 m^3 s^{-1}) based on Figure 2 of Ferster et al. (2018); orange dotted lines show boundaries over which flows were calculated. Northern boundary = 30°S. **(D)** general location of the major frontal systems of the Antarctic Circumpolar Current (ACC; SAF = red; APF = yellow; Southern ACC Front, SACCF = blue; Southern Boundary of ACC = SBACC = white), The dotted white line is from the schematic of Tamsitt et al. (2017) showing an idealized particle trajectory illustrating the spiraling pathway of upwelling of southward flowing deep-water in the ACC as it interacts with major topographic features (black arrows; see their **Figure 7** for details).

Tamsitt et al., 2017; Rintoul, 2018; **Figure 1D**). The formation, direction of rotation, and movement and longevity of the eddies vary in different Southern Ocean regions, while the physical properties and influence also vary with depth and may penetrate to >2,000 m (Frenger et al., 2015). Ekman transport moves water primarily northward (north-eastward) across the ACC and southward in areas closer to the continent, whereas Stokes drift can lead to some southward movement of surface waters and eddy associated transport can move surface waters in both directions (Ito et al., 2010; Holzer and Primeau, 2013; Dufour et al., 2015; Tamsitt et al., 2017; Fraser et al., 2018).

The pathways and time scales by which water and tracers enter and exit the Southern Ocean are a function of the ocean's full three-dimensional horizontal and vertical structure, thereby providing a very different perspective of connectivity that goes beyond the traditional two-dimensional view of ocean circulation (**Figure 1** and **Supplementary Table 1**). The major physical (oceanic and atmospheric) mechanisms and processes that generate cross-scale exchanges from local to regional, circumpolar and with the global ocean can be represented schematically [**Figure 2A**; developed from Niiranen et al. (2018), their Figure B1]. In the ocean, these involve spatially (horizontally and vertically) and temporally variable meridional flows associated with major ocean currents and water masses (**Figure 2A**), while regional and local processes (e.g., eddies, surface flows, and topographic interactions) also result in cross-frontal exchanges (**Figures 1**, **2A** and **Supplementary Table 1**). Atmospheric processes at different scales further influence exchanges between the Southern Ocean and wider global ocean regions (e.g., local and regional weather patterns, seasonality, and large-scale climatology), affecting the distribution of tracers (e.g., in aerosols and dust) and routes for more efficient and rapid travel

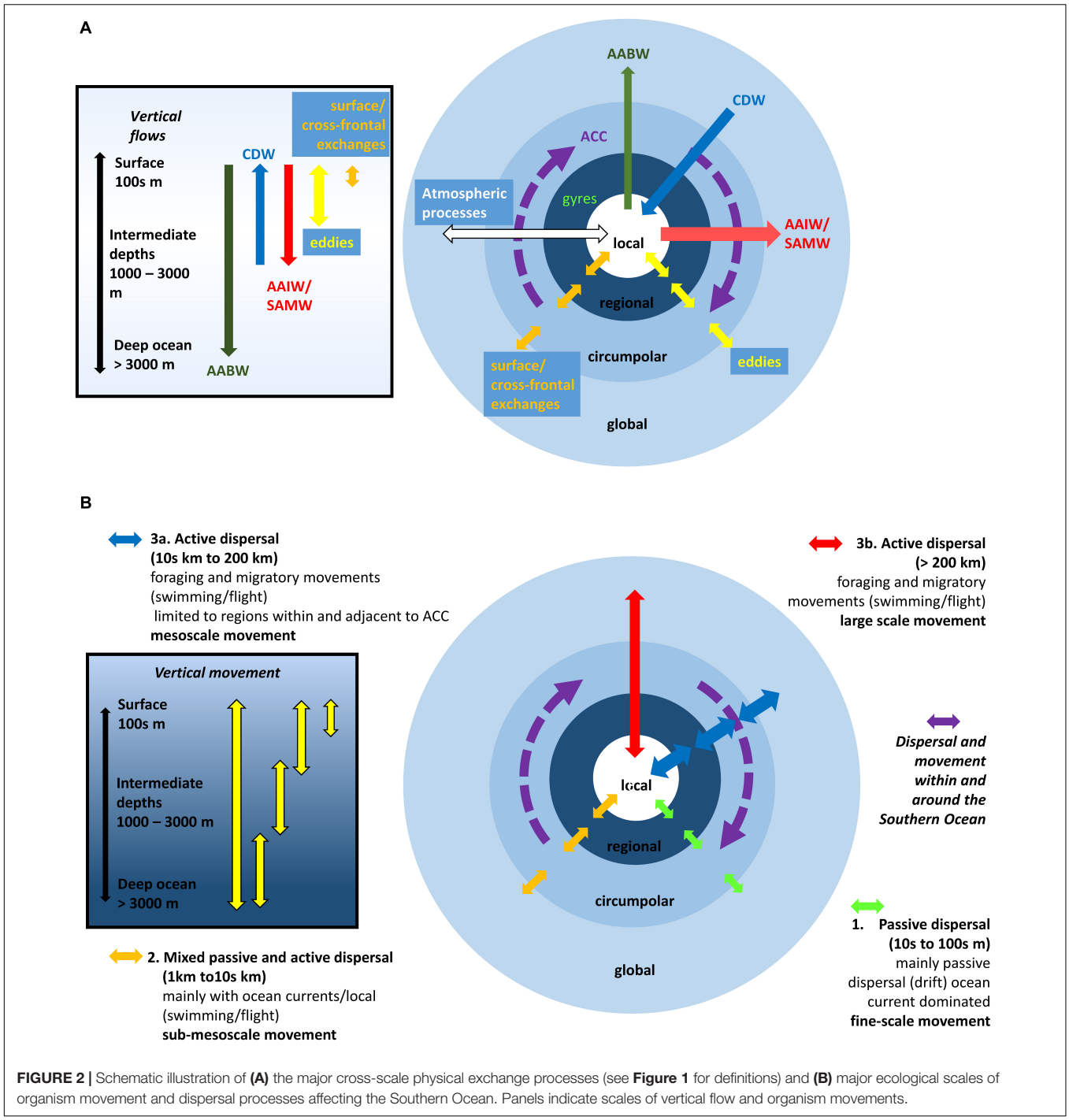

FIGURE 2 | Schematic illustration of **(A)** the major cross-scale physical exchange processes (see **Figure 1** for definitions) and **(B)** major ecological scales of organism movement and dispersal processes affecting the Southern Ocean. Panels indicate scales of vertical flow and organism movements.

by seabirds (Phillips et al., 2007b; Kirby et al., 2008; Egevang et al., 2010; Weimerskirch et al., 2012).

Biogeochemical Connectivity

The central role of the Southern Ocean in the global overturning circulation provides a direct connection with global biogeochemical cycles through the redistribution of biogeochemical properties (nutrients, carbon, and oxygen) amongst the major ocean basins and between the deep ocean, surface ocean, and atmosphere (Henley et al., 2020; see **Figure 1B**). Arguably, the most important role of the Southern Ocean in the Earth system is its regulation of climate through the exchange of CO_2 and other climate-active gases between the ocean and the atmosphere (Sabine et al., 2004; Marinov et al., 2006; Takahashi et al., 2012; Gruber et al., 2019). These exchanges are driven by physical and biological processes and their connectivity (Morrison et al., 2015) with oceanic regions to the north. For example, the Southern Ocean between 30 and

50°S is a major net annual carbon sink and the Southern Ocean as a whole has taken up ∼40% of the total oceanic uptake of anthropogenic CO_2 (Orr et al., 2001; Fletcher et al., 2006; DeVries, 2014; Frölicher et al., 2015).

In addition, nutrient export from the Southern Ocean, which is a function of a range of ecosystem processes, exerts an important control on global nutrient distributions, and therefore export production and oxygen and carbon budgets over large oceanic areas north of 30°S (Sarmiento et al., 2004; Marinov et al., 2006; Moore et al., 2018). Surface nutrient concentrations and ratios, particularly in the formation regions of Antarctic Intermediate and Subantarctic Mode Water (AAIW and SAMW), are transported northward, subducted into the ocean interior, and mixed through the thermocline into macronutrient-limited low-latitude surface waters, where they regulate primary production and phytoplankton species composition (Sarmiento et al., 2004; Marinov et al., 2006; Palter et al., 2010; Hauck et al., 2015, 2018). South of the Southern Boundary of the ACC upwelling region (SBACC; **Figure 1**), water masses move southward and can contribute to AABW formation, thus playing an important role in transferring carbon into the deep ocean (Marinov et al., 2006).

Iron is an important limiting micronutrient in the oceanic "high-nutrient-low-chlorophyll (HNLC)" areas of the Southern Ocean, occurring in low concentrations in surface waters and regulating the growth of autotrophic organisms (de Baar et al., 1990; Moore et al., 2013). Iron availability has a particularly strong impact on the uptake of the major nutrients (N, nitrogen; P, phosphorus; Si, Silicon) by diatoms, with iron limitation increasing the Si/N uptake ratio of diatom-dominated communities (Hutchins and Bruland, 1998; Takeda, 1998; Pondaven et al., 2000). This leads to a reduction in relative concentrations of silicon (as silicic acid) south of the SAF by the diatom-dominated primary production, such that surface waters exported northward from the Southern Ocean are Si-deplete and nitrogen- and phosphorus-rich (Treguer et al., 2018; Henley et al., 2020). This promotes non-diatom phytoplankton growth at lower latitudes, with implications for reduced carbon export compared to fast-sinking diatoms (Buesseler, 1998; Ducklow et al., 2001; Armstrong et al., 2009). Similarly, varying N/P uptake ratios of different phytoplankton species influence the N/P ratio of exported waters, with implications for carbon export at lower latitudes (Arrigo et al., 1999; Weber and Deutsch, 2010; Martiny et al., 2013). The spatial and temporal variability of oceanic connections (see section "Physical Connectivity," **Supplementary Table 1**) results in structure and variability in the biogeochemical connections. Combined with the physical variability, this generates inter-annual and seasonal variation in the concentration of nutrients, carbon, and oxygen entering the ocean interior.

Ecological Connectivity

Scales of Ocean Processes and Organism Movement

Evolutionary history is a major determinant of the distribution and ecological connectivity of modern Antarctic fauna. The rich contemporary fauna is considered to be largely endemic with *in situ* adaptation to local conditions occurring during the period of Southern Ocean cooling as Antarctica separated from the last Gondwanan connections 23–40 mya (Clarke and Johnston, 2003; Clarke and Crame, 2010; Fraser et al., 2012). Most Antarctic groups appear to have survived Pleistocene glacial cycles within the Antarctic region, for example, by sheltering in refugia created by polynyas, deeper waters, or geothermal environments (Convey et al., 2009; Allcock and Strugnell, 2012; Fraser et al., 2012, 2014). There are, however, many mobile seabird and marine mammal species that occur and breed both within and north of the APF (Hindell et al., 2020). The Southern Ocean's intense seasonality is a fundamental driver of life-cycle evolution and hence also a major influence on ecological connectivity (Clarke and Crame, 2010; Murphy et al., 2016; Varpe, 2017).

Passive and active dispersal, movements and migrations are a fundamental aspect of the dynamics of marine species and ecosystems (Nathan et al., 2008; Walther et al., 2015; Schlägel et al., 2020). Passive dispersal of organisms can reduce local accumulation and competition, moving organisms into regions that are more favorable allowing colonization of new habitats. Active movements and migrations allow organisms to shift habitats to cope with changes in environmental conditions, food availability and mortality, which involve trade-offs in terms of overall reproductive success (Clark and Mangel, 2000; Schlägel et al., 2020). A number of seabird and marine mammal species in the polar regions are seasonally migratory in order to access the optimal habitats for their life cycle (see section "Active Dispersal"). For example, some species of whales target colder areas with high densities of prey in the austral summer, and in the austral winter they occupy warm waters for calving, and possibly also skin regeneration (Pitman et al., 2020).

The major migratory movements of seabirds and whales occur over relatively short periods of a few weeks during the austral spring and autumn. This indicates that connectivity between regions will be particularly intense during these periods with concentrated patterns of movement and aggregation in Southern Ocean regions during spring. By moving and migrating the organisms can enhance reproductive success and maintain higher overall abundance. However, it also means that there are marked differences in local and regional abundance spatially and seasonally, with intense aggregation and hence high regional/local abundance in the summer habitats, but very low abundance in winter, while abundance increases in their winter habitats.

The multi-front structure of the Southern Ocean (**Figure 1**) limits the exchanges of material and organisms in the upper ocean from the most polar southern regions to areas north of the APF and SAF. However, there is much more extensive cross-frontal exchange than was previously understood, and frontal structures do not extend into the deep ocean (Frenger et al., 2015; Foppert et al., 2017; Chapman et al., 2020). Cross-frontal processes and current fows (**Figures 1**, **2A**) provide mechanisms and routes for transferring material and organisms into and out of the Southern Ocean, resulting in broad latitudinal zones of mixing of upper ocean communities. Dispersal of organisms, or particular life cycles stages, in (or above) the oceans results from a combination of physical and biological process interactions at different scales,

including passive and active movements. For organisms, as a broad simplification, the relative importance of advective versus active movement processes is a function of their size. Although there are clear exceptions to the general allometric relationship, small organisms tend to be more strongly influenced by physical advective processes, while larger organisms are more mobile and can overcome advective dispersal over smaller scales (Peters, 1983; Andersen et al., 2016; Hays, 2017). Organisms of every size have evolved adaptations that allow them to utilize spatial heterogeneities at different scales (horizontally and vertically) and temporal variability in advective processes to influence retention and dispersal to optimize access to favorable habitats and/or resources (Mann and Lazier, 2005; Costa et al., 2012; Shepard et al., 2013; Walther et al., 2015; Andersen et al., 2016; Hays, 2017). Although many of the exchanges we consider will be two-directional (north–south) and there is valuable information on dispersal and migratory movements of some species, particularly in terms of seasonal migrations of Southern Ocean predators, there has been little focus on the exchanges at most trophic levels.

We consider three scales of ecological connectivity linking the Southern Ocean and global ocean ecosystems based on the movement of Southern Ocean organisms (**Supplementary Table 2** and **Figure 2B**).

Passive Dispersal

The distribution of epipelagic planktonic organisms is primarily driven by passive dispersal, so cross-frontal exchange processes (e.g., eddy activity and surface currents) can greatly affect where they are found. As a result of the variability of these processes (see section "Physical and Biogeochemical Connections"), there are particular areas around the Southern Ocean where exchanges of planktonic organisms across frontal systems most frequently occur (Tamsitt et al., 2017). In areas between the APF and SAF, subduction processes (see section "Physical and Biogeochemical Connections"), move planktonic organisms northward from mode water formation areas (Jones et al., 2016). The success and survival of these expatriate plankton (e.g., Southern Ocean diatoms) depends on local physical and nutrient conditions (e.g., upwelling, cross-thermocline exchanges and silicic acid and iron concentrations).

Studies examining the partitioning of zooplankton communities over regional and circumpolar scales indicate that changes are coincident with the major frontal zones (Froneman et al., 1995; Pakhomov and McQuaid, 1996; Ward et al., 2003; Johnston et al., unpublished data). The SAF and APF can be strong barriers, and the APF is particularly significant as the main distribution limit for many of the true cold water Antarctic species (Deacon, 1982; Boltovskoy, 1999; Griffiths et al., 2009). However, latitudinal movements and variation of frontal positions and associated meandering and eddy shedding, particularly within the Polar Frontal Zone (PFZ), facilitate cross-frontal exchanges (Lutjeharms and Baker, 1980; Bryden, 1983; Heywood et al., 1985; Lutjeharms et al., 1985; Pakhomov et al., 1997; Chiba et al., 2001; Hunt et al., 2001, 2002; Bernard et al., 2007; Foppert et al., 2017). Eddies that drift some distance from their origin provide an effective means of transporting faunas into different water masses (Atkinson et al., 1990; Bernard et al., 2007) and can enhance zooplankton productivity and abundance, particularly at their peripheries (Bernard et al., 2007; Della Penna et al., 2018). Planktonic larvae of benthic species can cross such frontal zones in eddies (Clarke et al., 2005), and also have new and increasing passive opportunities on floating debris such as plastic (Barnes, 2002; Horton and Barnes, 2020). The result of these exchange processes is that there can be wide transition zones between warm- and cold-water communities where they mix to varying extents (Boltovskoy, 1999; Atkinson and Sinclair, 2000). The different plankton communities across the fronts are thus often represented by changes in the balance of taxa or in the abundance of individual species, rather than fundamentally differing faunas (Siegel and Piatkowski, 1990; Tarling et al., 1995; Ward et al., 2012).

Compared to epipelagic species, many mesopelagic species have wider-ranging distributions that are much less constrained by frontal boundaries (Proud et al., 2017; Sutton et al., 2017). Most mesopelagic species also encounter large temperature changes during their seasonal vertical migrations, compared to the comparatively small temperature change across the APF for example, and hence frontal boundaries do not represent faunal boundaries for these taxa (Proud et al., 2017; Sutton et al., 2017). Biogeographic schemes that work well for epipelagic species are therefore not appropriate for deeper dwelling species and many planktonic mesopelagic taxa (e.g., decapods, ostracods, and siphonophores) have distributions that are wider and more likely to cross frontal boundaries compared to their epipelagic counterparts (Angel and Fasham, 1975; Pugh, 1975, 1999; Fasham and Foxton, 1979; Angel, 1999).

Some benthic and intertidal species are now known to cross Southern Ocean fronts and enter Antarctic waters by rafting with buoyant materials at the very surface of the ocean (Fraser et al., 2018). Organisms floating at the surface are affected by Stokes drift, through the horizontal transport of particles with wind-driven surface waves (Fraser et al., 2018). Rafts of buoyant macroalgae, for example, can–through a combination of mesoscale eddies and storm-associated Stokes drift–cross into Antarctic waters from Subantarctic sources north of the APF, some carrying diverse invertebrate and other passengers (Avila et al., 2020).

Mixed Passive and Active Dispersal

A range of Southern Ocean plankton, fish and cephalopods species have cross-frontal distributions while foraging seabirds and marine mammals move across the APF to breed or feed or in shorter seasonal migrations (Catry et al., 2004; Murphy et al., 2007; Ashford et al., 2008; Della Penna et al., 2015; Hunt et al., 2016; Pistorius et al., 2017; Xavier et al., 2018; Saunders et al., 2019; Queirós et al., 2021).

The strong physical transition between warm and cold waters at the APF strongly limits the potential for southward movement of large migratory epipelagic fish species (Hunt et al., 2016). The fish fauna of the Southern Ocean is largely distinct from that north of the APF. The Antarctic fish fauna is primarily dominated by the notothenioid group (Matschiner et al., 2011), which has specific adaptations (Chen et al., 1997), allowing them

to exist in the coldest regions of the Southern Ocean. Several other species of fish and cephalopods do have distributions that cross the APF and/or the SAF with evidence of ontogenic shifts in habitats. A key aspect of a number of these species' life cycles is the importance of advection and physical processes of aggregation and dispersal in maintaining distributions. Mesoscale oceanographic processes, such as fronts, eddies and jets, can have a profound influence on the distribution, abundance, population dynamics and behavior of pelagic fish (Ashford et al., 2005; Petitgas et al., 2013; Hunt et al., 2016; Netburn and Koslow, 2018). Several demersal/semi-demersal fish species with pelagic eggs and larval stages depend on advection to transport offspring from spawning areas to suitable nursery areas, and zonal advection is important in maintaining connectivity amongst populations of such fishes (Ashford et al., 2012; Damerau et al., 2012; Young et al., 2012; Hop and Gjosaeter, 2013; Vestfals et al., 2014; Hunt et al., 2016; Petrik et al., 2016; Huserbraten et al., 2019; Mori et al., 2019). Although there is generally little exchange between fish fauna in the upper ocean across the APF, some species do move across the APF. For example, the commercially exploited Patagonian toothfish (*Dissostichus eleginoides*) is a species that shows population connectivity at the ocean basin scale and across the APF (Ashford et al., 2005, 2008, 2012). Spatial movements of organisms associated with ocean currents (and sea ice drift in polar waters) influence their distributions and hence susceptibility to transport into or out of the Southern Ocean. Vertical migrations by a range of zooplankton, fish and cephalopod species (see Caccavo et al., 2021; Johnston et al., unpublished data) involve interactions with water masses that may facilitate north-south exchanges across the APF.

Mesopelagic fish are ubiquitous in the world's ocean and comprise a substantial source of biomass (Irigoien et al., 2014; Saunders et al., 2019). Of the mesopelagic fish, lanternfish (Family Myctophidae; hereafter myctophids) are the most speciose and biomass-dominant group in most oceanic regions (Gjosaeter and Kawaguchi, 1980; Catul et al., 2011), including the Southern Ocean (Hulley, 1981; Lubimova et al., 1987), where they are important in pelagic food webs and biogeochemical cycles (Pakhomov et al., 1996; Murphy et al., 2007; Saunders et al., 2017, 2019; Caccavo et al., 2021). In parts of the Southern Ocean the majority of myctophid species either do not reproduce or their young do not recruit in waters south of the APF (Saunders et al., 2017), with the core populations of most myctophid species centered at predominantly sub-Antarctic, or temperate latitudes (Hulley, 1981; McGinnis, 1982; Loeb et al., 1993; Christiansen et al., 2018). This suggests that the relatively high biomass of myctophid fish in Antarctic waters appears to be sustained by mass immigration of adults from lower latitudes involving oceanographic and behavioral processes and interactions (Saunders et al., 2017). However, the level of connectivity between Antarctic and sub-Antarctic/temperate systems is also unlikely to be uniform for myctophid fish across the Southern Ocean (Koubbi et al., 2011; McMahon et al., 2019). Evidence that migrant individuals do not return from this southward journey and form sink populations in waters south of the APF was presented by Saunders et al. (2017), further highlighting the importance of such regional connectivity pathways in maintaining their distributions.

Some pelagic cephalopod species have distributions that encompass areas north and south of the APF (Xavier et al., 1999), which in some species involves ontogenetic shifts in habitat. Stable isotope analyses of carbon on different parts of the cephalopod beaks show that numerous species move from warmer waters to colder waters during their development (Queirós et al., 2020), indicating similar ontogenetic shifts in habitat to that observed in the mesopelagic fish community (Saunders et al., 2017). More generally, distribution modeling based on relationships with particular oceanographic conditions and analyses of the diets of predators of squid further indicates cross-frontal distributions (Xavier et al., 2016; Pereira et al., 2017). Analyses of the diets of predators of squid, stable isotope ratios, and species distribution models based on habitat preferences have confirmed these cross-frontal distributions around the Southern Ocean (Guerreiro et al., 2015; Xavier et al., 2016; Pereira et al., 2017).

Benthic species show both passive and active transport of organisms between the Southern Ocean and other oceans, e.g., pedunculate barnacles, "hitching a ride" as commensal epifaunal on birds, seals, and whales (Barnes et al., 2004). Shipping has increased passive riding on active transport into and out of the Southern Ocean (Lewis et al., 2003; Lee and Chown, 2009; McCarthy et al., 2019).

Active Dispersal

The migration of large numbers of seabirds and marine mammals into the Southern Ocean during spring to feed, and in many cases to breed, during the short summer period is part of the classical view of the operation of the ecosystem (Knox, 2007). However, major technological advances since the 1990s have greatly increased knowledge of the at-sea activity patterns and movements of a wide range of species (Phillips et al., 2007a; Hindell et al., 2020). During the austral spring/early summer, breeding seabirds and seals aggregate in large colonies on ice-free land in coastal regions around the continent and on islands further north. When young are being fed, foraging distance is restricted and demand for prey is most intense within a few hundred kilometers of the main breeding sites (Croxall et al., 1985; Murphy, 1995). However, during both incubation and chick-rearing, albatrosses and petrels travel long distances during extended foraging trips, including northward across the APF and SAF (Peron et al., 2010). For example, wandering albatross *Diomedea exulans* that breed south of the APF at South Georgia mainly forage in shelf areas off South America and in oceanic waters around the subtropical convergence (Xavier et al., 2004; Ceia et al., 2015). Some species breeding on sub-Antarctic islands north of the APF do the opposite, flying south to forage in the Southern Ocean (Peron et al., 2010).

At the conclusion of the breeding season, adults, and fledgling seabirds disperse across the Southern Ocean, keeping north of the advancing seasonal pack ice or migrating across the APF (Phillips et al., 2006; Weimerskirch et al., 2015). There is a general movement of animals which bred south of the APF into oceanic waters to its north during autumn and winter

(Croxall et al., 2005; Quillfeldt et al., 2013). This is to avoid the lower productivity, harsher weather, and shorter photoperiods during the austral winter, which limit the foraging of visual predators as well as phytoplankton growth: however, dispersal strategies vary greatly among species, breeding sites, and individuals (Delord et al., 2014; Weimerskirch et al., 2015; Phillips et al., 2016). A number of species migrate into coastal waters off South America, southern Africa, and Australasia, which are areas of high productivity and may also be associated with boundary currents or upwelling zones (Phillips et al., 2005, 2006; Quillfeldt et al., 2013). Other species undertake much longer winter migrations northward toward the equator, and a few even move into the Northern Hemisphere (Kopp et al., 2011). The observed patterns and routes of both foraging movements and long-distance migrations of seabirds are often associated with weather patterns as the birds use the wind for efficient travel between areas (Phillips et al., 2007b; Kirby et al., 2008; Egevang et al., 2010; Weimerskirch et al., 2012).

Most seabirds migrating from islands south of the APF in oceanic or continental shelf waters take varied routes across a broad front, but *trans*-equatorial migrants to or from the Northern Hemisphere often stay relatively close to continental coasts (Shaffer et al., 2006; Egevang et al., 2010; Kopp et al., 2011). The latter are some of the longest migrations of any organisms on the Earth (e.g., **Figure 3A**). Short-tailed shearwaters *Ardenna tenuirostris* tracked from Tasmania moved into the Southern Ocean after breeding, before flying north across the western Pacific Ocean to waters near Japan or further north in the Bering Sea (Carey et al., 2014). The classic example of a long-distance seabird migrant is the Arctic tern *Sterna paradisaea*, which breeds in Europe and the Arctic, then migrates in its non-breeding season to the Antarctic where it feeds in sea ice environments, thereby experiencing an endless summer (Egevang et al., 2010; Redfern and Bevan, 2020).

Cetaceans also migrate south to feed in the Southern Ocean in spring and move northward during autumn to breed at lower latitudes. Due to their size and mobility they can move large distances within the Southern Ocean to target areas of enhanced food availability (Branch et al., 2007; Horton et al., 2017, 2020; Andrews-Goff et al., 2018; Bestley et al., 2019; **Figure 3B**). It is not known whether their Southern Ocean entry points are diffuse or concentrated, because very few species have been tracked travelling into and out of the polar regions. Humpback whales *Megaptera novaeangliae*, are the best studied species in this respect; movement studies suggest a preference in some areas for particular migratory routes into the Southern Ocean for this Antarctic krill *Euphausia superba* feeding species. For example, in the southwest Atlantic region, humpbacks appear to follow a single southbound migratory route, consistent over multiple years and varying environmental conditions (Horton et al., 2020). Humpbacks tracked off east Australia follow multiple distinct migratory routes into the polar regions (Andrews-Goff et al., 2018), while whales migrating from Oceania (South Pacific) have more diffuse southbound movements (Riekkola et al., 2018), suggesting that regional patterns may vary depending on Southern Ocean food predictability. A number of pinniped species, such as Antarctic fur seals *Arctocephalus gazella* and elephant seals *Mirounga leonina*, have distributions that cross the PFZ, and a proportion of these populations move further north out of the Southern Ocean during winter (Hindell et al., 2020).

This large number of organisms (fish, cephalopods, seabird, and marine mammals) crossing the APF and PFZ during their life cycle or their seasonal migrations further connects the Southern Ocean to the rest of the globe. These animals constitute a recurrent dispersion vector of microorganisms such as bacteria, archea, fungi, and protists by transporting their attached microbiota in and out of the Southern Ocean [see examples in Mestre and Höfer (2021), and references therein].

IMPLICATIONS OF ECOLOGICAL CONNECTIVITY

Seasonal Shifts in Demand for Prey

With better estimates of abundance and much-improved knowledge of seasonal foraging and migration patterns in recent years, it is possible to broadly assess seasonal shifts in demand for prey of key groups of marine predators, including seabirds and cetaceans. We estimated the seasonal shift in and out of the Southern Ocean for these communities and their demand for prey in the Southern Ocean compared with waters north of the APF. Details of the data, methods, and concerns and caveats for calculations of seabird and cetacean demand for prey during and outside of the breeding season are given in the **Supplementary Material**. Calculation results are presented in **Supplementary Tables 3, 4** (seabirds and cetaceans, respectively). We have taken the APF as the major boundary for estimating movements, recognizing that many species will only move into sub-Antarctic regions south of the SAF. The calculations indicate the magnitude of seasonal movement and change in predator abundance, and food requirements in ice influenced polar waters and areas further north. However, these estimates are uncertain, and we regard them as the first set of illustrative estimates of prey demand, which will require further refinement, providing spatially and temporally resolved views of changes in distribution and demand for prey of different predator species.

Seasonal Changes in Prey Demand of Seabirds

We considered just those populations that breed in the Southern Ocean in our consumption estimates, primarily because of uncertainties associated with colony sizes and the proportion of time spent feeding south of the APF by many seabirds that breed north of the APF. However, demand for prey will also be high south of the APF for very abundant species that use these waters during part of their breeding or nonbreeding seasons, for example, short-tailed and sooty shearwaters *Ardenna grisea* from colonies in Australasia, and Antarctic prions *Pachyptila desolata* and thin-billed prions *P. belcheri* from sub-Antarctic islands (Shaffer et al., 2006; Quillfeldt et al., 2013; Carey et al., 2014; **Supplementary Material**). In total, we estimated that 51 million pairs of seabirds breed annually in the Antarctic region (south of the APF), which translates to an estimated 137 million individuals, including the other life-stages (sabbatical birds, immatures, and juveniles; **Figure 4A**

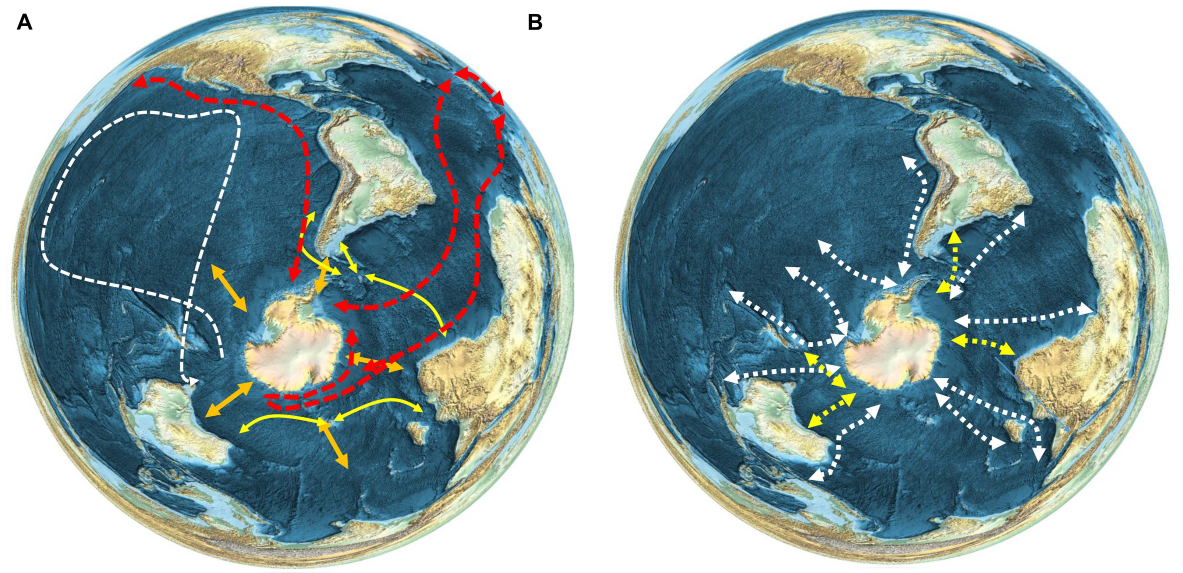

FIGURE 3 | Patterns of movement and migration of seabird and marine mammal species, **(A)** Seabirds (see text for references). Red–Arctic tern (*Sterna paradisaea*); White–short-tailed shearwaters (*Ardenna tenuirostris*); Yellow–black browed albatross (*Thalassarche melanophris*), wandering albatross *(Thalassarche chrysostoma*), white-chinned petrel (*Procellaria aequinoctialis*) and giant petrel (*Macronectes giganteus)*. Orange arrows show the general north-south seasonal migration of seabirds. **(B)** Whales. White–humpback whale (*Megaptera novaeangliae*) (Best et al., 1993; Zerbini et al., 2006, 2018; Robbins et al., 2011; Félix and Guzmán, 2014; Fossette et al., 2014; Rosenbaum et al., 2014; Garrigue et al., 2015; Guzman et al., 2015; Riekkola et al., 2018; Bestley et al., 2019; Horton et al., 2020); Yellow – southern right whale (*Eubalaena australis*) (Best et al., 1993; Zerbini et al., 2018; Mackay et al., 2020; Riekkola et al., 2021).

and **Supplementary Table 3**). During the breeding season, the at-sea distributions of most species are entirely south of the APF. Of the species which often forage north of the APF during breeding, most use oceanic waters, including grey-headed albatrosses *Thalassarche chrysostoma*, black-browed albatrosses *T. melanophris* and cape petrels *Daption capense* (Phillips et al., 2004). The few exceptions include white-chinned petrel *Procellaria aequinoctialis*, wandering albatrosses and to a lesser extent the giant petrels *Macronectes* spp., which frequently travel from South Georgia to the Patagonian Shelf or adjacent shelf-break (Phillips et al., 2006; Jiménez et al., 2016; Granroth-Wilding and Phillips, 2019). By comparison, as most or all individuals of many species are migratory, at-sea distributions during the nonbreeding season are largely or entirely (i.e., >80%) north of the APF. In most cases, this reflects their migration to sub-Antarctic, subtropical, or even tropical oceanic waters (Quillfeldt et al., 2013; Clay et al., 2016, 2018). The exceptions among the most abundant species from South Georgia are white-chinned petrels, which winter on the Patagonian Shelf or the Humboldt Upwelling system off Chile, and black-browed albatrosses, which winter mainly in the Benguela Upwelling system off South Africa and Namibia (Phillips et al., 2005, 2006).

Taking population sizes, at-sea distributions, and breeding schedules into account 870,000 seabirds from Antarctic colonies feed north of the APF for a total of 159 million bird-days during the breeding season (<0.01% birds in the north). In contrast, around 80 times as many seabirds–68.5 million–from Antarctic colonies move north of the APF for a total of 16,600 million bird-days during the nonbreeding season (51% of birds are in the north in winter; **Figure 4A**). In terms of biomass, this represents a flux of 18,000 tonnes of seabirds from Antarctic colonies to feed north of the APF in the nonbreeding season, compared with just 1,300 tonnes of seabirds which were feeding there during the breeding season.

The three species contributing to the great majority of this biomass movement in the nonbreeding season are the Antarctic prion, macaroni penguin *Eudyptes chrysolophus* and white-chinned petrel (8.1, 6.5, and 2.8 tonnes, respectively). Although the total number of seabirds north of the APF during the nonbreeding season is similar to the number that remains to its south (70 vs. 68 million individuals), the latter represents much greater biomass (151 vs. 19 thousand tonnes) of which the top five species (contributing 11–47 thousand tonnes) are all penguins; these are of course much heavier taxa than most of the migrant petrels. Small animals require considerably more energy than large animals for body maintenance per unit mass. Hence, the total energy required from food, and hence the total mass of prey consumed north and south of the APF for the seabirds from Antarctic colonies during the nonbreeding season is similar (1.07×10^{13} kJ and 1.79 million tonnes prey vs. 1.19×10^{13} kJ and 1.99 million tonnes of prey; 47% of the demand is in the north). This is in direct contrast to the breeding season when the relative energy and food intake of Antarctic seabirds south of the APF is 126 times that required to its north (56.5×10^{13} kJ and 9.42 million tonnes of prey vs. 0.4×10^{13} kJ and 74 thousand tonnes of prey; <0.01% in the north; **Figure 4A**).

Given the locations and sizes of their main colonies, the seabirds from south of the APF which feed to its north during

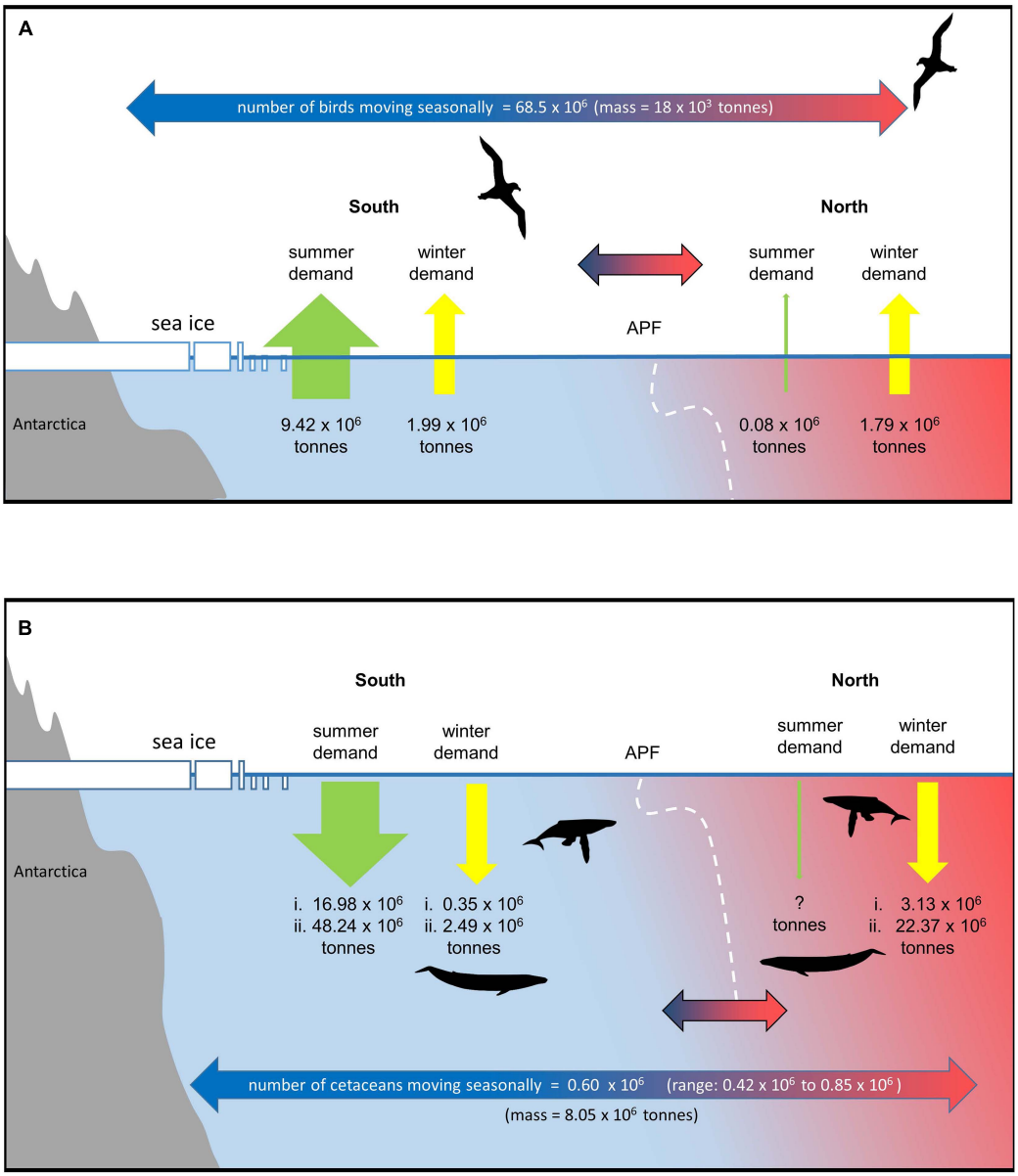

FIGURE 4 | Migration and seasonal changes in prey demand of predators that move seasonally in and out of the Southern Ocean (see text and **Supplementary Material** for details). The APF is taken as the nominal boundary. Information on population sizes and spatial shifts of many species is very limited and estimates are therefore uncertain and indicative. **(A)** seabirds, **(B)** cetaceans (assumes 90% of cetaceans move out of the Southern Ocean in winter (range based on available error estimates). Estimates of summer and winter demand south of the APF and winter demand to the north are based on two estimates of summer consumption rates and two estimates of winter:summer total consumption ratios [(i.) = low summer consumption rate and low winter:summer ratio, (ii.) = high summer consumption rate and high winter:summer ratio]. No estimate is given for summer demand north of the APF.

the breeding season are mainly in the Atlantic sector, although smaller numbers of seabirds also feed north of the APF in the Indian Ocean (Phillips et al., 2004, 2006; Wakefield et al., 2011; Granroth-Wilding and Phillips, 2019). The same broad geographical pattern applies during the nonbreeding season, i.e., the largest numbers and biomass of seabirds migrating north of the APF are in the Atlantic sector.

Excepting the south polar skua *Stercorarius maccormicki* and Wilson's storm petrel *Oceanites oceanicus*, the Antarctic seabird populations that move north of the APF remain in the Southern Hemisphere, predominantly in oceanic waters from the sub-Antarctic to the subtropics. In the Atlantic, those in oceanic waters will overlap with the southern portion of at-sea distributions of the huge seabird populations from the South Atlantic Islands. This overlap is greater during the nonbreeding season than the breeding season (Reid et al., 2013; Dias et al., 2017; Ronconi et al., 2018; Jones et al., 2020). Those Antarctic populations that move to a greater or lesser extent close to or

onto the Patagonian Shelf or into the Humboldt Current will overlap with huge local breeding populations of seabirds and many long-distance migrants from areas such as New Zealand or the Northern Hemisphere (Spear et al., 2003; Landers et al., 2011; Baylis et al., 2019; Ponchon et al., 2019). In the Indian Ocean, the situation is somewhat different in that the Antarctic seabird populations which feed north of APF overlap very extensively not just during the nonbreeding but also during the breeding season, with the major breeding populations of seabirds on island groups within a few 100 km of the APF (Delord et al., 2014; Reisinger et al., 2015). As such, it is perhaps only the most numerous of the migrant seabirds from the Antarctic region – Antarctic prion and macaroni penguin in oceanic waters, and white-chinned petrel on the Patagonian Shelf–that would have an impact on prey resources north of the APF compared to the demand of local or other migrant seabird species.

Seasonal Changes in Prey Demand of Cetaceans

Given the number, size and consumption rates of Southern Ocean cetaceans, the demand for prey in summer and shifts in winter are potentially very large (Reilly et al., 2004). Estimates of current population numbers and migration patterns of cetaceans are uncertain but there have been significant increases in estimates of abundance over the last 25 years (Jackson et al., 2008, 2016; IWC, 2016). Although uncertain, the available estimates are useful in considering the extent to which the demand for prey shifts seasonally across the APF. We estimate that there are ∼770,000 cetaceans in the Southern Ocean during the summer months, of which ∼667,000 are baleen whales. We assume that 90% of each baleen whale species move northward after summer (**Figure 4B** and **Supplementary Material**). Assuming an average body mass equivalent to that of an adult male, this represents a movement of $\sim 8.05 \times 10^6$ tonnes of whale biomass mass each year. As whales live a long time and build up body mass, this means that the carbon may be shifted from areas where it is produced and consumed to often distant regions where it is respired, excreted or lost when whales die (Roman et al., 2014).

For baleen whales we estimate summer consumption of between ∼17 and 48 million tonnes of prey south of the APF (**Figure 4B** and **Supplementary Table 4**). This is a higher estimate compared to those in earlier studies, resulting from the larger estimates of population size used in this study (Reilly et al., 2004; Branch, 2007; IWC, 2013, 2016; Trathan and Hill, 2016). Winter demand is highly uncertain. If we assume that 10% of baleen whales stay in the Southern Ocean during winter and continue to feed at summer rates, this results in a prey demand south of the front of between ∼0.35 and 2.5 million tonnes. The proportion of prey consumed outside the summer season is very uncertain; Lockyer (1981) estimated this to be 17%, but reviewing the consumption rate data available for whales, Leaper and Lavigne (2007) suggested that this is likely too low to satisfy the metabolic needs of whales. If the proportion of prey consumed outside of the summer season is 17% or double this value (34%) (Lockyer, 1981; Leaper and Lavigne, 2007; **Supplementary Material**), estimates of prey demand north of the front range from ∼3 to 22 million tonnes. Although the estimates of winter demand for prey are uncertain, the migration represents a large reduction in prey demand in the south and a very large movement of animal biomass, carbon and nutrients.

Food Web Connectivity

Both passive dispersal processes and active movements of organisms into and out of the Southern Ocean connect food webs in different ecosystems. These processes transfer nutrients, carbon, organic material, and organisms between systems and affect the biogeochemistry, productivity, structure, and functioning of the ecosystems (O'Gorman, 2016; Gounand et al., 2018a,b). This export of production from one ecosystem (source) can provide inputs into another, subsidizing local food webs' energy budgets. The relative importance of autochthonous (local) production and allochthonous (external) production is a subject often discussed in relation to horizontal transport (between locations) as well as vertical transport (benthic-pelagic coupling) of production within the Southern Ocean (Murphy, 1995; Ansorge et al., 1999; Froneman et al., 1999; Pakhomov et al., 2000; Perissinotto et al., 2000; Murphy et al., 2007, 2012; Hunt et al., 2016; Subalusky and Post, 2019; Treasure et al., 2019; McCormack et al., unpublished data) but there is little understanding of their operation or variability between the Southern Ocean and global ocean ecosystems.

The importance of individual organism and food web processes in biogeochemical cycles in Southern Ocean ecosystems is being elucidated (Murphy and Hofmann, 2012; Cavan et al., 2019; Henley et al., 2020). The passive and active movement of organisms have important impacts on biogeochemical cycles across scales (Henley et al., 2020). Biota cycle and store nutrients (especially iron) and carbon over widely-varying timescales, and hence also act as vectors transporting nutrients vertically, horizontally, and beyond the Southern Ocean. Whist carbon uptake by primary production is similar in magnitude to the direct uptake of CO_2 by solubility pump processes across the Southern Ocean, this organic carbon can be transferred into heterotrophic organisms, leading to rapid sequestration and long-term carbon storage in animal biomass, sediments or storage as refractory carbon in the deep ocean (Henley et al., 2020). The processes of vertical carbon export and sequestration associated with the biota (Boyd et al., 2019) and the carbon's fate depend on the interactions with the three-dimensional flow (Robinson et al., 2014). The movement of large mobile organisms also affects biogeochemical cycles in remote ecosystems through the input of nutrients and carbon (respiration, excretion, and mortality), while also acting as consumers, potentially affecting primary production and biogeochemical cycles (Roman et al., 2014; Doughty et al., 2016).

The migration of large numbers of predators, resulting in the annual northward and southward shifts in the distribution of upper trophic level biomass, is driven by the high-latitude Southern Ocean's intense seasonality. Dispersal out of the region during winter reduces the local demand for prey and hence the dependence of the remaining highest trophic level productivity on local Southern Ocean production. The mortality rates of

zooplankton, fish, and cephalopod populations may, therefore, also be significantly reduced during winter, especially in local shelf areas where summer demand is concentrated (Croxall et al., 1985; Murphy, 1995). Therefore, the effect of the mass movement of organisms and biomass is to reduce and disperse the demand for prey by mid- and upper trophic level species northward and out of the Southern Ocean during winter (**Figure 4** and **Supplementary Tables 3, 4**). However, the total mass of prey required by seabirds may not be that much lower; while adults no longer need to provision chicks, they need to replace plumage, which is energetically demanding and generally occurs during the nonbreeding season (Catry et al., 2013). Although they no longer provision young, their fledged offspring will expend energy feeding for themselves.

This seasonal pattern of movement also represents a major spatial transfer of energy, nutrients, carbon, and biomass across the APF and the SAF. It results in a seasonal pattern of concentration and dispersal of energy demand and increased intensity of food web interactions during the summer (**Figure 4** and **Supplementary Tables 3, 4**). Thus, food webs in the Southern Ocean are highly seasonal and inextricably connected with food webs further north, generating a seasonal interdependence between polar and lower-latitude regional ecosystems. This spatial connectivity is essential in determining the structure and functioning of food webs north and south of the APF. Movement of organisms between ecosystems will affect food web interactions in both areas, generating top-down impacts on lower trophic level and biogeochemical processes and competitive interactions between migrant and resident predators (van Deurs et al., 2016). These processes (advection and movement) coupling ecosystems across scale (metacommunities) are essential in maintaining ecosystems and affects their structure, functioning, biodiversity, and stability and resilience (McCann et al., 2005; Bauer and Hoye, 2014; Walther et al., 2015; Doughty et al., 2016; van Deurs et al., 2016; Bolchoun et al., 2017; Gounand et al., 2018a; Mougi, 2018, 2019; Dunn et al., 2019a).

Within the general pattern of northward movement of seabirds and cetaceans during autumn, a number of species move into eastern and western boundary areas around South America, southern Africa, and Australasia (**Figure 3**). Some species move along the coastal shelf areas or shelf edges, feeding in local food webs as they transit out of and into the Southern Ocean (Kopp et al., 2011; Andrews-Goff et al., 2018). Processes of food web connectivity are likely to be particularly strong in these areas associated with the ocean basin boundary regions, as these are also often areas of enhanced productivity (Croxall and Wood, 2002; Phillips et al., 2005; Peron et al., 2010). The predators can exploit shifting timings in peak productivity and food availability by migrating, although this brings them into competition with substantial resident populations of predators (see section "Seasonal Changes in Prey Demand of Seabirds"). The extent to which cetaceans impact remote regional ecosystems where they concentrate for breeding during the austral winter is unclear due to reduced feeding in the austral winter, but they still will respire, die, and be predated, and some species continue feeding year-round (Roman et al., 2014; Doughty et al., 2016).

HUMAN SYSTEMS CONNECTIONS

Southern Ocean ecosystems support a range of globally important ecosystem services. Ecosystem services are the benefits that humankind obtains from natural ecosystems and are generally grouped as provisioning (e.g., fishery products), supporting (e.g., nutrient cycling), regulating (e.g., climate regulation), and cultural (e.g., tourism). Assessments of the current and potential future status of Southern Ocean ecosystem services, together with decision-making considerations, are provided in Cavanagh et al. (2021a). The demand for, and importance of these services, for example, for supporting global food security, for recreation (i.e., tourism), and climate regulation, is expected to increase in the future (Rogers et al., 2020; Cavanagh et al., 2021a).

The three major areas of direct human interaction with Southern Ocean ecosystems that involve people's movement and the associated transfer of material or resources, including contaminants, microorganisms and pollutants (including plastics) are: (i) fisheries, (ii) tourism, and (iii) science activities. There are also transfers associated with national activities and logistics. These interactions are influenced by socio-economic and geopolitical factors, which also set the governance framework.

These operations provide economic activity and employment in countries across the world (Bertram et al., 2007), particularly in the Antarctic gateway ports (Bertram et al., 2007), and support extensive secondary industries, such as operation and maintenance of fishing and commercial tourism (IAATO, 2019) and science vessels. These operations generate carbon emissions through the movement of ships, aeroplanes, people, and associated resources (Amelung and Lamers, 2007; Farreny et al., 2011). Increased ship visits also potentially lead to a higher probability of invasive species introductions into Southern Ocean ecosystems (Lee and Chown, 2009; McCarthy et al., 2019; Morley et al., 2020; Grant et al., 2021). The accessibility of polar regions to human activities (fishing, tourism scientific activities, and shipping) is becoming greater with warming and reduced sea ice distribution and timing induced by climate change (IPCC, 2019; Meredith et al., 2019; Cavanagh et al., 2021a,b).

Fisheries

The Southern Ocean has long played a major role in global production of goods from marine species, with a sequence of exploitation that includes seals, whales, finfish, and krill (Grant et al., 2021). It has also featured heavily in the global rise of illegal, unreported and unregulated (IUU) fishing in the mid-1990s. Global demand led to the near extirpation of Antarctic fur seals in the early 19th century, the great whales during the 20th century, and a number of groundfish (notothenid species, including *Notothenia rossii*) in the 1970s and 1980s. The rapid rise of Antarctic krill fishing in the 1970s led to the negotiation of the Convention on the Conservation of Antarctic Marine Living Resources (the "krill" convention) because of fears of overfishing of krill and potential damage to the ecosystem as a whole (Miller, 1991).

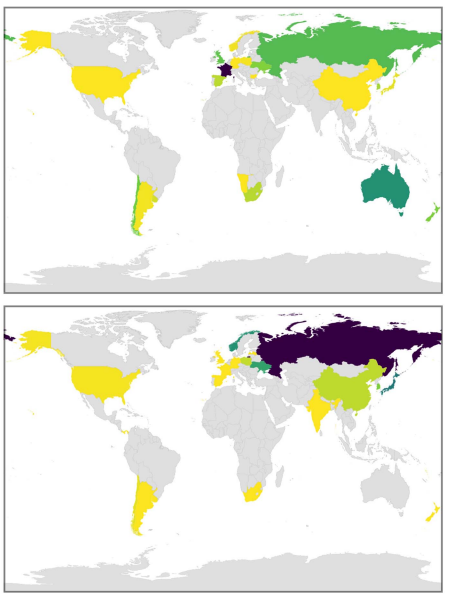

FIGURE 5 | Total catches of the two current major Southern Ocean fisheries over the historical period (1970s to present day) for each Flag State (catch records from all years, CCAMLR): **(A)** toothfish (*Dissostichus* spp.) and **(B)** Antarctic krill (*Euphausia superba*).

Recent assessments of Southern Ocean ecosystem services have emphasized the global significance of Southern Ocean fisheries (Cavanagh et al., 2021a). Over the period of the fishing operations (1970s to present), catches in the two main fisheries [toothfish (*Dissostichus* spp.) and Antarctic krill] have been taken by vessels registered in states on every continent and in Northern and Southern Hemispheres (**Figure 5**). The total catch of all species in 2018/19 was 406 thousand tonnes (CCAMLR Statistical Bulletin, 32, see their Table 4.1). The mean annual wholesale value of Southern Ocean toothfish fisheries was US$206.7 million per year for the period from 2011 to 2015 (CCAMLR, 2016), and Antarctic krill (*Euphausia superba*) had a first-sale value of between US$100 to 416 million in 2017/2018 (Cavanagh et al., 2021a). Currently, krill catches makeup <0.5% of the global marine fisheries catch (GAMFC), although it has been suggested that potential catch could be equivalent to >10% of GAMFC (Nicol and Foster, 2016).

Tourism

The Southern Ocean is home to 90% of the world's penguin species, 50% of the world's baleen whale species, and includes 80% of the total area of high seas Marine Protected Areas (Boonzaier and Pauly, 2016). The unique biodiversity is a significant driver of tourism, which has increased rapidly over the last 30 years. Over the last decade, the number of commercial tourism voyages almost doubled (223 in 2010–2011, 432 in 2019–2020), while passengers carried on ships has more than doubled (33,438 in 2010–2011, 74,120 in 2019–2020; IAATO, 2019). As a result, the tourism industry directly impacts Southern Ocean ecosystems in terms of ship traffic, landings, and site visits, with current operations, concentrated on the Antarctic Peninsula (Bender et al., 2016; Pertierra et al., 2017; Grant et al., 2021). Tourism has a global footprint in that movement of people to join commercial tourism ships involves air travel to South America (Ushuaia and Punta Arenas), Africa (Cape Town), Australia (Hobart), and New Zealand (Christchurch), or via flights to the South Shetland Islands where visitors may join cruise vessels without having to experience a potentially rough crossing of the Drake Passage (known as fly/cruise tourism; Bertram et al., 2007; IAATO, 2019; **Figure 6**). The operations of commercial tourism to the Antarctic provide economic activity and employment in countries across the world and particularly the Antarctic gateway ports (Bertram et al., 2007; **Figure 6**).

Science

Southern Ocean ecosystems are an increasing focus of international scientific activities as highlighted by the international investment in a new generation of ice-capable research vessels and the construction of new coastal research stations on the continent's margins (COMNAP, 2017). Furthermore, there has been a rapid increase in the development and deployment of remote and autonomous systems for increasing observations of these ecosystems across multiple spatial and temporal scales (Newman et al., 2019). This increased scientific activity involves extensive inflows into Southern Ocean regions of ships, airplanes, people, and associated resources, while outflows include biological samples, specimens, and data. It also involves national investments that contribute to the support of communities and businesses as well as fundamental scientific endeavors. The Southern Ocean and Antarctic scientists' global community supports personnel and associated businesses, government and governance structures, non-governmental organizations, and other bodies worldwide.

Society and Culture

People across the world have long had a fascination and concern for Antarctica and the Southern Ocean from the heroic era in the late 19th and early 20th Centuries (Larson, 2011), to the rise of science (Walton, 2005), and the advent of the ATS with its orientation toward the conservation of the region (Hanifah et al., 2012; Hughes et al., 2018). The development and implementation of the Madrid Protocol in 1998 was the result of a global effort to provide long-term protection to the Antarctic environment south of 60°S, instituting a ban on mining in the region in perpetuity, which was in contrast to the negotiations at the time for a convention to regulate mining activity (Scully, 2011). The strength of commitment of Antarctic Treaty nations to these principles was reaffirmed in 2016 in a declaration on the 25th Anniversary of the signing of the Protocol (ATCM, 2016) confirming the central values of peace, science and conservation in the region, as well as the importance of the region to the global system. Antarctica and the Southern Ocean also have cultural links to indigenous cultures, and the expression of ecosystem science through art (Roberts et al., 2021). In recent times, there has been an extensive media and cultural focus on the Southern Ocean as a unique, fragile, and threatened environment. This has and continues to contribute to developing global public

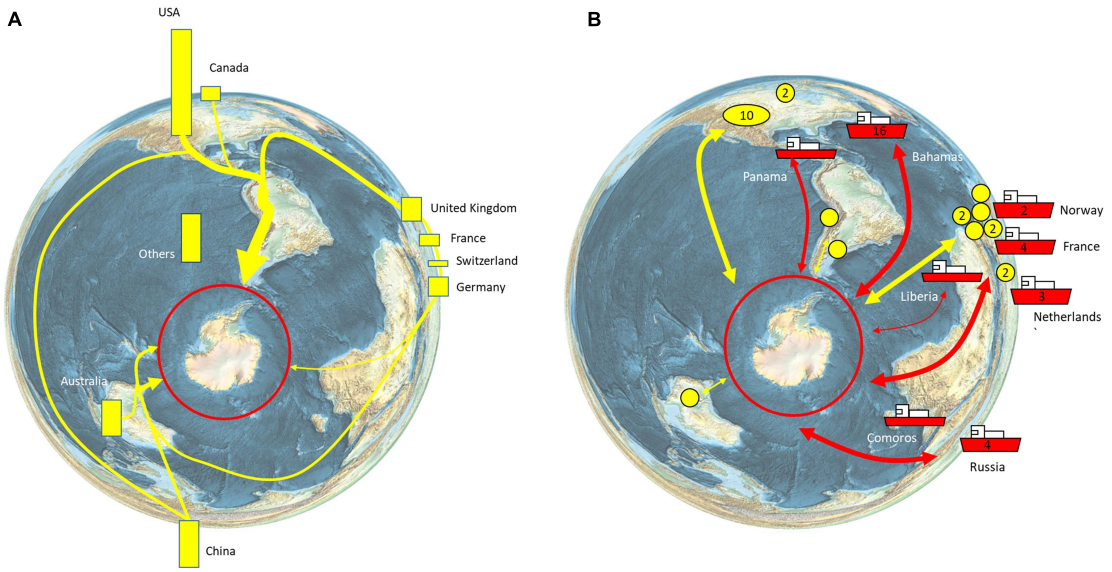

FIGURE 6 | Global connections of the Antarctic tourism industry. **(A)** Nationalities of tourists. 55,489 sea-borne tourists, of more than 100 different nationalities, visited Antarctica during the 2018–2019 season. The nationalities of the tourists are shown as bars, with bar length indicating the relative percentage of all tourists (IAATO, 2019, their Table 2). The major routes of travel/arrival are indicated schematically. **(B)** Country of registration of tourism vessels (ships with country of registration label; number of vessels where more than 1 is registered is indicated on the hull). The yellow circles indicate the region of the operator (numbers are given for more than 1 operator in a country (IAATO, 2019, their Appendix 2).

awareness and understanding of how the oceans and associated ecosystems will be affected by anthropogenically driven climate and ocean change.

Governance

The various instruments of the ATS regulate all activities in the area south of 60°S (the Antarctic Treaty area), except for whaling, which is managed by the IWC under the Convention on the Regulation of Whaling (*1946*). The primary instruments in the ATS are the Antarctic Treaty (*1959*) with its Protocol on Environmental Protection (*1991*), the Convention on the Conservation of Antarctic Seals (*1972*; CCAS), which is not now active, and CCAMLR (*1980*; CAMLR Convention). The area of jurisdiction of CCAMLR was extended to the Antarctic Convergence (APF) in order to encompass the region thought to contain most of the Antarctic marine ecosystem. The instruments of the ATS are open to accession by nations.

The management bodies of the two active components of the ATS are the Antarctic Treaty Consultative Meeting (ATCM) and CCAMLR. Currently, there are 54 signatory Parties to the Antarctic Treaty, of which 29 Parties have demonstrated "substantial research activity" within Antarctica and thereby attained consultative status which includes participation in governance decision-making. The engagement of nations with the Treaty represents approximately two thirds of the global population. The underlying focus of the ATCM and CCAMLR has been conservation of the region (Hanifah et al., 2012; Press et al., 2019).

The importance of the Southern Ocean is recognized in some global governance arrangements. These have included consideration of managing high seas fish stocks through regional fisheries management organizations (RFMOs) and harmonizing the management of migratory species and shared stocks through the UN Fish Stocks Agreement (*1995*). Although external to the UN system, CCAMLR is recognized as the regional management organization responsible for managing fisheries in the Southern Ocean[1]. While there are exchanges of information with RFMOs to the north of CCAMLR, there remains to be formal arrangements about shared interests such as fishing for toothfish and the incidental mortality of seabirds (Anon, 2017).

CCAMLR has developed work programs for managing the marine environment, including taking steps to establish marine protected areas, a request from under the Convention on Biological Diversity (SC-CAMLR, 2005), and to conserve Vulnerable Marine Ecosystems arising from the UN Resolution 61/105 in 2006 (SC-CAMLR, 2007), although much work remains in this regard (Anon, 2017; Chown and Brooks, 2019). While CCAMLR and the ATCM remain the regulatory bodies, the recent review of CCAMLR in 2017 recommended that CCAMLR give more attention to demonstrating its preeminent role globally by establishing relationships with external bodies that not only have an interest in Antarctica and the Southern Ocean, a call gaining increasing support (Chown and Brooks, 2019; Dodds, 2019), but also to gain support for global actions that will help CCAMLR achieve the long-term conservation of the region (Anon, 2017). Unlike the ATCM, CCAMLR has yet to establish a program on the effects of climate change, including establishing a relationship with the UN Framework Convention on Climate Change, on the effects of climate

[1]http://www.fao.org/fishery/topic/166304/en

change on the conservation of Antarctic biota (Anon, 2017; Cavanagh et al., 2021b).

WHY SOUTHERN OCEAN ECOSYSTEMS MATTER AND WHY THEY ARE A PRIORITY FOR THE FUTURE

Southern Ocean ecosystems are inextricably connected in global ocean ecosystems and are important in Earth system processes and human socio-economic systems. Southern Ocean ecosystems connect across multiple trophic levels and temporal and spatial scales that are interconnected by physical, ecological and human exchange processes (**Figure 7**). Physical processes connect habitats and influence biogeochemistry and productivity (**Figures 2**, **7**), which underpins the flow of energy and carbon through regional food webs. Bio-physical interactions and ecological processes (**Figures 2**, **7**) of dispersal (drift) and active movement (behavior, foraging, and migration) connect ecological systems across scales. Human systems exchange by movement of people, materials, resources, contaminants and pollutants (including plastics). These processes are influenced by a series of proximate (e.g., fisheries and atmospheric greenhouse gas concentrations) and ultimate drivers (e.g., food security and population change). The physical, ecological and human exchange processes are affected by climate change, thereby generating potential feedback effects, with consequences for Southern Ocean and global systems (**Figure 7**).

Over the coming decades, changes in Southern Ocean overturning circulation and bottom water formation will happen and will affect global circulation and biogeochemical cycles (IPCC, 2019; Meredith et al., 2019; Morley et al., 2020). These physical changes will undoubtedly impact the supply of nutrients and carbon to Southern Ocean surface waters, and their redistribution horizontally and vertically within the Southern Ocean and to the north (Henley et al., 2020 and references therein). Warming and freshening of the mode and intermediate waters north of the ACC will propagate northward into the interior of the global ocean (IPCC, 2019; Meredith et al., 2019).

Projections based on coupled biogeochemical-ocean circulation models suggest that Southern Ocean primary productivity is likely to increase because of ocean warming and increased iron inputs, but these projections are uncertain and the projected changes vary with latitude (Hauck et al., 2015; Leung et al., 2015; Boyd, 2019; IPCC, 2019; Meredith et al., 2019; Henley et al., 2020; Pinkerton et al., 2021).

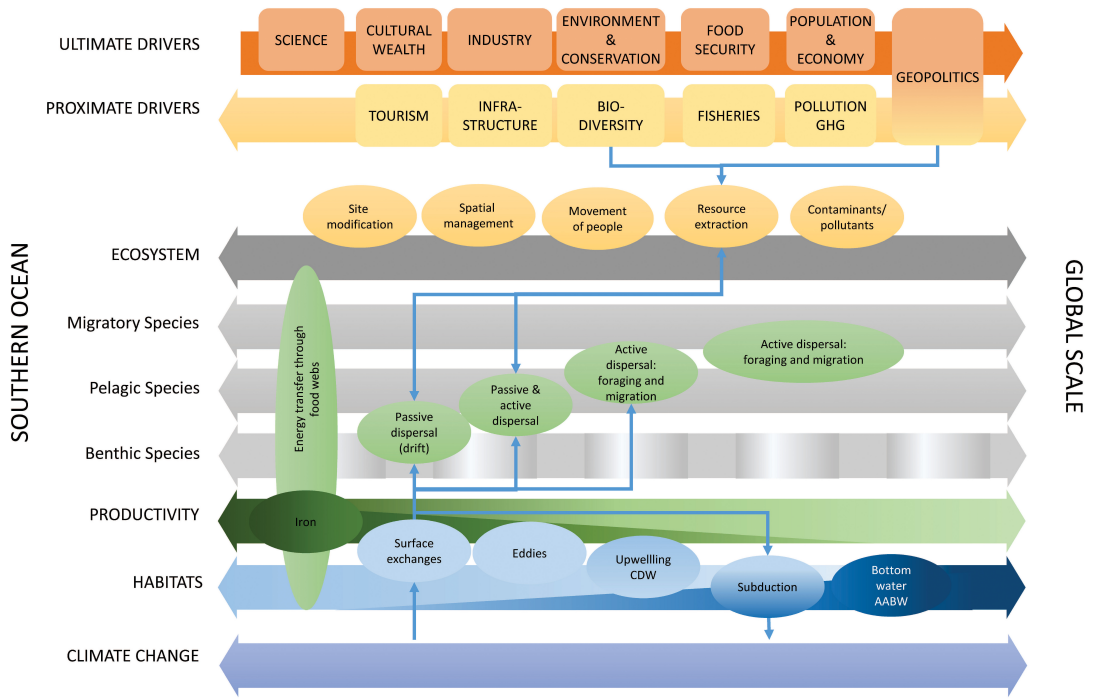

FIGURE 7 | Summary figure of the role of exchange processes (colored ellipses: physical–blue, ecological–green, and human–orange) across interlinked biophysical dimensions (large horizontal arrows) from the Southern Ocean scale to the global scale, the drivers of change in these exchange processes across different dimensions (ultimate and proximate), overlaid with an example of connections and feedbacks across these exchange processes (thin blue arrows). Green shading for iron supply and exchange, and dark blue shading for AABW indicate the decreasing and increasing importance, respectively, of these exchange processes from the Southern Ocean to the global scale. GHG, greenhouse gases. Spatial scale (i.e., from the scale of the Southern Ocean to the global scale) is represented as a continuum rather than a specific demarcation between the Southern Ocean and the rest of the globe, noting that such demarcations are generally geopolitical constructs (with some links to physical ocean features) but that the ecological dimensions and exchange processes represented here occur across many scales. The positions of boxes showing drivers and exchange processes along the horizontal arrows give an indication of whether those are more specific to the Southern Ocean or extend to regional and global scales.

A more productive Southern Ocean overall has the potential to increase the biological uptake of CO_2, with large-scale consequences for biogeochemistry and ocean-climate feedbacks (Del Castillo et al., 2019), although the extent to which this can modulate the effects of carbon emissions later this century is uncertain (Del Castillo et al., 2019; Rogers et al., 2020; Cavanagh et al., 2021a). Importantly, shifts in the location of primary production and the phytoplankton community composition can influence this outcome. Moreover, the dynamics of phytoplankton in the Southern Ocean will impact productivity elsewhere in the world. Increased production in the Southern Ocean could result in reduced quantities of exported macronutrients, and therefore reduced production elsewhere (Holzer and Primeau, 2013; Primeau et al., 2013; Hauck et al., 2015; Bronselaer et al., 2016; Keller et al., 2016; Moore et al., 2018). Further, uncertainty in future changes in Southern Ocean biogeochemistry is compounded by uncertainties in the changes to phytoplankton assemblages in the region (Pinkerton et al., 2021).

As Southern Ocean phytoplankton communities shift southward under global warming, the uptake of nitrogen is expected to be greater relative to phosphorus, leading to a decrease in the N/P ratio of water masses exported to the north (Arrigo et al., 1999; Weber and Deutsch, 2010; Martiny et al., 2013), which would reduce productivity in lower latitudes with potential large-scale implications for carbon export and budgets in those regions (Weber and Deutsch, 2010; Martiny et al., 2013; Hauck et al., 2015, 2018). Conversely, shifts to diatoms in the subantarctic could increase the N/P ratio of exported waters. Similarly, changes in the Si/N ratio of exported waters, driven by phytoplankton species shifts, changes in iron availability and ocean acidification effects on diatom silica production, are also expected to impact upon primary production, phytoplankton species composition and carbon export throughout the low-latitude oceans (Mosseri et al., 2008; Petrou et al., 2019; Henley et al., 2020). The effect of enhanced productivity in the Southern Ocean may lead to reductions in total export of nutrients from the Southern Ocean, resulting in the trapping of nutrients (Moore et al., 2018), with a consequent reduction in productivity across the rest of the global ocean affecting global oxygen and carbon budgets and food webs (Holzer and Primeau, 2013; Primeau et al., 2013; Hauck et al., 2015; Bronselaer et al., 2016; Keller et al., 2016). Nutrient biogeochemistry can also be modified by changes in microbial processes or shifts in community composition, abundance, distribution, behavior, and/or trophic interactions of phytoplankton, zooplankton and higher organisms (Azam et al., 1991; Lavery et al., 2010; Maas et al., 2013; Sailley et al., 2013; Ratnarajah et al., 2014; Schmidt et al., 2016; Cavan et al., 2019; Bestley et al., 2020; Henley et al., 2020; Caccavo et al., 2021; Pinkerton et al., 2021; Johnston et al., unpublished data).

Ocean acidification resulting from increased uptake of CO_2 is expected to occur earlier in the Southern Ocean than other ocean regions (Orr et al., 2005; McNeil and Matear, 2008; Feely et al., 2009), and has already been observed across a number of Southern Ocean regions e.g., (Bednarsek et al., 2012; Takahashi et al., 2014). Around 30% of Southern Ocean surface waters are expected to be affected by ocean acidification by 2060 (Hauri et al., 2016). As well as altering biota, food webs and ecosystem functions within the Southern Ocean (Gutt et al., 2015; Henley et al., 2020), the northward export of waters undersaturated with carbonate ions could promote the harmful effects of ocean acidification in the lower-latitude oceans to the north (McNeil and Matear, 2008; Feely et al., 2009).

Food webs in the Southern Ocean and their connectivity to other systems are changing (Murphy et al., 2012; Constable et al., 2014; Meredith et al., 2019) with consequences within (see McCormack et al., unpublished data) and outside the Southern Ocean. The connectivity of ecosystems through transport and movement has the potential to transfer the signals of those changes between ecosystems. Changes in small and large-scale ocean dynamics will affect cross-frontal exchange and the dispersal of plankton. Such changes in the rates of mixing between polar, sub-polar and subtropical waters may also potentially disrupt the life cycles of fish and cephalopod species that cross oceanic fronts during development, thus affecting their role in Southern Ocean food webs (Murphy et al., 2007; McMahon et al., 2019; Saunders et al., 2019; Abreu et al., 2020). The APF is not expected to undergo major changes in location in the coming century (Meijers et al., 2019b), potentially limiting the southward extension of the distributions in the Southern Ocean of pelagic fish species from farther north (Boyce et al., 2008). However, changes in cross-front exchanges due to increases in eddy intensity may allow more frequent opportunistic incursions further south of some species. Modeling suggests that warming coastal and shelf waters around Antarctica (Griffiths et al., 2017) is likely to result in colonization and establishment by diverse non-native species, and have important consequences for Antarctic ecosystems and food webs (but many native species may also benefit from initial warming see Morley et al., 2019).

Southern Ocean waters have the fewest established non indigenous species (NIS) of any large region, which does reflects the general level of geographic and oceanographic exchange (Clarke et al., 2005). Nevertheless vector density for potential NIS travel is increasing, either through shipping (Lewis et al., 2003; McCarthy et al., 2019) or rafting on plastic debris (Barnes et al., 2018). Sustained presence of any given NIS within the Southern Ocean requires not just transport, but transfer, establishment, year-round survival and reproduction. Hughes et al. (2020) considered a list of >100 species thought to pose risk of invasion to Antarctica. They considered that 13 were high risk in terms of likely establishment and severity of impact, if successful. The consequences of NIS spread in the Southern Ocean are still unclear because each is likely to be species identity and local area dependent and may have considerably lag phases. However, Hughes et al. (2020) think the situation is highly concerning (see also Grant et al., 2021), especially as native species are already under pressure from many other interacting stressors (Gutt et al., 2015; Rogers et al., 2020).

The analysis of seabird and whale movement in this study is a first attempt to estimate the magnitude of the summer-winter movement of large numbers of predators into and out of the Southern Ocean. Large uncertainties are associated with these estimates, but the scale of the migration and its ecological importance in connecting ecosystems across the Southern

Hemisphere is clear. The demand estimates also highlight that changes affecting predators in the Southern Ocean will be transferred out of the region and impact areas across oceanic and coastal regions on the east and west basin boundaries.

The population sizes of some Southern Ocean species of seasonally migrating predators have undergone major changes over the last few decades, and these are expected to continue in the future. The most profound ecological changes are associated with recovering populations of the great whales that were exploited to very low numbers in the 19th and 20th centuries (Noad et al., 2019). The steady population increases observed over the last 2 decades in several species of great whales (Tulloch et al., 2019) will affect Southern Ocean ecosystems as well as those in shelf regions along the east and west coasts of South America, Africa, and Australasia (Rosenbaum et al., 2014; Noad et al., 2019; Zerbini et al., 2019). As whale populations recover from historical harvesting, the increased demand for prey may increase competition in local food webs, and change the balance of the upper trophic level community. Changes in predator populations will also generate shifts in the absolute and relative numbers of seabirds and marine mammals of different species moving along migration routes.

Threats to Southern Ocean ecosystems from potential future human activities, together with the recovery of historically harvested species and the natural high variability of Southern Ocean ecosystems, will generate major challenges for conservation and management (Chown et al., 2012; Hughes et al., 2018; Chown and Brooks, 2019; Dunn et al., 2019b; McCarthy et al., 2019). The major threat to the structure and functioning of ecosystems in areas south of the APF is from climate change (IPCC, 2019; Meredith et al., 2019), and there are major uncertainties about the directions, magnitude and time scales of impacts. Recent assessments indicate that climate change generally poses a medium to high level of risk for the capacity of the Southern Ocean to support ecosystem services under future climate change (Cavanagh et al., 2021a). Increased pressures may also be exerted on the region by tourism and by increases in global demand for food (FAO, 2018). Pollution is also a potential threat and may increase associated with increased activity through a range of local and global sources, such as oil-spills, marine debris, and ocean and atmospheric transport of microplastics and heavy metals (Grant et al., 2021). Human activities within the region are managed within a mandate to conserve the region (Hughes et al., 2018), but global socio-economic and political processes (**Figure 7**) will determine the extent to which these threats are realized. In the short-term, the number of visitors may increase although the negative consequences of COVID-19 on tourism and science activities may last for some years (Hughes and Convey, 2020).

CONCLUDING COMMENTS

Ecological processes interact with the full three-dimensional physical structure of the Southern Hemisphere ocean and atmosphere to produce a continuum of connected ecosystems and food webs with intense seasonal dynamics rather than distinct food webs. The two-directional connections between Southern Ocean regional ecosystems and wider Southern Hemisphere and global ocean ecosystems affect the stability and resilience properties and responses to change of these connected ecosystems, forming a "meta-ecosystem" in the global ocean. This ocean-scale ecosystem connectivity and interdependence will influence Earth system-level responses to climate change on time scales of decades to millennia. However, the current generation of Earth system models does not consider the importance of such large scale ecological connectivity and potential feedbacks (Eyring et al., 2016; IPCC, 2019). There is a major need to improve understanding of species ecology, ecosystem structure and functioning and seasonal dynamics throughout the Southern Ocean and how this interacts with the biogeochemistry in the 3-dimensional ocean and the links with global ocean ecosystems (**Box 1**). Within this there are key questions about how important such north-south ecological exchange processes and energy flows are in Southern Ocean and global ecosystems and carbon budgets and what are the major routes, vectors, magnitudes (and variability) of transfer.

The ecological connectivity between Southern Ocean and global ocean ecosystems underpin the processes that maintain essential ocean ecosystem functions and services and are important in maintaining human societal and economic processes within the Earth system (Steffen et al., 2020; Cavanagh et al., 2021a). The effects of change and decision making across the global ocean will affect Southern Ocean ecosystems, and in turn, decisions made for the Southern Ocean will affect ecosystems and human systems across the planet. Geopolitics will affect the ability of CCAMLR and other international bodies (Dodds, 2019) to make decisions that will be required as climate-driven changes become clearer, and the pressures from increased direct human impacts increase driven by demand and increased accessibility.

There is an urgent need to develop conservation and management consortia between CCAMLR and adjacent bodies that operate at Southern Hemisphere scales (Anon, 2017). The ecological connectivity of Southern Ocean and global ocean ecosystems has important implications for decision making for conservation and management in the Southern Ocean and across the Southern Hemisphere. Managing the Southern Ocean in isolation does not consider the potential effects of that management on people and regions outside of the Southern Ocean, nor does it recognize the effects that actions external to the region have on the dynamics of Southern Ocean systems. Maintaining connectivity of populations, food webs, and the flow of genes across scales will also help to support ecological resilience to climate change. Prediction and management of the impacts of human activities and climate change on Southern Ocean ecosystems requires a view that recognizes and incorporates the connectivity and linkages of these ecosystems to global ocean ecosystems.

Such large-scale connections between ecosystems will be important throughout the world's oceans in developing conservation and management approaches and understanding the impacts of change (Dubois et al., 2016; Gounand et al., 2018b; Young et al., 2018; Dunn et al., 2019a; Kenchington et al., 2019;

BOX 1 | Knowledge gaps and future research priorities.

Global Connectivity. There is an urgent need to develop quantitative understanding of the global connectivity of Southern Ocean ecosystems. With changes already occurring in ecosystems in the Southern Ocean and across the Southern Hemisphere the impacts of change are being transferred into and out of the Southern Ocean with variability in that transfer both spatially and temporally. With Earth system models poorly representing Southern Ocean systems, and signals within the Southern Ocean being confounded by the potential for ecological connectivity, new approaches are required to understand the impacts of change in Southern Ocean ecosystems and the consequent effects in the wider Earth system and to manage and adapt to the global consequences of that change. Developing such approaches to consider two-way ecosystem connectivity and impacts of change should be an important focus for international research communities, including the science programs of the Scientific Committee on Antarctic Research (SCAR), the Integrating Climate and Ecosystem Dynamics in the Southern Ocean programme (ICED) and the global Integrated Marine Biosphere Research programme (IMBeR).

Three-Dimensional View. Detailed information is available to highlight the three-dimensional nature of Southern Ocean circulation, and understanding of how it is likely to change over the next half century is sufficient to investigate and quantify the biogeochemical and ecological implications for ecological connectivity and ecosystem services from the Southern Ocean (see section "Southern Ocean Connections" and **Supplementary Table 1**). More information is particularly required on the pathways of exchange and especially the subregional nature of the connections from the Southern Ocean to remote areas of the global ocean. The priority is to identify and focus research in these subregions where connectivity is most likely to influence the internal dynamics of Southern Ocean ecosystems and has greatest influence in the global ocean. We also need to improve our understanding of how individual species and food webs operate in the full three-dimensional Southern Ocean, in the sea ice and full depth ocean, and how these processes influence biogeochemical cycles, particularly in the APF and SAF frontal zones. Quantifying fluxes is a priority and more direct measurements and full-depth analyses are required of the nutrient, carbon and biological properties of waters flowing across the regions of the APF and SAF, how these are produced, modified and impact ecosystems in remote regions. The development of time-series observations is important, as the exchange processes will show strong seasonal and interannual variability and we need to start developing base-lines against which to assess future changes.

Cross-Frontal Exchange. There is little information on the magnitude of cross-frontal exchanges in maintaining or influencing the dynamics of most Southern Ocean biota, and how these exchanges influence trophic structure, particularly in ecosystems outside of the Southern Ocean. The importance of these movements of large numbers of seabirds, marine mammals and possibly larger fish in connecting Southern Ocean and wider Southern Hemisphere and global ocean ecosystems has generally not been considered. The calculations in this study of seasonal movement of seabirds and cetaceans and associated shifts in the demand for prey into and out of the Southern Ocean (see section "Implications of Ecological Connectivity") show that these are important in both Southern Ocean and remote regional ecosystems. However, these preliminary calculations also highlight the uncertainty associated with such calculations and the need to improve assessments of seasonal changes in abundance, distribution and energy and prey requirements. Understanding winter-time habitat use by predators is a crucial, understudied, element of this. This requires focused studies of subregional ecosystems of the Southern Ocean, examining the spatial operation of food webs and how these vary seasonally, and how extra-Southern Ocean processes impact on these. Ensuring the Southern Ocean Observing System (SOOS) program has observations that can be used to specifically assess exchange processes would be a valuable step. However, new approaches aimed at quantifying energy and carbon flows and the connectedness of ocean ecosystems are also required. Developing observation networks in regions where ecological exchanges are most intense may be valuable, for example, the major boundary and coastal current regions appear to be particularly important in some of the major biogeochemical and ecological exchange processes (see sections "Physical and Biogeochemical Connections" and "Ecological Connectivity"). Such regions would be areas where enhanced observation networks of biogeochemical and ecosystem processes could be deployed, including, for example, networks of moorings or autonomous vehicles and seabird and marine mammal tracking systems.

Modeling Ecological Connectivity. Ultimately, the only way to examine the role of ecological connections in food webs across the wide range of spatial and temporal scales required is through the development of system-level ecological models. Such models are needed to quantify the relative importance to ecosystem services of local and remote change, and for projecting future ecosystem states based on projected changes to the Earth system. There are few models available that can be used to assess ecological connectivity across multiple trophic levels within food webs. This requires the development of dynamic models of food webs across scales, which link physical, biogeochemical and ecological processes. A key aspect of this will be the development of high-resolution models of local and regional whole ecosystem processes operating within larger scale models (e.g., circumpolar or global) to allow seasonal and spatial (horizontal and vertical) connectivity to be examined. Moreover, these models are needed to assess the probabilities of invasive marine species becoming problematic in the Southern Ocean and for better understanding the infiltration and impact of plastics in the system. Current Earth system models do not take account the connectedness of oceanic ecosystems, its potential role in transferring impacts of change and the influence of cross-scale ecological exchanges on local and regional ecosystem stability and resilience. Earth system models are required that explicitly include cross-scale ecological interactions and whole ecosystem processes to allow analyses of their direct and indirect influence on climate processes and impacts of change.

Human Pressures. Southern Ocean ecosystems are likely to be affected by global pressures from future changes within human systems. Current human activities that involve transfers of people and material in and out of the Southern Ocean have a global footprint. Improved understanding is required of the national and international drivers of these processes in order to develop projections of how such activities may develop in the future, particularly as a result of climate change and population increases. Such understanding will be crucial for generating scenarios and shared socio-economic pathways of future change that can be used in conjunction with climate projections to inform future decision making for the Southern Ocean and throughout the global ocean.

Governance. At present insufficient attention is given to cross-system connections by regulatory bodies within and surrounding the Southern Ocean. There is an urgent need for the further development of conservation and management measures that encompass multiple regional systems and conservation and management bodies. Given the connectivity between Southern Ocean and global ocean ecosystems and the two-way effects, developing activities within the Antarctic Treaty System will be important. Taking account of the importance of Southern Ocean ecosystems and their connectivity in the wider Earth system will also be important for regulatory bodies that consider ecosystems across the Southern Hemisphere and throughout the global ocean.

Xu et al., 2019; Zuercher and Galloway, 2019; Guihou et al., 2020). However, oceanic ecosystems' ecological connectivity may be particularly important in the high-latitude and seasonal polar ocean ecosystems (Niiranen et al., 2018). It is clearly a major aspect of the structure and functioning of Southern Ocean ecosystems, which are already undergoing major

change. Those changes will impact areas north of the APF and SAF and across the Southern Hemisphere and have global consequences. Developing a quantitative understanding of global ocean ecosystems' connectedness and role in determining responses to change, including impacts on climate processes, is an urgent requirement for improving the representation of ecological processes in Earth system models. Understanding the impacts of change in the Southern Ocean and managing and adapting to the global consequences of that change requires new approaches to studying ocean ecosystems that consider the connectedness of global ocean ecosystems (**Box 1**). Developing such a global perspective requires the integration of research communities and ocean management activities, linking Southern Ocean and global research communities. That is a priority of the Integrating Climate and Ecosystem Dynamics in the Southern Ocean programme (ICED), which is part of the global Integrated Marine Biosphere Research programme (IMBeR), and co-sponored by the Scientific Committee on Ocean Research (SCOR), Future Earth and the Scientific Committee on Antarctic Research (SCAR). This is important not only from a Southern Ocean perspective, but is also required for the development of Earth System analyses and management across the global ocean, which needs to take account of Southern Ocean ecosystem processes to improve understanding, future projections and ocean governance.

The Southern Ocean has not been remote for a long time, and its regional ecosystems have never been separate. The pathways of connection and feedback are important in the Earth system and in human systems. We now have an advanced understanding of local ecosystem processes and the importance of interactions across scales, and how this affects their structure and functioning, including food web interactions and processes. Yet current analyses and models of ocean ecosystems and their responses to change often assume that such systems are only local and affected by the bottom-up physical impacts of changing environmental conditions.

This analysis shows that Southern Ocean ecosystem processes are inextricably linked to global ocean ecosystems across many scales. This conceptual shift in understanding has global implications for assessing, analysing and modeling ocean ecosystems (Bauer and Hoye, 2014; Walther et al., 2015; van Deurs et al., 2016; Gounand et al., 2018a; Dunn et al., 2019a). Given the scale of the exchanges, the amount of nutrients, carbon and energy being transferred and the number and biomass of organisms moving over large areas of the ocean, these processes are likely to be important in both the direct climate-related processes (i.e., biogeochemical cycles and carbon budgets) and in determining resilience properties of ecosystems across scales and hence responses to change, with potentially indirect impacts on climate processes (Bauer and Hoye, 2014; Doughty et al., 2016). Analyses and models are required that implicitly consider the scale of ecological process connections across multiple trophic levels and how these affect ecosystem properties of stability and resilience and their responses to variability and change at local, regional, ocean basin, and global scales.

DATA AVAILABILITY STATEMENT

The data used in the study are available in the cited literature. Further details of methods and data and additional references are included in the **Supplementary Material**. The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

This work involved synthesising information from previously published studies.

AUTHOR CONTRIBUTIONS

EM initiated and coordinated the project and led the writing of the manuscript to which all authors contributed. NJ, EH, AC, and SH contributed substantially to the development, coordination, and writing of the manuscript. EM, RP, and JJ developed the prey demand calculations. EH, AC, JM-T, RT, and ST contributed to development of the figures. RP, JJ, JM-T, RT, RC, GT, RS, DB, DC, SC, CF, JH, KH, CS, ST, PT, and JX contributed significantly to the development of ideas, writing of the manuscript, and completion of the figures. All authors have approved the version for submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.624451/full#supplementary-material

Supplementary Data Sheet 1 | Supplementary details of methods used to calculate seasonal changes in seabird and cetacean demand for prey with additional references. Supplementary tables presenting information on ocean exchange processes, scales of movement of Southern Ocean organisms and seabird and cetacean demand calculations and associated additional references.

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From Data to Marine Ecosystem Assessments of the Southern Ocean: Achievements, Challenges, and Lessons for the Future

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Southern Ocean ecosystems offer numerous benefits to human society and the global environment, and maintaining them requires well-informed and effective ecosystem-based management. Up to date and accurate information is needed on the status of species, communities, habitats and ecosystems and the impacts of fisheries, tourism and climate change. This information can be used to generate indicators and undertake assessments to advise decision-makers. Currently, most marine assessments are derivative: reliant on the review of published peer-reviewed literature. More timely and accurate information for decision making requires an integrated Marine Biological Observing and Informatics System that combines and distributes data. For such a system to work, data needs to be shared according to the FAIR principles (Findable, Accessible, Interoperable, and Reusable), use transparent and reproducible science, adhere to the principle of action ecology and complement global initiatives. Here we aim to provide an overview of the components of such a system currently in place for the Southern Ocean, the existing gaps and a framework for a way forward.

Keywords: Southern Ocean, open science, MEASO, biodiversity data accessibility and use, action ecology

INTRODUCTION

The Southern Ocean covers ∼10% of the global ocean and plays a pivotal role in biogeographic processes. It is an essential contributor to oceanic primary production and biodiversity, exports nutrients and oxygen to the world's ocean basins, and plays a central role in global ocean circulation (Xavier et al., 2016). The world's oceans have seen tremendous change in the last 30 years, including changes to species, communities, habitats, and ecosystems (collectively referred to as ecosystem changes). These underpin critical Southern Ocean ecosystem services, including (but not limited to) climate regulation, fisheries, tourism, and aesthetic value (Grant et al., 2013; Cavanagh et al., 2021).

The Antarctic Treaty System includes the Protocol on Environmental Protection to the Antarctic Treaty (also known as the Madrid Protocol) and the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). The Treaty recognises "the intrinsic value of Antarctica, including its wilderness and aesthetic values and its value as an area for the conduct of scientific research, in particular, research essential to understanding the global environment" (Protocol on Environmental Protection to the Antarctic Treaty 1991, Article 3.1), while CCAMLR aims to ensure the "rational use" of marine living resources subject to "principles of conservation" (CCAMLR, 1980, Article II). As such, there is an urgent need to balance the impact of cumulative stressors and the continued use of marine ecosystem services provided by the Southern Ocean (Grant et al., 2013). Furthermore, there is a strong spirit of international cooperation ingrained within the Framework of the Antarctic Treaty, including the stipulation that "Scientific observations and results from Antarctica shall be exchanged and made freely available" (Antarctic Treaty 1959, Article 3).

The second UN Decade of Ocean Science for Sustainability (2021–2030) has begin in 2021 and focuses on developing "the science we need for the ocean we want" (IOC, 2020). The Decade is closely linked to the United Nations 17 Sustainable development goals (SDG) established in 2015 as a universal call to action to end poverty, protect the planet and ensure that all people enjoy peace and prosperity by 2030. SDG such as SDG 2 Zero Hunger and SDG 8 Decent Work and Economic Growth will have to be balanced with SDG 13 Climate Action and SDG 14 Life Below Water.

Biodiversity is a fundamental aspect of marine ecosystem health, and it upholds many ecosystem functions and services. Changes in species distribution and abundance form the foundation of ecosystem changes at the level of habitats, species, communities, and food webs (Brasier et al., 2019). In turn, these complex ecosystem changes will also affect the marine ecosystem services reliant upon them.

Managers and policymakers need access to the right tools to make informed decisions. An integrated end-to-end system where each component builds upon, and is informed by the other parts, represents the optimum tool for this job. Translating these observations and knowledge into policy-ready advice requires a system that allows the selection of indicators, conducting of assessments, making of predictions or projections, and making the appropriate decisions (Benson et al., 2018; Muller-Karger et al., 2018b; Canonico et al., 2019).

In an effort to optimise biodiversity monitoring initiatives, two synergistic global efforts identified specific priority variables for monitoring life in the sea and on land: Essential Ocean Variables (EOVs) through the Global Ocean Observing System (GOOS), and Essential Biodiversity Variables (EBVs) from the Group on Earth Observations Biodiversity Observation Network. These efforts strive to form the basis of efficient and coordinated monitoring programs worldwide (Muller-Karger et al., 2018b) while allowing for regional-scale monitoring frameworks and "essential variables" to be developed concurrently. Within that broader context, the Southern Ocean Observing System (SOOS) led the creation of Southern Ocean specific ecosystem Essential Ocean Variables (eEOVs; Constable et al., 2016). These variables are defined as the derived measurements required to study, report, and manage biodiversity change, designed to play the role of brokers between research and monitoring initiatives and decision-makers.

These different types of variables serve as a guide for the data necessary for monitoring changes in biodiversity. While they all share a common rationale, there are differences between these frameworks. EOVs look at biomass and diversity, and cover and composition. EBVs focus on genetic composition, species populations, species traits, community composition, ecosystem function, and ecosystem structure. eEOV's focus on general ecosystem properties such as spatial arrangements of taxa, food-web structure and function, and anthropogenic pressures.

Toward an Integrated Marine Biological Observing and Informatics System

Developing the information needed for marine ecosystem assessments to understand the impact of changes on the Southern Ocean marine ecosystem [such as the Marine Ecosystem Assessment for the Southern Ocean (MEASO)] requires an integrated system of marine biological observations and informatics as defined by Benson et al. (2018) that are compatible with global systems but also address the specific properties of the Southern Ocean. They propose a cyclical architecture (**Figure 1**) where each component is connected to and helps to inform the other components. The system should build upon existing platforms and standards, adding to them where needed. Furthermore, such a system cannot be static but must enable the inclusion of new methods and ideas. It also needs to be transparent and traceable, which can be achieved by ensuring that data, algorithms and tools are shared according to the FAIR principles (Findable, Accessible, Interoperable, and Reusable; Wilkinson et al., 2016). Central to such a system is a minimal set of variables using comparable methods across time and space (EOVs, EBVs, and eEOVs) and relies on monitoring and use of shared protocols. Data needs to adhere to international standards (such as the Darwin Core standard) and fit the FAIR principles. It also requires analytical algorithms, tools, and workflows that are shared and include documented provenance.

The principles of open and free data are ingrained in the Antarctic Treaty. At a global level, the benefits of open and free data are ever more recognised, and data policies encouraging data sharing have been widely adopted. The FAIR principles provide guidelines for data management that give data greater value and enhance their propensity for reuse and sharing, at scale by machines. As such, they provide a framework for integrative scientific discovery and policy utilisation. Furthermore, the FAIR principles can be applied to non-data assets such as analytical workflows.

Following the principles of action ecology (White et al., 2015), policymakers and managers tasked with overseeing the Southern Ocean require timely responses to their needs and questions. Those responses need to: (1) address the most pressing ecological problems, (2) include transdisciplinary input from a range of researchers and stakeholders, (3) be conducted in open

FIGURE 1 | Conceptual representation of the different components of an integrated system for the Southern Ocean centred around Essential Variables (EOVs, EBVs, and eEOVs) and linked to the FAIR Principles (red) and IPY data vision (purple).

access ways, and (4) use technology and globally integrated data resources, such as the Ocean Biodiversity Information System (OBIS) and the Global Biodiversity Information Facility (GBIF). By incorporating the key characteristics of action ecology, the scientific community can ensure their efforts are efficiently and effectively incorporated into policy and management. Focusing on rapid analysis, using publicly accessible resources, and open access methods leads to shorter intervals between data and knowledge as well as opportunities for incorporating slight adjustments and re-running analyses.

At the start of the UN Decade, we have a unique opportunity to develop a framework that can support decision making for the Southern Ocean. In this paper, we examine the resources that currently exist, the gaps in the resources, and provide a perspective on how we can work together to develop data management and e-science facilities that can link biodiversity observations and biodiversity change modelling to inform decision making (Beja et al., in press). This paper complements the "audit" of the materials and methods available for the first MEASO provided by Brasier et al. (2019). It does not aim to identify specific data gaps, it rather seeks to provide a set of recommendations on the shape and principles of an integrated marine biological observing and informatics system that should underpin future MEASOs with a strong focus on biological data.

HISTORICAL PERSPECTIVE

The Southern Ocean has a long history of exploration and scientific activities (**Figure 2**). The expeditions of Cook and Ross to the Southern Ocean in the late 18th and early to mid-19th century marked the onset of intensive exploration of this region. The observation by Cook of large numbers of seals and whales in high latitudes led to a rush of sealers toward the Southern Ocean. From 1784 onward, they would hunt in the region of South Georgia, the Falkland Islands, Cape Horn, the South Sandwich Islands, and the coast of South America. By 1825, some populations of fur seals were close to extinction, and sealers began hunting elephant seals and some species of penguins for their oil. 1904 saw the start of extensive exploitation of all seven species of whales found in the Southern Ocean (Walton, 2013).

While the scientific focus of the first (1882, 1883) and second (1932, 1933) International Polar Years was firmly on the Arctic region, there was an increase in exploration of the Antarctic and the Southern Ocean, starting with the Belgica expedition (1897–1899) and ending with the Discovery Investigations (1924–1951). These expeditions of the early age of Antarctic exploration form the basis of the current records of Southern Ocean biodiversity (Griffiths, 2010; Brasier et al., 2019).

The global increase in collected data, especially during the second Polar Year, and subsequent loss of collected data during the Second World War made the need for a World Data Centre clear (Beja et al., in press). During the International Geophysical Year (IGY, 1957–1958), nations collaborated on earth science topics across the globe. One of the requirements set out by the IGY was that "all observational data shall be available to scientists and scientific institutions in all countries" (Odishaw, 1959). This led the International Council of Scientific Unions to develop the World Data Centres, which were reformed in 2008 to the World Data System that we know today. Unlike the previous polar years, this IGY included 18 months of fieldwork

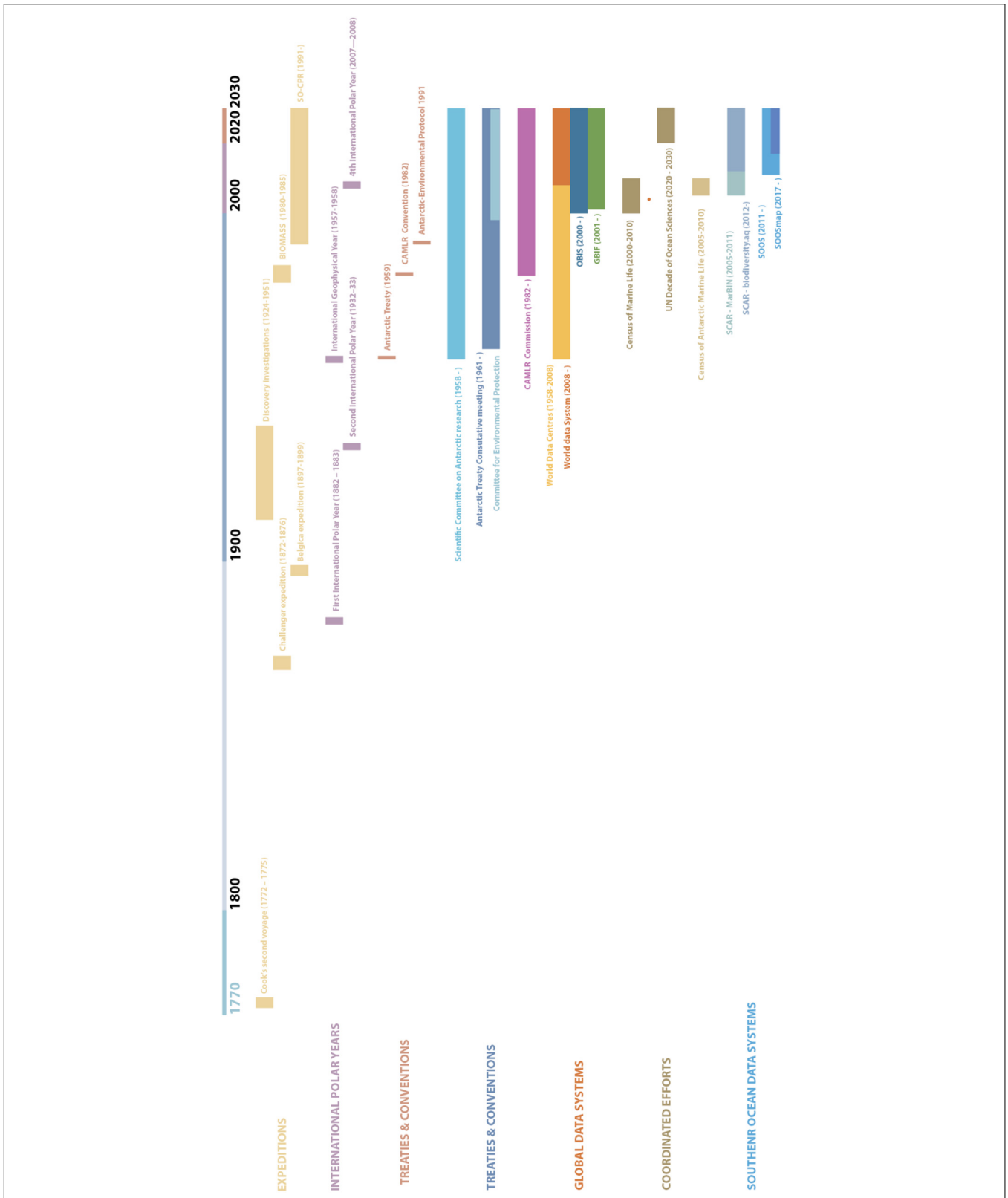

FIGURE 2 | Historical timeline of activities toward an Integrated end to end system in the Southern Ocean. This includes expeditions, International Polar Years, Treaties and conventions, and data systems collaborations within a global context and the context of the Southern Ocean.

in the Antarctic. As a result, the IGY is also referred to as the 3rd International Polar Year (Bailey, 2013). Besides the development of the World Data Centres, this also led to the establishment of the Scientific Committee of Antarctic Research (SCAR) by the International Council of Scientific Unions. The 12 countries involved in the Antarctic component went on to sign the Antarctic Treaty in 1959. This treaty set apart the Antarctic continent and surrounding oceans (the area south of 60°S) for peaceful scientific collaboration (Walton, 2013).

Within the Antarctic Treaty System, two instruments were established to promote the preservation and conservation of living resources in the Southern Ocean. The first was the "Measures for the Conservation of Antarctic Fauna and Flora," agreed in 1964, which entered into force in 1982. This was followed by the "Convention for the Conservation of Antarctic Seals" (agreed in 1972; entered into force 1978) with the objectives of protection, scientific study, and rational use of Antarctic seals, and to maintain a satisfactory balance within the ecological system of the Antarctic treaty area.

Meanwhile, the sub-Antarctic was characterised by intensive harvesting of finfish from the late 1960s to the mid-1970s, along with the emergence of interest in the large-scale exploitation of Antarctic krill, *Euphausia superba*. As the most notable research activities into krill stemmed from the Discovery Investigations in the late 1920s and 1930s, there was no adequate information concerning the biology and stocks of these resources. This led to the Biological Investigations Of Marine Antarctic Systems and Stocks (BIOMASS) project initiated by SCAR in 1972, which resulted in various internationally coordinated expeditions from 1980 to 1985. Discussion within the Antarctic Treaty on the Conservation of Antarctic Marine Living resources commenced in 1975 and led to the establishment of the Commission for the Conservation of Antarctic Marine Living Resources in 1982 (El-Sayed, 1994).

Technological advances from the 1980s to the early 2000s saw an important shift in terms of data management. The increasing use of the internet and email in the 1990s created a shift from paper to digital resources and set the scene for another international effort. By the start of the 21st century, there was a growing need to coordinate large-scale access to biodiversity data. This led to various initiatives both on land and in the marine realm.

Sequencing of proteins and DNA started in earnest in the 1970s but was a time-consuming and costly process. Nevertheless, comparisons between different research groups lead to various unexpected discoveries. By the late 1970s, there was a growing consensus for the development of an international database of nucleic acid sequence data. In 1982, Genbank was started with funding from the National Institute for Health. Similar initiatives were initiated in Europe (European Molecular Biology Laboratory) and Japan (DNA Data Bank of Japan). Currently, these three groups collaborate under what is known as the International Nucleotide Sequence Database Collaboration.

Building upon a request from the Antarctic Treaty Consultative Meeting (1985), SCAR established the *ad hoc* Committee on the Coordination of Antarctic data. This led to the development of the SCAR-COMNAP *ad hoc* Planning group on Antarctic data Management in 1992, which then became the Joint Committee on Antarctic Data management (JCADM) in 1997. JCADM established the Antarctic Master Directory as part of the Global Change Master Directory in 2000 (Taco De Bruin, Pers Comm.).

Under the International Union for Biological Sciences the Taxonomic Database Working Group (TDWG) was set up in 1985 focussing on data standards for plant taxonomic databases. Over the years, this working group has expanded its scope to include general taxonomic data (1995) and ultimately developing standards for publishing and integrating biodiversity information. This included a loosely defined set of terms that can be considered the first iteration of the Darwin Core Standard. This set of terms was further developed, and in 2009, the first ratified Darwin Core standard was published (Wieczorek et al., 2012). While the acronym is still used, the standards have had various name changes in order to better represent the ongoing activities, and as of 2006, they are known as Biodiversity Information Standards.

The Census of Marine Life was a decadal global effort (2000–2010) to assess and explain the diversity, distribution, and abundance of life in the oceans (Costello et al., 2010). The Census was divided into various regional programmes, such as the Census of Antarctic Marine Life (CAML). The Census paved the way for various initiatives related to marine biodiversity data; two of the most important developments were the creation of the OBIS and the World Register of Marine Species.[1] In 2000, OBIS was launched as a framework where scientists and others can discover both historic and new data on species distributions and abundances in the world's oceans (Grassle, 2000). Twenty years later, OBIS remains one of the principal legacies of the Census. The World Register of Marine Species, created in 2007, aims to "provide freely online the most authoritative list of names of all marine species ever published." Several separate portals within it with a taxonomic or regional focus, have expanded the scope of its holdings from extant marine species and now also include non-marine and/or fossil representatives.

The Global Biodiversity Information System (GBIF) was created in 2001, based on recommendations to the Organization for Economic Cooperation and Development (OECD, 1999). They recognised that worldwide access to biodiversity data and information could provide many economic and social benefits and enable sustainable development by providing sound scientific evidence. Equally, it recognised that an international mechanism was needed for this purpose. GBIF aggregates freely and openly available species occurrence data from around the world and makes it available for use in research and policymaking (Robertson et al., 2019).

The (CAML; 2005–2010) was a 5-year international project that focused attention on the ice-bound oceans of Antarctica, and which coordinated 18 research voyages in Antarctica during the IPY and/or within the CAML life-span (Schiaparelli et al., 2013). It was part of both the IPY and the CoML (Gutt et al., 2010). The main objective of CAML was to understand the biodiversity of the

[1] www.marinespecies.org

Southern Ocean and set reference baselines to allow subsequent measurements of change.

The 4th International Polar Year (2007–2008) demonstrated that the volume of data that was collected was less of a challenge than its heterogeneity and the cultural diversity of the collectors, making the challenge sociological as much as it was technical. Thus, a vision was developed that (polar) data should be Discoverable, Open, Linked, Useful, and Safe (Parsons et al., 2011).

The SCAR Marine Biodiversity Network (SCAR-MarBIN) was an information network that was part of the IPY data ecosystem that had these principles deeply ingrained in its development. SCAR-MarBIN was a sister project to the CAML (Danis et al., 2013). It was initiated to establish a web-based inventory of the Antarctic marine biodiversity focusing on three main data types: taxonomy, biogeographic data, and metadata (Danis et al., 2013). It was quickly adopted by SCAR and is the regional node of both the OBIS and GBIF. Building upon a first block contributed by Clarke and Johnston (2003), the first Register of Antarctic Marine Species was compiled and published (De Broyer and Danis, 2011) in 2005 as a thematic node of the World Register of Marine Species mentioned above. As the scope expanded beyond the marine environment, SCAR-MarBIN developed into the SCAR Antarctic Biodiversity Portal,[2] a Register of Antarctic Species as part of the World Register of Marine Species, and the Lifewatch Taxonomic Backbone.

The Marine Biodiversity Observation Network (MBON) is a "coalition of the willing" who agree to share knowledge and know-how to evaluate changes of biodiversity in the ocean, including data, products, protocols and methods, data systems and software. MBON was established as a theme of the GEO BON (Group on Earth Observation Biodiversity Observation Network) in 2014. In 2021, SCAR Antarctic Biodiversity Portal was recognised as a regional MBON node.

The rise of molecular techniques to study living organisms (especially microorganisms such as phytoplankton and bacteria) led to an exponential increase in nucleotide sequence data, including genes, genomes, and metagenomes. To develop standards for the description of these data, the Genomics Standards Consortium was established in 2005, in parallel with the workings of the TDWG. The development and community ratification of the Minimum Information on any (x) Sequence (MIxS) data standard by the Genetics Standards Consortium (Yilmaz et al., 2011) links important metadata like DNA extraction and sequencing protocols, as well as environmental measurements to the nucleotide sequences, which is fundamental to its correct use and interpretation.

The SOOS is an international collaboration under the auspices of SCAR and the Scientific Committee on Oceanic Research (SCOR) to collect and deliver sustained and coordinated observational data on dynamics and change of Southern Ocean systems to researchers and other stakeholders, including governments and industries. Launched in 2011, its tasks include the design, advocacy, and implementation of observing and data sharing systems (Meredith et al., 2013). SOOS has defined its vision and begun improving the coordination of observing efforts through Regional Working Groups, which coordinate the collection of observations, Capability Working Groups, which solve particular technical challenges, and a Data Management Sub-Committee, which coordinates data sharing systems for polar and oceanographic data centres (Newman et al., 2019). In 2017, SOOS collaborated with the European Marine Observation and Data Network Physics group to create SOOSmap, a portal of standardised datasets for waters south of 40°S. SOOS, SCADM, and the Arctic Data Committee are collaborating to design a best-practice approach to implementing schema.org for discovery metadata for all disciplines, with the goal of establishing single-window dataset search tools.

BUILDING THE SYSTEM

Monitoring

Logistical challenges inherent to biological sampling in the Southern Ocean have resulted in a strong bias in the distribution of sampling locations. Due to unfavourable conditions during the Antarctic winter, including extended darkness and sea ice cover, sampling is mostly undertaken during summer. Even in summer, high sea ice concentrations are a limiting factor, with sampling gaps corresponding to areas with sea ice concentrations above 20% (Griffiths et al., 2014). Furthermore, sampling is often concentrated around continental shelves, islands, research stations, and the logistical routes to access them.

Primary biodiversity data about the Antarctic ecosystem can originate from different sampling schemes with different geographic, taxonomic and temporal coverage resulting in five broad categories: limited monitoring data, extensive and intensive monitoring schemes, ecological field studies, and remote sensing (Proença et al., 2017). In addition, an increasing number of automated detection mechanisms have greatly benefited from technological developments in recent decades, such as camera traps, biotelemetry, biologgers, and biogeochemical Argo floats and various automated vehicles, such as automated underwater vehicles or unmanned aerial vehicles. These technologies minimise the environmental impact of research and allow sampling of various kinds of high definition still and moving images, sound, environmental DNA (e-DNA) or biogeochemical measurements (Miloslavich et al., 2018; Canonico et al., 2019).

Extensive monitoring schemes in the Southern Ocean are limited, and most of them are usually focused on specific regions. As such, they may not be representative of ecosystems in other areas of the Southern Ocean. In the Peninsula region, there are roughly ten major sustained research efforts, including the United States Antarctic Marine Living Resources and Long Term Ecological Research Network programs which commenced in 1986 and 1990, respectively. These programs, along with long term operations by Chile, Argentina, United Kingdom, China, Poland, and others, have lent insight into comprehensive knowledge on productivity, zooplankton, benthic community, birds, marine mammals, and physical parameters regarding sea ice and temperature (see e.g., Henley et al., 2019 and references

[2] www.biodiversity.aq

within). They also tend to happen on timescales where any follow-up sampling may be years later. One notable exception of a long term, extensive monitoring scheme is the SCAR Southern Ocean Continuous Plankton Recorder Survey was established in 1991 by the Australian Antarctic Division to map the spatial-temporal patterns of plankton biodiversity and use the sensitivity of plankton to environmental change as early warning indicators of the health of the Southern Ocean (Hosie et al., 2003; Pinkerton et al., 2020). The current dataset comprises over 47,600 segments, each representing the laboratory analysis of zooplankton samples within water filtered by a Continuous Plankton Recorder while it travelled approximately five nautical miles.

CCAMLR established its Ecosystem Monitoring Program (CEMP) in 1989 to "detect and record significant changes in critical components of the marine ecosystem" and "distinguish between changes due to harvesting of commercial species and changes due to environmental variability" (CCAMLR).[3] The program focuses on marine predator species that rely on fish or krill resources and are used as indicators for ecosystem changes: Adélie (*Pygoscelis adeliae*), chinstrap (*P. antarcticus*), gentoo (*P. papua*) and macaroni penguin (*Eudyptes chrysolophus)*, black-browed albatross (*Thalassarche melanophris*), Antarctic (*Thalassoica antarctica*) and cape petrel (*Daption capense*), and Antarctic fur seal (*Arctocephalus gazella;* CCAMLR).

Another data collection method is utilised by MEOP (Marine Mammals Exploring the Oceans Pole to Pole) and other projects. The MEOP consortium consists of several international initiatives that started as part of the International Polar Year in 2008. Marine mammals, e.g., elephant seals, are equipped with CTD sensors and collect oceanographic data on their foraging trips around Antarctica (Treasure et al., 2017). Data is publicly available under.[4] Tracking data from these and other studies were included in the Retrospective Analysis of Antarctic tracking data (RAATD) – the first analysis of circum-Antarctic tracking data that was executed under the auspices of SCAR (Hindell et al., 2020; Ropert-Coudert et al., 2020).

Satellites can measure phytoplankton productivity and biomass and even roughly estimate functional composition based on reflectance spectra that contain the characteristic absorption, scattering, and fluorescence signatures of major algal groups (Muller-Karger et al., 2018a). Although some satellite products of continental Antarctica are available at resolutions of tens of metres or finer, satellite-derived data for the Southern Ocean tends to be much coarser in spatial resolution. Varying daylight hours and polar winter, floating sea ice, and cloud cover also limit the seasonal resolution and geographic distribution of data. Satellites cannot provide a depth-integrated view of the ocean as they only observe surface waters. Deep chlorophyll maxima, as the name suggests, are located in the subsurface, and so open ocean regions typically appear low in satellite-derived chlorophyll (Blondeau-Patissier et al., 2014). Satellite-based instruments are also limited in the aspects of the ecosystem that are directly observable. Although satellites are able to cover vast areas and obtain near real-time information on coarse phytoplankton patterns, they are currently not sufficient for a continuous and fine-scale assessment of the Southern Ocean ecosystem.

As an extension of the existing Argo programme, a global network of biogeochemical Argo floats collect vertical water profiles of oxygen, nitrate, pH, chlorophyll-a concentration, suspended particles, and downwelling irradiance (Organelli et al., 2017). In the Southern Ocean, several international programmes regularly deploy new floats, including the Southern Ocean and Climate Field Studies with Innovative Tools (France) and the Southern Ocean and Carbon and Climate Observations and Modeling (United States) projects.

Most of the biological observations available for the Southern Ocean stem from commercial fishery activities and scientific expeditions. In 1992, CCAMLR adopted a Scheme of International Scientific Observation which established a framework for independent fisheries observers to collect data aboard commercial fishing vessels (2020).[5] All toothfish and icefish fisheries require 100% observer coverage and krill fisheries require 50% observer coverage. Observers collect data on catch composition, biological measurements of target and by-catch species (e.g., length), gear configuration, any incidental mortality of birds or mammals, and any indications of vulnerable marine ecosystems (e.g., through coral pieces found on fishing gear). Observers also collect samples, such as otoliths, to use in later age and growth studies. Further, following a standardised tagging protocol (see text footnote 5, 2020), observers assist in deploying tags on fish and skates and recording information on tag recaptures – this is essential given that CCAMLR uses these tag and recapture data to inform stock assessments for toothfish. The data collected by observers feed directly into knowledge development and management products (see below) but are not publicly available.

Protocols

With the establishment of CCAMLR, it was realised that to effectively regulate the harvesting of Antarctic living marine resources, the effect of such harvesting on species would have to be monitored. The species of primary interest are those which prey on the commercially harvested species (currently Antarctic krill *Euphausia superba*, toothfishes *Dissostichus eleginoides* and *D. mawsoni*; and mackerel icefish *Champsocephalus gunnari*), such as birds and seals. The Working Group on Ecosystem Monitoring and Management (WG-EMM) is responsible for the design and coordination of the monitoring programme and the analysis and interpretation of the data arising from it. Since the establishment of CEMP standard methods in 1987, CCAMLR has collected data from over 50 combinations of sites, species, and parameters. At least eight members are currently involved in acquiring data. For some series, data are available from the late 1950s, but most data series start in the mid-1980s when CEMP was initiated. In August 1997, a new edition of the CEMP Standard Methods was produced following substantial revision of most methods and the adoption of a number of new standard

[3]https://www.ccamlr.org/en/science/ccamlr-ecosystem-monitoring-program-cemp

[4]http://www.meop.net/database/

[5]www.ccamlr.org

methods. It included observation protocols and techniques, as well as a set of reference materials.

Scientific expeditions in the Southern Ocean are often ecological field studies; they address specific scientific questions and often have specific sampling schemes; it may take several years or even decades before an area is visited again. Such one-off expeditions result in limited comparability, but a few major multi-national scientific programmes have tried to standardise survey methods. These include the BIOMASS project, which collected comparable data during 34 cruises involving 13 countries and three field experiments (El-Sayed, 1991), and CAML, which suggested a number of standardised protocols that all 18 participating expeditions agreed to for all habitat types and biological realms (De Broyer and Koubbi, 2014).

(Biological Data) Standards

Standards provide one way of organising information across projects and time, making data more FAIR. For biological data, the Darwin Core standard has become one of the most widely used, and is implemented by OBIS, GBIF, and others. Darwin Core was initially developed for museum collection data but has since expanded to document a range of biodiversity data from metagenomics to sampling event and species abundance metrics (Wieczorek et al., 2012). The Darwin Core standard and other biological data standards are managed by the non-profit Biodiversity Information Standards consortium (through its Taxonomic Databases Working Group), in which various stakeholders are represented.

The Darwin Core standard consists of a set of well-defined terms that refer to different aspects of the data, such as the identity of an observed taxon (scientificName), the location of the observation (decimalLatitude, decimalLongitude, locality,…), and the time (year, month, day, and time). Other terms provide further details and metadata on observations, sampling events, or sampled material. The format for datasets that uses Darwin Core terms is called "Darwin Core Archive," which is a self-contained zipped folder that consists of a set of text files (CSV tables) that hold the data, a simple XML document that describes how these files are organised, and a metadata XML file following the Ecological Metadata Language (EML). The data CSV files in a Darwin Core Archive are linked in a star-like manner, with one core data file surrounded by any number of "extensions." The core data may consist of species occurrences, sampling events, checklists, or material samples. At the same time, the extensions are used to provide additional information or measurements that are usually specific to a study, sampling campaign, or experimental set-up.

OBIS has pioneered an extension to Darwin Core that records measurements or facts about the species occurrences as well as about the events in which the occurrences were observed (De Pooter et al., 2017). With this extension, data managers can document, in a standardised way, information like catch per unit effort or percentage cover, as well as abiotic measurements like temperature and salinity. Moreover, this extension includes fields for documenting links to vocabularies helping to disambiguate text descriptions of sampling methods or aggregations.

The use of different sampling methods and gear significantly affect the collection of species (and reported abundance). This means that one single method is not sufficient to sample all biodiversity and also that results need to be integrated. For data to be useful in a broader context, it is necessary to document and classify where and how they are sampled, which sampling gear is used, and how the data are processed.

Nucleotide sequence data is also commonly used for biodiversity assessments, especially for studying microorganisms or when implementing non-invasive species detection strategies based on e-DNA. There is a well-established practice of making the sequence data available (FASTA or FASTQ) in repositories under the International Nucleotide Sequence Database Collaboration. However, while the Genetics Standards Consortium developed a standard to describe associated metadata and environmental measurements (MIxS; Yilmaz et al., 2011), this information is often lacking.

Since nucleotide and biodiversity data standards evolved in different communities, they are currently not fully compatible. The Darwin Core standard is historically based on Linnaean taxonomy. Microbial or e-DNA biodiversity currently includes taxa known only from their sequences and have no formal morphological description and Linnaean name. Therefore, the integration of this molecular-based data is non-trivial. With the advent of event-core as part of Darwin Core, the integration of non-Linnaean biodiversity data becomes more feasible. There is currently a strong ongoing interest to integrate such data (e.g., OBIS and GBIF). Furthermore, efforts are underway to harmonise standards, e.g., by the Genomic Biodiversity Working Group created by the TDWG and the Genetics Standards Consortium to harmonise Darwin Core and MIxS terms.

More recently, in the United Nations Decade on Ocean Science framework, the Oceans Best Practices System aims to enhance the management of methods across research and support the development of best practices.[6] Typically, regular meetings and working groups, combined with raising issues to provide feedback, are the primary mechanism by which community consensus is built around adopting and developing data standards and best practices. In turn, such standards are fundamental to international collaboration scientific projects or biodiversity monitoring schemes, where data needs to be interoperable between research groups, observation stations and time. However, Tanhua et al. (2019) note that many best practices in ocean data management are currently poorly defined and that much work is needed to identify and promote the adoption of best practices.

Accessibility

The vast size of the Southern Ocean, its remoteness relative to human populations, the extreme weather conditions, and the costs of operating research vessels all strongly constrain our ability to regularly sample biota. Consequently, access to data from expeditions and chemo-physical observation systems is vital to cover sufficient space and time for ecosystem

[6]https://www.oceanbestpractices.org

assessments. The need for open and accessible data is mandated by the Antarctic Treaty System, which has led to several initiatives to promote FAIR data and tools to increase the discoverability and accessibility of open data. The largest resource for finding Antarctic metadata and data is the Antarctic Master Directory, curated by the Standing Committee on Antarctic Data Management of SCAR.

For CCAMLR's Convention area, all summary catch and fishing effort statistics since 1970 are made publicly available in the annual Statistical Bulletins. In addition, CCAMLR receives data from scientific observers onboard fishing vessels, research survey data, and the CCAMLR Ecosystem Monitoring Program (CEMP; Caccavo et al., 2021). In contrast to the summary statistics, these high-resolution fishery and research data are not made available to those outside of CCAMLR due to commercial confidentiality concerns by fishing members. However, permission to access this data can be requested in accordance with the Rules for Access and Use of CCAMLR Data.

A direct access point for finding Antarctic and Southern Ocean biodiversity data from research expeditions, such as species occurrence observations or nucleotide sequence data, is the SCAR Biodiversity.aq portal. Biodiversity.aq is part of the European LifeWatch ERIC infrastructure and is the regional thematic node of OBIS and GBIF, to which data are published and made discoverable. Biodiversity data can also be downloaded through Application Programming Interfaces (APIs) such as R packages, like robis (Provoost et al., 2019), rgbif (Chamberlain and Boettiger, 2017), and spocc (Chamberlain, 2021).

SOOSmap[7] is a web portal that makes standardised environmental datasets available for waters south of 40°S. For an overview of available datasets see **Table 1**. It collates physical, chemical, and biological observations into a single portal to maximise interdisciplinary data discovery. This involves both developing new data-sharing connections for widely distributed data types (e.g., oceanographic mooring data is held in dozens of separate data centres, and stored in multiple standard and non-standard formats) and, where no standards have yet been agreed to, developing data-sharing tools that allow a standard to be developed (e.g., data from the SCAR Plastic in Polar Environments Action Group is served to SOOSmap via a simple online spreadsheet).

Modelling and Analysis

As discussed earlier, and despite continuing increases in data collection, publishing efforts, and the development of new data capture technologies, data support for marine ecosystem assessments in the vast and remote Southern Ocean remains challenging. Observations are often sparse or biased in aspects such as spatial (horizontal and vertical), temporal (seasonal, interannual), taxonomic, and trophic level coverage. Data limitations, coupled with the increasing need for sophisticated assessment outputs, means that moving from marine ecosystem data to an ecosystem assessment increasingly involves some form of modelling. Here we use the term "model" in the inclusive sense of Constable et al. (2016) to include conceptual, qualitative, statistical, empirical, and dynamic mathematical models.

Models have differing utility depending on the type and details of the model but may assist in processes such as identifying change within a set of observations, identifying causal mechanisms (attribution of change), and testing our understanding of systems. A model's ability to make inferences can also help alleviate issues of data coverage. This can take the form of interpolation, where the model is used to make estimates within the domain of the existing data, effectively filling in gaps. This can include the provision of information regarding ecosystem processes that cannot easily be directly observed. Inferences can also be predictive; applied to a broader domain than encompassed by existing data. Predictions can extrapolate to new geographic areas, different time periods, and operational regimes representing perturbations beyond previously observed states. Prediction can be used for forecasting or hindcasting ecosystem properties and behaviour over time, evaluating scenarios (e.g., management interventions, climate change), and exploring the consequences of observed change.

A cornerstone of the scientific method is transparency, reproducibility of scientific results and provenance (Ma et al., 2014; Toelch and Ostwald, 2018). The critical importance of modelling and analysis to ecosystem assessments means that any informatics system must support the integration of data with analysis pipelines. Furthermore, internet-based technologies have not only led to an increase in data sources and data volumes but also increased availability of sophisticated analytical methods. As such, the limits of the traditional reporting mechanisms of material and methods have been surpassed and require a new approach to describe the what, how, when, where and why of an analysis to ensure the complete reproducibility of a scientific analysis. To achieve this, not only the data needs to be open and FAIR but also the tools that have been used to generate the results. Notably, efforts to this effect must support the development of appropriate software tools (e.g., Borregaard and Hart, 2016) and also strive to build supportive and inclusive communities that empower users to apply and build on these tools (Boettiger et al., 2015).

Knowledge

As noted above, Southern Ocean ecological monitoring – and thus knowledge – is concentrated at specific locales (e.g., the Western Antarctic Peninsula) and/or focused on specific species (e.g., commercially valuable species). Due to these long-term comprehensive research efforts, climate change trends are most evident in the western Antarctic Peninsula (e.g., Hendry et al., 2018). However, these changes and related impacts on the ecosystem remain complex and difficult to disentangle from other human impacts, such as fishing and tourism, which are also concentrated in the region (Hogg et al., 2020).

Due to ongoing commercial fisheries and scientific research in the Southern Ocean, extensive data has been collected regarding the basic life history of toothfish and krill. The above noted US Antarctic Marine Living Resources program has led long-term surveys of krill, lending insight into age, growth and recruitment

[7] http://soosmap.aq/

TABLE 1 | Aggregated and standardised data products currently available through SOOSmap to support ecosystem assessments in the Southern Ocean.

Category	Data type	Example sources
Bathymetry	Bathymetry base layer	http://www.ibcso.org/data.html
	Bathymetric surveys	https://maps.ngdc.noaa.gov/viewers/bathymetry/ http://www.ibcso.org/data.html
Biology	Continuous Plankton Recorder Tows	https://data.aad.gov.au/aadc/cpr/ http://www.globalcpr.org/
	Sea ice chlorophyll	https://data.aad.gov.au/metadata/records/ASPeCt-Bio
	KRILLBASE	http://dx.doi.org/10.5285/8b00a915-94e3-4a04-a903-dd4956346439
	CCAMLR Ecosystem Monitoring Program (CEMP)	https://search.earthdata.nasa.gov/portal/soos/search?q=cemp (metadata)
	SCAR plastic in polar environments	https://www.scar.org/science/plastic/resources/
	Penguin count data (MAPPPD)	http://www.penguinmap.com/mapppd
Physics	MEOP seals	http://www.meop.net/database/
	Argo	http://www.jcommops.org
	GO-SHIP	http://www.jcommops.org
	Tide gauges	http://www.psmsl.org/gloss/ http://www.psmsl.org/data/obtaining/stations/data_source_guide.php
	XCTD/XBTs	http://marine.copernicus.eu/ http://www.aoml.noaa.gov/phod/goos/xbtscience/southern.php https://www.nodc.noaa.gov/GTSPP/access_data/index.html
	OceanSITES	http://www.jcommops.org
	Moorings	http://soosmap.aq/
	Satellite SST	http://cpom.org.uk/ http://icdc.cen.uni-hamburg.de/1.html
	CTDs	http://marine.copernicus.eu/ www.seadatanet.org www.emodnet.eu
	Gliders	http://www.ego-network.org/dokuwiki/doku.php?id=public:dataaccess
	Drifting Buoys	http://www.jcommops.org http://www.ipab.aq
	Ships of opportunity	http://www.jcommops.org
	Sea ice concentration	https://resources.marine.copernicus.eu/documents/PUM/CMEMS-OSI-PUM-011-009.pdf
	Ferrybox	http://www.coriolis.eu.org/Data-Products/Data-Delivery
	Saildrone	https://www.saildrone.com/data
	NECKLACE (glacial basal melt rate)	http://soos.aq/images/soos/activities/endorsement/NECKLACE-web.pdf

Please note that for many data types, even data in standard formats may not yet be fully aggregated, so SOOSmap is working with data centres to arrange additional data feeds.

(e.g., Kinzey et al., 2019), as have other nations. For toothfish, data collection has mainly been fisheries-dependent, yet has also lent insight into age, growth, maturity, and other basic life history parameters (e.g., Hanchet et al., 2015). Nevertheless, even in these well-studied species, major gaps and uncertainties remain. For toothfish, uncertainties around connectivity and ecosystem dynamics remain, including impacts on predator and prey populations (e.g., Abrams et al., 2016). In addition, significant gaps remain in the status of bycatch species caught in toothfish fisheries, including for macrourids, skates, and sharks (SC-CAMLR, 2018), and in understanding the role of toothfish in the diets of killer whales (Pitman et al., 2018) and Weddell seals (Salas et al., 2017).

Overall, with limited exceptions noted above, considerable gaps exist in our data collection and thus in our knowledge of Antarctic marine systems. For example, a baseline estimate of Antarctic marine biodiversity has yet to be completed (Chown et al., 2017; Chown and Brooks, 2019). Further, even when data regarding status and trends exists, the drivers behind these trends can be unclear. For example, Adélie penguin (*Pygoscelis adeliae*) populations are in some places stable while in other places they are declining (e.g., parts of the western Antarctica Peninsula)

or increasing (e.g., in the Ross Sea; Che-Castaldo et al., 2017). The drivers behind this variation are not well understood but are likely a combination of climate change impacts, commercial fishing, and potentially historical whaling and the resulting prey release (e.g., Ainley et al., 2017; Hinke et al., 2017). The status of pack-ice seals Ross (*Ommatophoca rossii*), crabeater (*Lobodon carcinophaga*), Weddell (*Leptonychotes weddellii*), and leopard seal (*Hydrurga leptonyx*) remains understudied and largely unknown (e.g., Southwell et al., 2012). The status of Southern Ocean whales, many of which were heavily exploited in the 20th century, also remains uncertain. Some species are estimated to be recovering (e.g., humpback whales, *Megaptera novaeangliae*), others lack data sufficient for assessment (e.g., fin whales, *Balaenoptera physalus*), and others are still considered critically endangered (e.g., Antarctic blue whale, *B. musculus intermedia;* Thomas et al., 2016).

New innovations and applications are lending knowledge and insights into Antarctic marine systems. For example, satellite remote sensing has been incredibly useful at identifying, and estimating the distribution and abundance of penguins (Fretwell et al., 2012), and seals (LaRue et al., 2011). These efforts may provide cost-effective innovations for monitoring in the future, including for marine protected areas (MPAs; LaRue et al., Submitted). Acoustics are also offering new insights with potential applications for population monitoring for krill (Reiss et al., 2020) and whales (Miller and Miller, 2018). Southern Ocean applications of computational approaches and modelling are also providing new insights. For example, applications of Bayesian methods reveal insight into circumpolar abundance trends for Adélie penguins (Che-Castaldo et al., 2017) and earth system models are beginning to reveal longer-term changes in krill growth throughout the Southern Ocean (Sylvester et al., 2021). Applications to better understand the status and the drivers of Southern Ocean species and ecosystems are urgently needed, especially in light of the growing human impacts in the Southern Ocean.

The knowledge gaps highlighted above do not reduce the urgency for management actions that will protect and sustain Southern Ocean ecosystems into the future. Such actions must be based on the best available science, accommodating the uncertainties associated with current knowledge. Uncertainty will always be present to some degree and does not necessarily preclude action from being undertaken. Management processes must engage with uncertainty and seek to undertake robust actions to it wherever possible (Press, 2021). Future priorities, therefore, include not only an increased capacity for knowledge generation and delivery of products into management but also improvements in methods and applications of decision making under uncertainty. Innovations in encapsulating knowledge into products that are usable by managers are also urgently needed.

Products

Knowledge and data products should help inform management and guide the implementation of monitoring protocols. Beyond FAIR data sharing principles, best practices exist for action ecology and actionable science (Beier et al., 2017). Action ecology calls for transdisciplinary input, closing the gap between findings and implementation, using the best available technology, and providing policy-ready recommendations (White et al., 2015). Actionable science can be defined as the data, analyses, projections or tools needed to support decision-making (Beier et al., 2017). The key principles of actionable science comprise credibility (i.e., sound science), saliency (i.e., relevance to management), and legitimacy (i.e., inclusive of stakeholder objectives and values (Cash et al., 2006; Beier et al., 2017)). Co-production of actionable science involves iterative collaboration between scientists, managers, and other stakeholders and offers a model for effective collaboration when managers (e.g., CCAMLR or Antarctic Treaty Parties) need to base multi-faceted decisions on complex scientific information (Sylvester and Brooks, 2020). These best practices for FAIR principles, action ecology, and actionable, co-produced science may help in achieving effective products for decision-making but have not necessarily been used to their full extent in Southern Ocean applications.

CCAMLR and the Antarctic Treaty Consultative Parties (with advice from the Committee on Environmental Protection) manage the Southern Ocean, with the exception of some subantarctic islands under national jurisdiction. The scientists in these fora primarily either work for their national governments or serve on a delegation to CCAMLR or the ATCM. Further, some data—especially data collected through fisheries management—remains out of the public domain yet is often required for analyses and products such as stock assessments and independent reviews that are key to management processes. These arrangements can be challenging for scientists external to their national delegations but who produce valuable knowledge and wish to engage in co-production, thus limiting the scope of input to these management bodies.

One potential avenue for the ATCM and CCAMLR to increase their capacity for management-ready science products could be to more actively facilitate the engagement of a greater cross-section of the scientific community. For example, in the spirit of FAIR principles, Fisheries data should be linked to detailed, findable metadata and, wherever feasible, made more easily accessible for analysis by independent scientists. SCAR provides an illustration of the value of this approach as, especially in the ATCM, they are often invited to present data and products to help inform specific management. For example, SCAR provided an in-depth report regarding the impact of drones on wildlife which helped inform the adoption of ATCM Resolution 4 (ATCM, 2018), "Environmental Guidelines for operation of Remotely Piloted Aircraft Systems in Antarctica." SCAR also hosts the Antarctic Environments Portal,[8] which provides concise, technically accurate, politically neutral summaries of the current state of knowledge that are accessible and understandable to policymakers. These examples illustrate SCAR's role as a bridging organisation, delivering science-based products in the form of analyses, white papers, or others.

An end-to-end system in the Southern Ocean can further create more opportunities for independent science (and scientists) to feed into their management process. While

[8]www.environments.aq

BOX 1 | Key Messages for Policy Makers.

Key Message 1

The Southern Ocean is an important contributor to global oceanic biodiversity and nutrient, oxygen, and primary production. It also plays a central role in global ocean circulation, which is in turn a key climate driver. A clear understanding of Southern Ocean change and dynamics is therefore important to understanding the world's oceans.

Key Message 2

Understanding dynamics and change in the Southern Ocean requires an end-to-end system of observations, data management, scientific analysis, and policy advice. So far as possible, this system should be assembled from existing platforms and standards, and it must be transparent and traceable. To do this, the data, algorithms, and tools should all be shared according to the FAIR principles (Findable, Accessible, Interoperable, and Reusable).

Key Message 3

Existing biodiversity observations are strongly biased both spatially and temporally because of access issues caused by the remoteness and size of the Southern Ocean, the inhospitableness of winter weather, and sea ice. Observations are also biased toward taxa of particular interest to managers (e.g., commercially valuable species and their prey). Thus, observations are concentrated in ice-free areas along access routes to research stations and in the summer months. Information about biodiversity in other regions and seasons or about more obscure taxa is very sparse. Future observing efforts should be endeavour to reduce these biases.

Key Message 4

Most of the biological observations in the Southern Ocean are collected by scientific expeditions and commercial fishing activities. While the data from scientific expeditions is increasingly available through FAIR data systems, much of the data collected by fisheries observers remains inaccessible to scientists external to CCAMLR. Long gaps between repeat scientific expeditions to particular regions means that much of the publicly accessible data has very low temporal resolution. Increased repeat sampling will improve the ability of scientists to understand changes in species distribution and populations.

Key Message 5

Community-agreed standards for sampling methods and data management processes allow data from multiple projects to be integrated into an aggregated data product which can allow scientific questions to be analysed across time and space. Scientists and observers should be using existing standards or developing new ones, where needed, to allow maximal reuse of reanalysis of their observations by the global community.

Key Message 6

A system to support future ecosystem assessments in the Southern Ocean must address the knowledge and data gaps caused by sampling bias, non-standardised sampling methods and data management processes, and by data being kept out of the public domain.

scientists external to these bodies can publish papers, data sets, or other products, they are often not received or used in management. Currently, The participants in these fora primarily either work for their national governments or serve on a delegation to CCAMLR or the ATCM, and so an independent scientist could not present a paper for consideration by these bodies other than through a national government. This process could be more open, transparent and streamlined. Fisheries data, in the spirit of FAIR principles, should be linked to detailed, findable metadata and, wherever feasible, made more easily accessible for analysis by independent scientists. Secondly, independent scientists working with Southern Ocean data could work to follow best practices for co-production of actionable science. This would result in the creation of credible science products that are salient to the needs of the managers, and legitimately include stakeholder views.

The recent proposal for a marine protected area in the western Antarctic Peninsula provides a similar example. The preparation of that proposal, including the creation of data layers and products, was conducted mainly by national scientists but did include input from independent scientists and other stakeholders (Sylvester and Brooks, 2020).

CONCLUSION

Biodiversity data is a critical aspect of any integrated Marine Ecosystem assessment. Within the Southern Ocean, limited availability of biodiversity data will remain an issue as the region is remote and is characterised by harsh environmental conditions. This necessitates an internationally collaborative approach that is, fortunately, ingrained within the Antarctic Treaty. International initiatives such as CAML and the 4th IPY have contributed to sharing protocols and applying data standards, resulting in the mobilisation of data with global networks like OBIS and GBIF. During CAML and IPY, there was a strong focus on historical data and the development of a baseline assessment of the Southern Ocean (De Broyer and Koubbi, 2014). The wealth and volume of new data associated with new technology represent a huge challenge with increased demand on informatics, requiring high capacity computing capabilities.

Data infrastructures such as SCAR-MarBIN/SCAR Antarctic Biodiversity Portal, the Antarctic Master Directory, SOOS, and SOOSmap make Southern Ocean data findable and accessible and are well linked to the relevant international data communities. However, ensuring that data are interoperable and reusable remains a complex task. A key aspect to achieve this will be the application of open science principles to the whole research cycle. Furthermore it requires the engagement of all stakeholders and most noteworthy policymakers (**Box 1**).

The application of EBVs, EOVs, or eEOVs represents a strong way forward in the monitoring and assessment of Southern Ocean Ecosystems. However, these Essential Variables will require prioritising specific variables and the data to be collected at the level of CCAMLR. This will require close collaboration between policymakers and researchers and the application of the action ecology to get the scientific input we need for the Southern Ocean we want.

AUTHOR CONTRIBUTIONS

AV coordinated the text contributions, wrote the introductory, and finalised the manuscript. PB, CB, HG, SH, BR, and MS contributed to the writing and editing of the manuscript. All authors contributed to the article and approved the submitted version.

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REVIEW
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Southern Ocean Food Web Modelling: Progress, Prognoses, and Future Priorities for Research and Policy Makers

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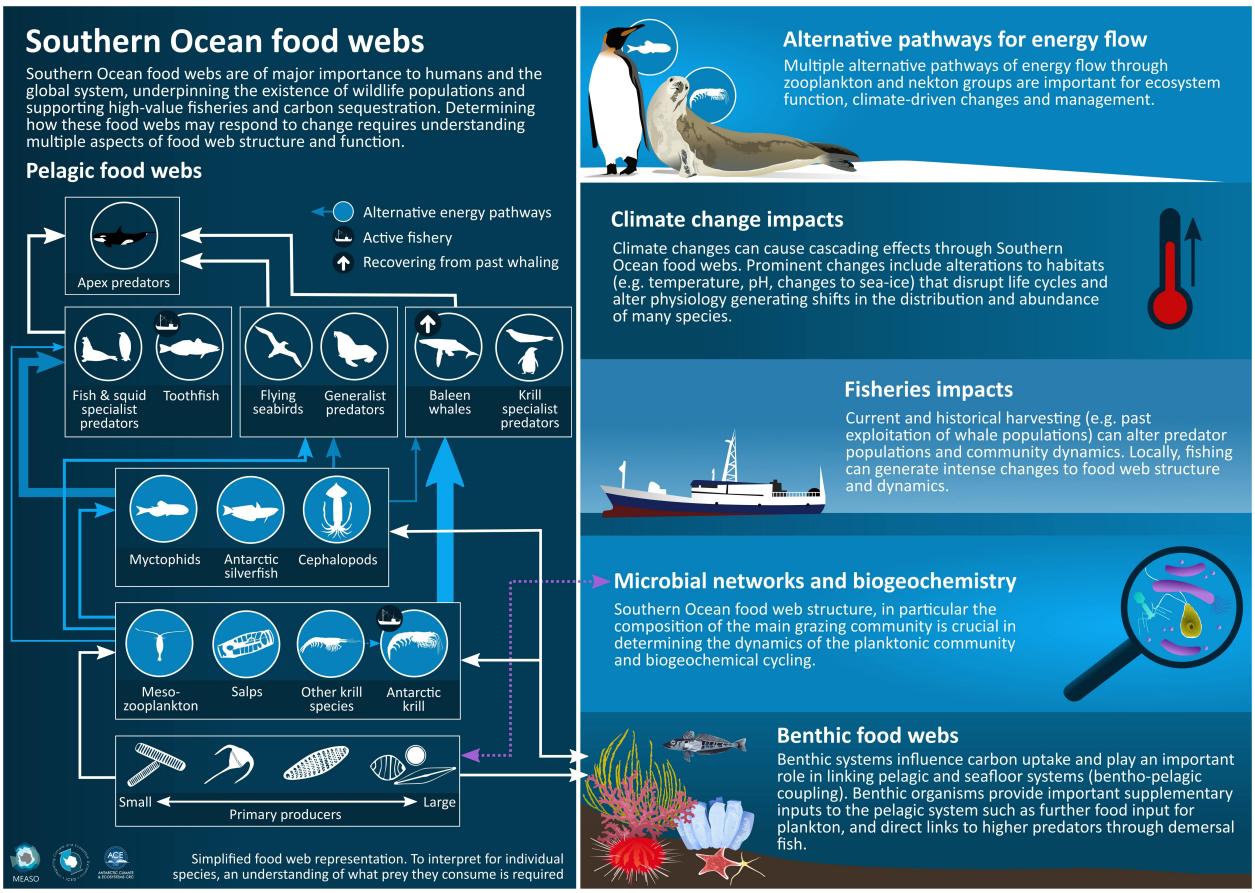
Globally important services are supported by Southern Ocean ecosystems, underpinned by the structure, function, and dynamics of complex interconnected and regionally distinctive food webs. These food webs vary in response to a combination of physical and chemical processes that alter productivity, species composition and the relative abundance and dynamics of organisms. Combined with regional and seasonal variability, climate-induced changes and human activities have and are expected to continue to drive important structural and functional changes to Southern Ocean food webs. However, our current understanding of food web structure, function, status, and trends is patchy in space and time, and methods for systematically assessing and comparing community-level responses to change within and across regional and temporal scales are not well developed. Insights gained from food web modelling studies—ranging from theoretical analyses of ecosystem resilience and adaptation, to qualitative and quantitative descriptions of the system—can assist in resolving patterns of energy flow and the ecological mechanisms that drive food web structure, function, and responses to drivers (such as fishing and climate change). This understanding is required to inform robust management strategies to conserve Southern Ocean food webs and the ecosystem services they underpin in the face of change. This paper synthesises the current state of knowledge regarding Southern Ocean pelagic food webs, highlighting the distinct regional food web characteristics, including key drivers of energy flow, dominant species, and network properties that may indicate



GRAPHICAL ABSTRACT | Graphical summary of multiple aspects of Southern Ocean food web structure and function including alternative energy pathways through pelagic food webs, climate change and fisheries impacts and the importance of microbial networks and benthic systems.

system resilience. In particular, the insights, gaps, and potential integration of existing knowledge and Southern Ocean food web models are evaluated as a basis for developing integrated food web assessments that can be used to test the efficacy of alternative management and policy options. We discuss key limitations of existing models for assessing change resulting from various drivers, summarise priorities for model development and identify that significant progress could be made to support policy by advancing the development of food web models coupled to projected biogeochemical models, such as in Earth System models.

Keywords: ecosystem models, food web assessment, marine policy, Antarctic, ecosystem-based management

INTRODUCTION

Southern Ocean marine ecosystems support globally important values and services such as the sequestration of atmospheric carbon, commercial fisheries, polar biodiversity, the existence of iconic wildlife populations, and cultural connections (Grant et al., 2013; Cavanagh et al., 2021; Murphy et al., 2021; Roberts et al., 2021). These unique ecosystems and the services they support are underpinned by the structure, function, and dynamics of complex interconnected and regionally distinctive food webs (McCormack et al., 2020; Hill et al., 2021). Food web structure can be understood in terms of energy transfer and biomass flow between different components of the ecosystem, either flowing from primary producers to top predators in the pelagos or exported to the benthos through the sinking of detritus and dead organisms as well as through active transport, thereby serving as an energy source for many benthic organisms (Isla et al., 2006). These energy pathways connect different trophic levels, geographic places, as well as the water column and benthic

environment. The types of pathways also determine how much energy and biomass ends up in different parts of the system—both spatially and within the trophic structure—whether that be in the form of the bodies of iconic wildlife and fished species, or in the form of carbon that is sequestered in deep waters through sinking and mineralisation. As such, food web ecology has considerable relevance to policy makers, as management decisions have to rely on knowledge of food web structure and function to predict and mitigate the effects of change (Constable et al., 2017; Trebilco et al., 2020).

Understanding and predicting the dynamics of Southern Ocean food webs is challenging, complicated by a myriad of direct and indirect (networks of) interactions amongst species, many of which have highly variable spatial and seasonal dynamics (Murphy et al., 2012). Combined with this variability are the past, current, and future effects of climate-induced changes (Morley et al., 2020) and human activities (Grant et al., 2021) on habitats and biology in the Southern Ocean (Constable et al., 2014; Turner et al., 2014). These drivers of change can cause rapid and significant effects on species, habitats, broader ecosystem functioning, and resilience. The complex adaptive nature of oceanic ecosystems further complicates our ability to determine the range of responses that food webs may exhibit to perturbations.

Most Southern Ocean species have broad distributions with trophic interactions varying across seasons, regions, and habitats. Such variation impacts trajectories of network reorganisation following disturbances, illustrating the importance of accounting for spatial heterogeneity (Cordone et al., 2020; also see Section " Ecological Network Models" and **Box 1** for a description of ecological networks and network modelling in a food web context). Whilst it is impossible to empirically document the spatial variability and scales of all trophic interactions across the Southern Ocean, significant progress has been made in recent decades toward characterising Southern Ocean food webs at a regional scale (see **Figure 1** for locations). Here, we consider that Southern Ocean food webs include species that wholly reside in the Southern Ocean, south of the Subtropical Front (Morley et al., 2020), as well as migratory species that obtain much of their sustenance within the Southern Ocean, such as whales and flying birds (Constable, 2005).

Two parallel activities have been expanding over the last decade since the programme Integrating Climate and Ecosystem Dynamics of the Southern Ocean (ICED) first reviewed the gaps and priorities for understanding Southern Ocean food webs and what was needed to support decision-makers (Murphy et al., 2012). The first set of activities relates to building a greater depth of understanding of food web linkages using enhanced diet studies involving isotopes, genetics, and other trophic markers (e.g., McCormack et al., 2019a; 2020). The second has been the development of models of multispecies interactions, food webs, and ecosystems, derived from diet and foraging studies (discussed in section "Current Developments in Food Web Modelling"). Insights gained from the modelling studies, ranging from theoretical analyses of ecosystem resilience and adaptation to qualitative and quantitative descriptions of food webs, have assisted in resolving patterns of energy flow and the ecological mechanisms that drive food web structure and

BOX 1 | Network science as a powerful approach to describe the structure and dynamics of food webs.

Network science has become a powerful interdisciplinary approach for describing, quantifying, and analysing the structure and function of ecological communities. Through application of well-developed mathematical concepts from graph theory (Iñiguez et al., 2020), network science approaches allow for the exploration of questions across various ecological scales, ranging from individual species to community-level analyses (Poisot et al., 2016). Graph theory, the branch of mathematics concerned with pairwise relations between objects, has provided a range of measures to quantify and interpret interactions, scaling from pair-wise interactions between species to complex whole ecosystem approaches (Delmas et al., 2019).

Network science has been applied across various spatial scales in the Southern Ocean from characterisation of the general Antarctic food web (Carscallen and Romanuk, 2012; de Santana et al., 2013) to more localised studies of the complexity, structure, and function of several coastal and open-ocean ecosystems. Important insights have been gained into mechanisms for energy flow, the relative importance and traits of individual species and the influence of environmental variables (e.g., sea-ice) on the structure of local food webs (Jacob et al., 2011; Marina et al., 2018a; Rossi et al., 2019). Evolving state-of-the art techniques are opening up new possibilities of applying network science to investigate Southern Ocean food webs that go beyond simple measures and correlation analysis. Based on the concept of causal networks (Runge et al., 2019) and complex adaptive systems (Griffith, 2020; Eyring et al., 2021), they have the potential to help identify the causal effects on food web structure and functioning from the complex interplay between environmental and human induced changes on food webs.

We consider that there are a range of future applications of network science building on the progress to date. Priority areas of research include: (1) A generic food model should be developed as a common structural base for further work and as a base for collective knowledge (Murphy et al., 2016). This can initially be a qualitative or semi-quantitative food web model (see section "Qualitative Modelling and Network Approaches"). (2) Quantifying the interaction strengths or fluxes in food webs. This is currently considered difficult for the Southern Ocean requiring intensive experimental and observational efforts. A viable solution is to extend the qualitative model or use a more sophisticated model and use mathematical proxies to calculate interaction effects such as energy fluxes. One approach is to assume that energy fluxes are driven by a top-down effect (energy demands of top predators). This can also be extended to a general model using allometric rules (Gauzens et al., 2018). (3) Extending species-based food web models to ones based on body-size architecture and species traits (e.g., Blanchard et al., 2017). For instance, this has the potential to identify critical interactions and linkages between energy pathways that stabilise food webs (e.g., Blanchard et al., 2011; Brose et al., 2019). (4) Deciding on a common group of measures to characterise the different regional properties of Southern Ocean food webs and to feed into research and monitoring plans such as for Marine Protected Areas. Four metrics from graph theory that are applicable are Degree, Betweenness centrality, Google Page Rank, and Modularity. (5) Uncovering the building blocks of Southern Ocean food webs regionally and across gradients applying the network science concept of motifs and higher-order connectivity patterns (Benson et al., 2016). These patterns have important consequences to dynamic stability and how food webs may adapt to perturbations. (6) Extending Southern Ocean food web research to include social- ecological interactions including governance. (7) Integrating more sophisticated network science analysis with whole ecosystem models. For instance, to identify which species or traits are more important for transferring the complex effects of multiple stressors (Griffith et al., 2018). (8) Developing a circumpolar and/or regional Dynamic Bayesian Networks as a Decision Support tool to help establish potential adaptation strategies.

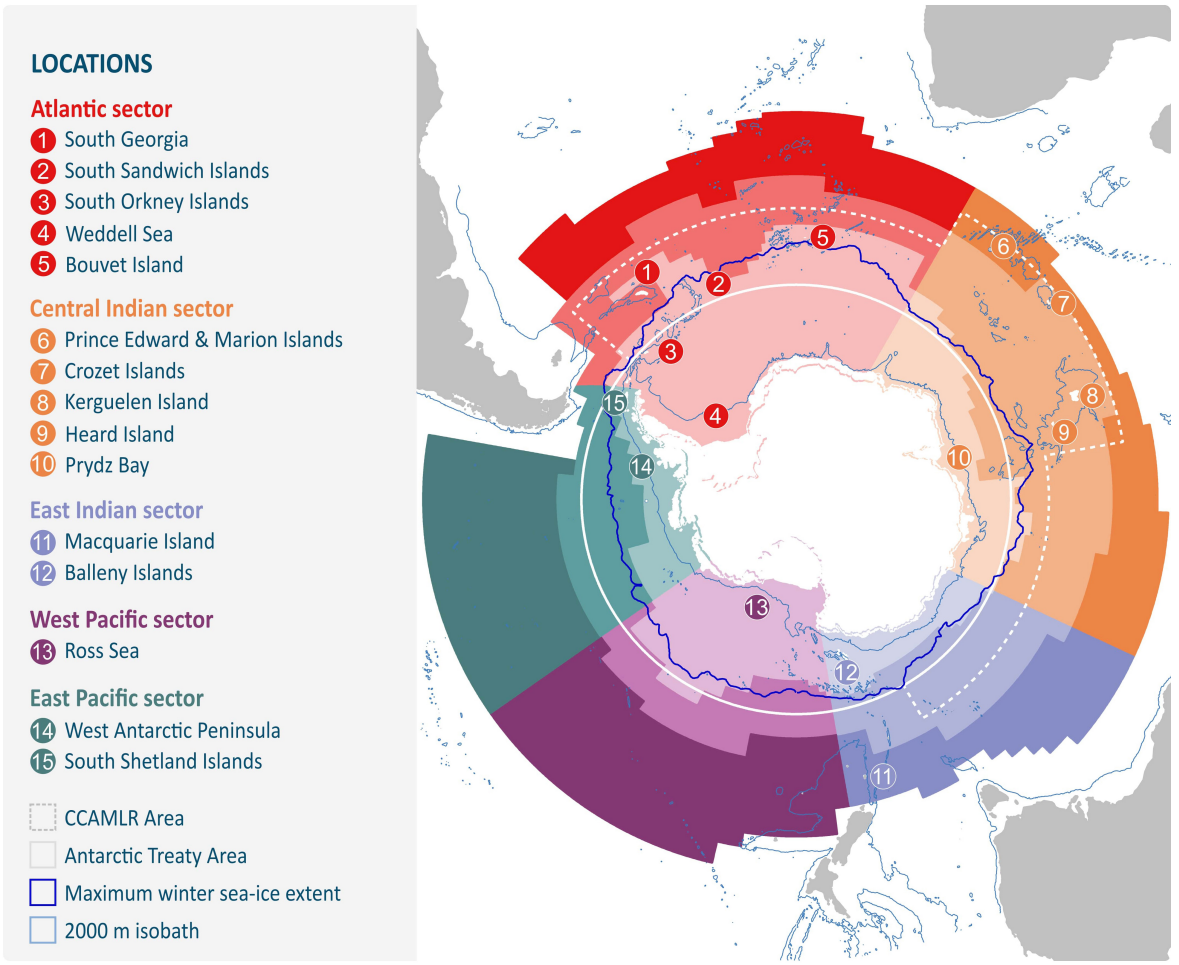


FIGURE 1 | Boundaries for the Marine Ecosystem Assessment for the Southern Ocean (MEASO) areas including five ocean sectors (Atlantic, Central Indian, East Indian, West Pacific, and East Pacific) each with three zone divisions. Sectors are divided meridionally. Zones extend from the coast to the Southern Antarctic Circumpolar Current Front (Antarctic Zone), to the Subantarctic Front (Subantarctic Zone) and to the Subtropical Front (Northern Zone). Islands are marked in white. Antarctica includes ice shelves. Antarctic Treaty is denoted by the solid white line and the area of the Convention on the Conservation of Antarctic Marine Living Resources is shown with a dashed line, which approximately follows the Antarctic Polar Front. The 2,000 m isobath is shown in light blue with the approximate position of the maximum winter sea ice extent shown in dark blue. Numbers refer to locations mentioned throughout the manuscript or with relevance to food web studies and correspond to those listed in the key.

function at a regional level (**Figure 2**; previously reviewed in Murphy et al., 2012).

The interactions of individual species with prey, including foraging ecology, are examined in detail in other papers associated with the Marine Ecosystem Assessment for the Southern Ocean (MEASO, 2020). In this paper, we contribute to MEASO by evaluating the current state of food web and ecosystem modelling for supporting assessments of current and future change in Southern Ocean ecosystems and for informing decisions relating to the management and conservation of those ecosystems. We divide this contribution into a further five sections. Section " Approach" details the approach we have taken and its rationale. Section "Characterising Southern Ocean Food Webs" examines regional variations in the characteristics of Southern Ocean food webs, including key drivers of energy flow and the dominant species giving rise to different energy pathways, regional variation in the relative importance of those pathways and how those pathways may change. In section "Attributes of Food Web Models for Supporting Policy," we examine the attributes of food web models for supporting policy by examining food web (network) properties that may provide indicators of change as well as system resilience. We describe how food web and ecosystem models can be used to inform policy makers on scenarios for and risks in the future, what field measures are needed to help validate models and refine them over time, and how the models can be used to test the efficacy of management strategies. Section "Current Developments in Food Web Modelling" reviews the current developments in food web modelling and their capabilities in supporting policy, and the key issues to be resolved in building models to support policy. Lastly, section "Concluding Remarks—Addressing Needs of Policy Makers" considers the capability of food web and ecosystem

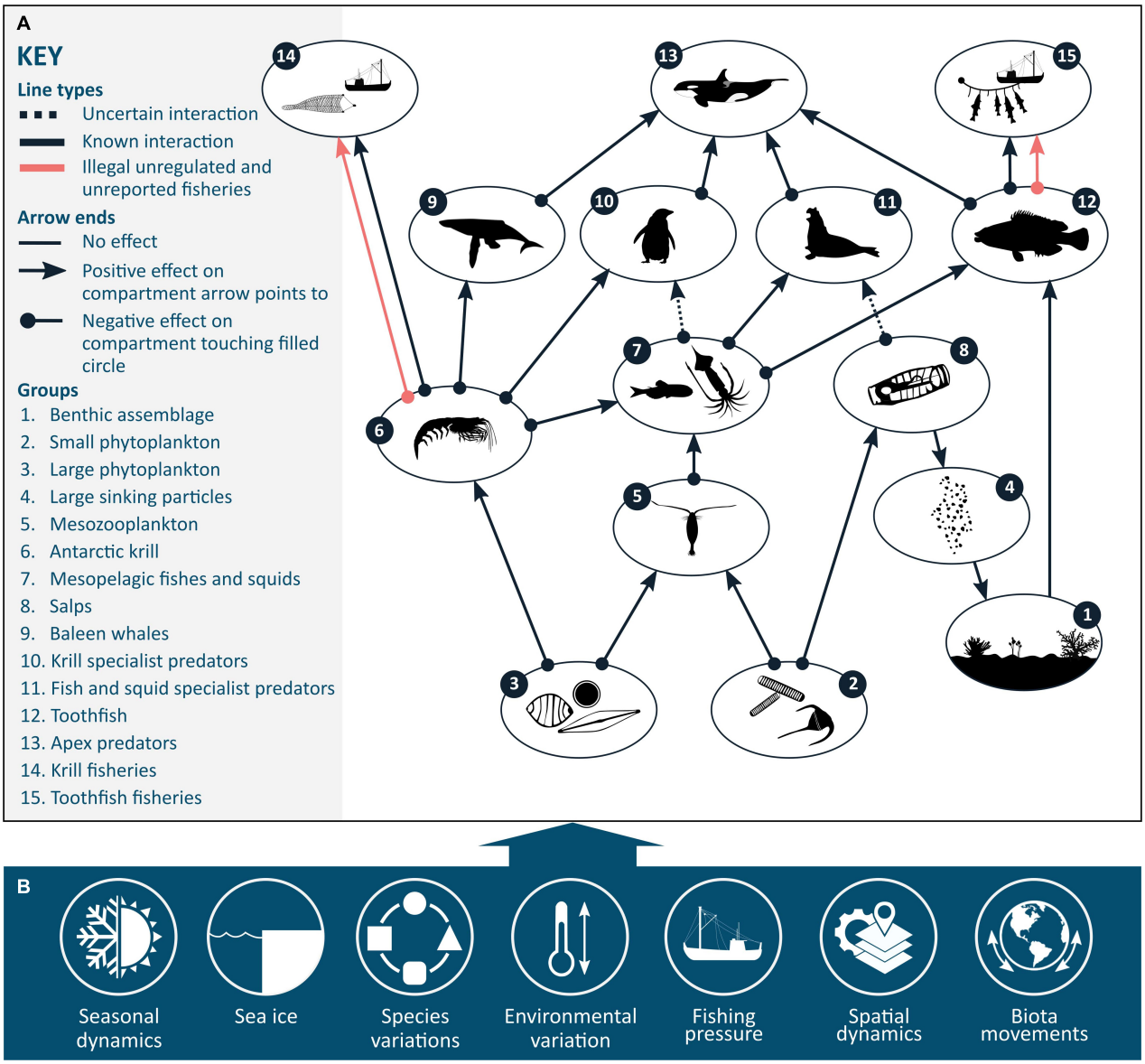


FIGURE 2 | (A) Simplified representation of a Southern Ocean food web, incorporating links to dependent fisheries. **(B)** Key controls underlying food web dynamics. Figure adapted from Trebilco et al. (2020).

models to address topical issues, current constraints/limitations, and outlines priorities for model development.

APPROACH

The focus of this paper is on progress in development of modelling of Southern Ocean food webs as part of the broader ecosystem. In this context, food web models incorporate representation of all trophic levels, the potential for competition within trophic levels, and non-trophic transfers such as bentho-pelagic flux. This definition may be seen to include biogeochemical models that typically include representation of nutrients (N), primary production (P), secondary production (Z = zooplankton), and carbon export (D = detritus). In this paper, we do not review biogeochemical models in detail but instead consider the models that help address policy questions relating to food web interactions at higher trophic levels, which need greater flexibility in considering (unpacking) different functional groups and relationships.

While not always the case, we have in mind that food web models are informed by, if not embedded within, end-to-end ecosystem approaches to modelling. In that respect, compartments of the model would typically involve interactions between physics, chemistry, and biology, where food webs would be the biological part. The term "food web" relates to energy

flow. In this respect, the interpretation of "food web" needs to be broader than a trophic network but also include the potential for non-trophic mortality or competition for resources other than food. These processes are common within the benthic environment, where benthic disturbance and competition for space may be important for structuring benthic assemblages and their influence on benthic-pelagic coupling and carbon sequestration. That said, the ability to include models of non-trophic interactions is poor at present for Southern Ocean ecosystems, despite some important progress over the last decade (e.g., Kéfi et al., 2015). As a result, we focus this review on pelagic food webs, taking note wherever possible of what needs to be done to improve the representation of benthic processes and bentho-pelagic coupling in Southern Ocean ecosystem dynamics.

Our discussion of progress in Southern Ocean food web modelling is informed by broader reviews of marine ecosystem and food web modelling elsewhere (e.g., Fulton and Link, 2014; Melbourne-Thomas et al., 2017; Fulton et al., 2019) and by the knowledge of Southern Ocean biological interactions contained within the MEASO research topic (MEASO, 2020) and other recent reviews. We do not undertake similar reviews here but summarise those reviews in **Table 1**. Instead, we describe the important characteristics of Southern Ocean food webs that should be represented in models and the attributes that models need to have to support policy. Finally, we consider the progress being made toward that level of modelling and the gaps and priorities for the future.

CHARACTERISING SOUTHERN OCEAN FOOD WEBS

Despite the highly dynamic nature of Southern Ocean ecosystems at a large geographic scale, consistent patterns in food web structure exist (Murphy et al., 2012). Such regularities can help determine ecosystem functioning (e.g., productivity, nutrient cycling, energy flow) (Griffith et al., 2019). Identifying these consistent patterns and their links to function contributes to our understanding of the key controls that underlie food web dynamics (**Figure 2**). One of the most common descriptions of food web structure and function is the relative importance of various species and trophic relationships in dictating how energy flows through an ecosystem (i.e., energy pathways). Multiple studies have described the various energy pathways that exist within Southern Ocean ecosystems, with their dominance varying across regions and between seasons (Ballerini et al., 2014; Suprenand and Ainsworth, 2017; Dahood et al., 2019; McCormack et al., 2019b, 2020; Hill et al., 2021).

The food chain from phytoplankton through Antarctic krill (*Euphausia superba*) to various marine mammal and bird species is typically dominant in Antarctic food webs (Hill et al., 2006; Murphy et al., 2012; McCormack et al., 2020). This represents an efficient energy pathway from primary producers to higher trophic levels, with the potential to sustain a large biomass (Clarke, 1985). Such central dependence of higher trophic levels on krill is unique to the Antarctic, leading to krill often being classified as a key "forage fish" in the context of general ecosystem model structure (Essington and Plagányi, 2014; Plagányi and Essington, 2014). For instance, the diets of baleen whales include a more diverse range of prey species (e.g., fish) in other systems such as the northern hemisphere. The importance of Antarctic krill in providing the majority of energy needed to sustain higher trophic level production has been well demonstrated in various regions such as the Antarctic Peninsula (Ballerini et al., 2014; Dahood et al., 2019).

In addition to the archetypal krill pathway, alternative pathways exist for this transfer of energy to top predators; these pathways sustain other predators less reliant on krill, notably toothfish, toothed whales, and a number of seals, penguins, and flying birds (**Figure 2A**; Atkinson et al., 2004; Murphy et al., 2016; McCormack et al., 2019b, 2020; Subramaniam et al., 2020a), or provide alternative pathways to the suite of krill dependent predators (e.g., Saunders et al., 2019). Various studies have emphasised the importance of these alternative configurations for energy flow, usually involving various combinations of other zooplankton, fish, and squid species (Ballerini et al., 2014; Suprenand and Ainsworth, 2017; Dahood et al., 2019; McCormack et al., 2019b). These diverse energy pathways maintain a range of ecosystem services (e.g., high-value fisheries, carbon sequestration; Cavanagh et al., 2021) where distinct suites of species provide unique contributions (Barnes and Sands, 2017; Constable et al., 2017). However, what determines the relative dominance of different energy pathways in space and time generally remains poorly understood (Constable et al., 2017).

Southern Ocean food webs are highly temporally and spatially variable across multiple scales (Murphy et al., 2012). There is marked seasonality, which varies in intensity from the permanently ice-covered region of the southern Weddell and Ross Seas (see **Figure 1**) to the northern areas of the Polar Frontal Zone and Sub-Antarctic Front. There is also a high level of interannual variability in regional ocean temperatures and sea ice conditions associated with atmospheric variation across the Southern Hemisphere. The asymmetric nature of the Antarctic continent and the complex bottom topography results in varied patterns of ocean circulation and seasonal sea ice dynamics across the Southern Ocean. This temporal and spatial variability generates different physical and chemical conditions, which are crucial determinants of regional food web structure (Murphy et al., 2012). There is also, however, a high degree of connectivity among regions as a result of transport in association with both ocean currents and sea ice drift along with the movement of organisms during development, foraging and migration (**Figure 2B**; see also Murphy et al., 2012; Thorpe et al., 2019; Treasure et al., 2019). This combination of variability and openness of ecosystems across multiple scales challenges simple definitions of regional boundaries between food webs, and hence also characterisation of the structure of food webs (McCormack et al., 2020).

Insights gained from regional analyses of food web structure and the mechanisms for energy flow (McCormack et al., 2020; Hill et al., 2021) have provided the foundation for developing a generalised view of Southern Ocean food webs, one that highlights the importance of alternative energy pathways and regional variability in the relative importance in those pathways

TABLE 1 | Summary of review papers that inform modelling of Southern Ocean food webs and ecosystems.

Model subject	Reviews
Model development	Murphy et al., 2012; Fulton and Link, 2014; Melbourne-Thomas et al., 2017; Fulton et al., 2019; Rogers et al., 2019; Geary et al., 2020
Biogeochemistry	Post et al., 2014; Cavan et al., 2019; Henley et al., 2020
Primary producers	Alvain and Ovidio, 2014; Deppeler and Davidson, 2017; Pinkerton et al., 2021
Zooplankton	Atkinson et al., 2012b; Angel and Blachowiak-Samolyk, 2014; Hosie et al., 2014; Kouwenberg et al., 2014; Lindsay et al., 2014; Roberts et al., 2014; Swadling, 2014; Zeidler and De Broyer, 2014; Schaafsma et al., 2018; Pinkerton et al., 2020
Krill	Atkinson et al., 2012a; Cuzin-Roudy et al., 2014; Siegel, 2016; Meyer et al., 2020
Fish and squid	Kock et al., 2012; Duhamel et al., 2014; Rodhouse et al., 2014; Caccavo et al., 2021
Flying birds	Ropert-Coudert et al., 2014; Bestley et al., 2020; https://www.acap.aq/
Penguins	Ratcliffe and Trathan, 2011; Ropert-Coudert et al., 2014; Borboroglu and Boersma, 2015; Hindell et al., 2020; Bestley et al., 2020
Seals	Trites and Pauly, 1998; Southwell et al., 2012; Ropert-Coudert et al., 2014; Bestley et al., 2020; Hindell et al., 2020
Whales	Trites and Pauly, 1998; Leaper et al., 2008a,b; Ropert-Coudert et al., 2014; Bestley et al., 2020; Hindell et al., 2020
Benthic systems	Brasier et al., 2021; Part 5 of the Biogeographic Atlas of the Southern Ocean (Wiencke et al., 2014)
Local drivers	Grant et al., 2021

(Murphy et al., 2012). For example, Murphy et al. (2013) drew upon earlier quantitative food web analyses (Hill et al., 2012; Sailley et al., 2013; Ballerini et al., 2014), to compare ecosystem structure in two major regions: South Georgia and the west Antarctic Peninsula. They showed structural similarity in the food webs, highlighting the importance of ecological connectivity across the Scotia Sea from sea ice dominated regions in the south to warmer open ocean regions in the north. Despite the similarities, the study also emphasised that the dominant species at mid-trophic levels involved in the major pathways of energy flow are not the same across the different habitats (Murphy et al., 2013). In northern regions, and north of the Polar Front, copepods and mesopelagic fish (myctophids or lantern fish) are key mid-trophic levels species, while across much of the Antarctic Circumpolar Current (ACC) south of the Polar Front, Antarctic krill become a dominant feature with mesopelagic fish less so. In the most southerly areas of regular sea ice cover, it is ice-krill and silverfish that are the most important mid-trophic level species (Murphy et al., 2013, 2016; Ballerini et al., 2014; McCormack et al., 2019b). Squids can also be important in some areas (Subramaniam et al., 2020a). Salps have long been considered to be an alternative dominant herbivore to Antarctic krill (Murphy et al., 2012), possibly even competing but more likely occurring in different water masses (Johnston et al., in this research). The role of salps in the food web is less known but becoming increasingly recognised as an alternative energy pathway to krill and copepods in some areas (Kelly et al., 2020).

Further comparative analysis of the structure and pathways of energy in food webs at South Georgia and the west Antarctic Peninsula was undertaken by Murphy et al. (2016, **Supplementary Information**). The study reanalysed food web data, re-aggregated the species and groups into size groups and recalculated energy flows between groups. The study further demonstrated the basic similarity of food web structure and the crucial role of Antarctic krill in both ecosystems. The comparative analysis of these food webs suggests that the South Georgia food web is more dependent on external productivity (e.g., import of secondary production from external regions) than that in the west Antarctic Peninsula region. This may, however, reflect differences in initial food web analysis and data rather than real differences between the actual food webs.

The view that polar pelagic food webs are dominated by relatively few major pathways of energy flow involving a small number of mid-trophic level species was further developed for the wider Southern Ocean and polar regions more generally in Murphy et al. (2016). They noted that the crucial role that these key mid-trophic level species play in Southern Ocean food webs is related to their life history traits and the associated habitats in which they dominate. This led to the recommendation that development of understanding of polar food webs and the impact of change not only requires analyses of food webs but also quantitative studies and models of the life history processes of the key species (Murphy et al., 2016).

Major gaps remain in information on food web structure for most areas of the Southern Ocean and on the species involved in major flows of energy, the degree of sub-system connectivity (e.g., pelagic—benthic—sea-ice) and seasonal changes in interactions. An increased focus on the development of comparative analyses of food web structure will be crucial for improving understanding and generating and validating models for projecting the potential impacts of future change. A concerted and systematic effort is required to quantify and compare food web structure and variation throughout the Southern Ocean (Murphy et al., 2016; Newman et al., 2019). Such studies would also need to quantify the seasonal and interannual variation, food web subsidies (input of external energy: allochthonous production) and inter-food web connectivity (Murphy et al., 2007, 2013, 2016; Treasure et al., 2019). Understanding of the life-histories of many of the less-studied key mid-trophic level species is improving (e.g., Moteki et al., 2017; Queirós et al., 2018; Groeneveld et al., 2020; Kelly et al., 2020; Lin et al., 2020; Saunders et al., 2020; Zhu et al., 2020), however, for most species, quantitative understanding of life-cycles and population dynamics is still very limited (Constable et al., 2014, 2017). Models of distribution and population processes of these species are required to provide inputs into food web models.

ATTRIBUTES OF FOOD WEB MODELS FOR SUPPORTING POLICY

Assessing variability and change in Southern Ocean food webs and their underlying causes is required to inform policy and guide management. Constable et al. (2016) discuss four general, inter-related classes of ecosystem properties relevant to food web structure and function that may be used to develop statements on status and trends to inform policymaking:

1. *Primary production*: Production of organic material by photosynthetic and chemosynthetic autotrophs.
2. *Structure*: Abundances of taxa in space and time, related to patchiness of the organisms; size structure of populations and functional groups; relationships between biota (including trophic connections); and processes/responses that give rise to structure (note that the meaning of "structure" here encompasses both food web network structure and the structure of populations).
3. *Production*: Production of organic material at different trophic levels of the food web in a region. This may include factors that affect production such as non-trophic interactions and disease.
4. *Energy transfer*: Efficiency in transferring/utilising energy in the food web, which will need to account for spatial and temporal overlap of consumers and resources, which in turn will be affected by habitat characteristics and behaviour.

Climate-driven changes in physical and chemical conditions are expected to generate shifts in the distribution of organisms during the coming decades, which will affect food web structure as a consequence (e.g., Hill et al., 2012; Murphy et al., 2012, 2013, 2016; Ballerini et al., 2014; Suprenand and Ainsworth, 2017; Dahood et al., 2019; McCormack et al., 2019b). Developing projections of change in food web structures will require models that can represent the major alternative structures and energy transfer pathways that exist now or may occur in the future, requiring a nuanced understanding of potential shifts in the food web. Development of models for multiple regional food webs with a high degree of species resolution is useful for improving understanding. However, given the current relatively poor state of knowledge of the structure of food webs throughout much of the Southern Ocean, and the low resolution of models used to generate future projections, such high-resolution food web modelling is less useful at this time for considering large scale, Southern Ocean-wide responses to change. Instead, a more generalised and generic approach, in which the major components of food webs throughout the Southern Ocean can be represented in a single model structure, is likely to be more useful in generating projections and understanding the potential impacts of future change (Trebilco et al., 2020). In current ocean-scale models, biogeochemical processes and plankton dynamics are represented by generalised and often very simple models that can capture major structural and process variations. A similar approach has been proposed for Southern Ocean ecosystems, aiming to generate generic representations of the wider (meta-) food web that provides a basis for predicting the major pathways of energy flow and food web structure in different regions and the potential impacts of future change (Murphy et al., 2012, 2013, 2016).

A challenge for researchers and for observing systems is to identify and measure meaningful indicators of these ecosystem properties. So-called *ecosystem Essential Ocean Variables* (eEOVs) are defined as biological and ecological variables selected for regular measurement by observing systems, that can be used as indicators of status and change in ecosystem properties (as well as to attribute the causes of change), and that are feasible to collect at appropriate spatial and temporal scales (Constable et al., 2016). eEOVs can also inform the development of ecological models (e.g., qualitative, statistical/empirical, dynamic mathematical models) to support assessments. The identification of eEOVs for Southern Ocean ecosystems is an ongoing process (Newman et al., 2019; Muelbert et al., to be published in this research topic) and the identification of key data streams that constrain biological energy pathways by better characterising the transfer of mass through food webs, into carbon export, and into fish stocks has been identified as a priority to inform Southern Ocean ecosystem modelling, assessment, and management (Constable et al., 2017; Newman et al., 2019).

Indicators of food web processes of utility to policy making can also relate directly to Southern Ocean ecosystem services (Cavanagh et al., 2021). For example, Trebilco et al. (2020) considered four types of indicators relating to ecosystem services, using network models to investigate their response to perturbations in a simplified food web. These indicators included target species of fisheries (Antarctic krill and toothfish), predator groups of conservation importance (krill specialists such as Adelie penguins, and fish/squid specialists such as elephant seals), baleen whales and carbon export potential. Modelling changes in these indicators under different scenarios for climate change impacts and human use can help in identifying where there might be counterintuitive changes in ecosystem services due to feedback effects in Southern Ocean food webs.

CURRENT DEVELOPMENTS IN FOOD WEB MODELLING

Food web and ecosystem models have been fundamental and highly influential to the provision of robust, policy-relevant scientific advice about status and change, particularly in the context of ecosystem-based management of fisheries (Essington and Plagányi, 2014). Such models continue to be used in assessments of change, investigations of causality and the prediction of potential impacts. These models vary in their representation of ecological systems, ranging from conceptual models, qualitative mathematical models, statistical algorithms, and dynamic quantitative simulation models (see Fulton and Link, 2014 for a review of model types and applications) (**Figure 3**). They allow for the exploration of alternative conservation and management strategies in relation to achieving specified objectives. Through synthesising information and

representing an ecosystem or species in a coherent form, particular questions of interest can be explored to generate scientific advice.

Whilst modelling approaches and applications across the Southern Ocean vary considerably in scope (i.e., socio-ecological and spatial representation), each provide a degree of insight into various aspects of Southern Ocean food webs. This section discusses approaches to modelling Southern Ocean ecosystems, outlining the insights and gaps highlighted by various models (published following Murphy et al., 2012) in relation to food web structure, function, and change. The key limitations of these existing models and their potential to be integrated in support of Southern Ocean food web assessments to inform policy are evaluated in section "Concluding Remarks—Addressing Needs of Policy Makers."

Qualitative Modelling and Network Approaches

Qualitative Models

Qualitative models can help to capture, communicate, and represent knowledge of food webs. They can be used in a multi-step process starting with a simple conceptual model of the pair-wide relationships (e.g., feeding interactions) for specific research questions, to being used in "real time" workshop sessions to collectively pool knowledge across many researchers and stakeholders. To date, these models have been used for the Southern Ocean to identify interactions to aid quantitative model development and for assessing the consequences of simulated changes on interaction pathways (Melbourne-Thomas et al., 2013a; Goedegebuure et al., 2017; **Figure 3**). These types of models remain underutilised in the Southern Ocean context particularly for integrating and communicating food web research results along with other concepts and research results to aid policy decisions (e.g., Trebilco et al., 2020). Decision-support software (e.g., www.mentalmodeler.com; or QPress in R, Melbourne-Thomas et al., 2012; https://github.com/SWotherspoon/QPress) exist that allow a scenario interface to be easily developed to allow stakeholders to run and compare changes under different potential scenarios representing collective knowledge and then revisit and revise in the light of new information.

Ecological Network Models

Network science, meaning the study of interactions to quantify the structure and dynamics of complex systems such as food webs (see Box 1), has proved useful in evaluating the diverse effects of climate change (i.e., local extinctions, sea-ice dynamics) on the structure and functioning of Southern Ocean food webs (Jacob et al., 2011; Cordone et al., 2018; Rossi et al., 2019). A comparison between pelagic regions in the Arctic and Antarctic using standard network measures such as degree distribution (frequency distribution of the number of trophic links) suggests that the most connected prey species in Antarctic food webs, such as *E. superba* are more vulnerable to extinctions (de Santana et al., 2013). Network science suggests that many food webs exhibit the so-called "small-world" pattern that involves high clustering and short interaction path lengths between species conferring resistance to perturbations (such as species removal) (Montoya and Solé, 2002). Marina et al. (2018b) studied the prevalence of such a property in food webs of two Southern Ocean locations: Potter Cove (South Shetland Islands) and Weddell Sea. Interestingly, Potter Cove and the Weddell Sea food webs showed opposite results, meaning that the latter network presents a "small-world" pattern while the former does not. This implies that understanding how each local food web self-organises is essential to gain precise knowledge about the impact of perturbations (e.g., climate change) on local food web structure and function.

Two recent studies of Arctic food webs using a network science approach suggest that polar food webs can self-organise through new interaction pathways. What had previously been considered as a system-wide regime shift with changing climate and species invasion was shown to be limited to changes in a limited set of species interactions (Yletyinen et al., 2016). In another study, the core ecological processes of an Arctic food web have been shown to be resilient to cumulative perturbations (ocean warming, decreasing sea-ice and arrival of invasive species) by the self-organisation of direct and indirect species prey interactions. Both studies caution that the resilience may be short-lived (Griffith et al., 2019; Yletyinen, 2019). Resilience in this case is defined from a complex adaptive systems perspective (Hagstrom and Levin, 2017) that the resilience of food webs to on-going perturbations emerges from the dynamic self-organisation of small-scale interactions. It remains unclear if Antarctic food webs show a similar pattern to perturbation. A probabilistic model that accounts for trophic structure, colonisation, and extinction events from the Antarctic metaweb suggests that the modification of habitats due to climate change will probably modify individual populations distributions and abundances (Saravia et al., 2021). However, food web structure could rearrange without producing abrupt changes (regime shifts) (Saravia et al., 2021). This may be due to internal dynamical feedback (Suweis and D'Odorico, 2014; Ward et al., 2018).

Dynamic Modelling

Modelling Key Species and Trophic Interactions

Developing a suite of models that vary in scope and their spatial and socio-ecological representations (**Figure 3**) is required to support management approaches in complex ecological systems (Murphy et al., 2012; Fulton et al., 2015; Melbourne-Thomas et al., 2017). Through offering varying representations of ecological scales (e.g., individual, local, regional, global) and dimensions (e.g., physical, ecological, social, management) (**Figure 3**), integrated modelling approaches can provide flexibility for supporting decision making and for constraining the abstracted views developed for an ecosystem (Murphy et al., 2012; Melbourne-Thomas et al., 2017). Insights gained from models that focus on particular species of interest (see **Table 2** for Southern Ocean examples) can provide knowledge into key food web processes and guide the development and implementation of multi-species management tools (Plagányi, 2007).

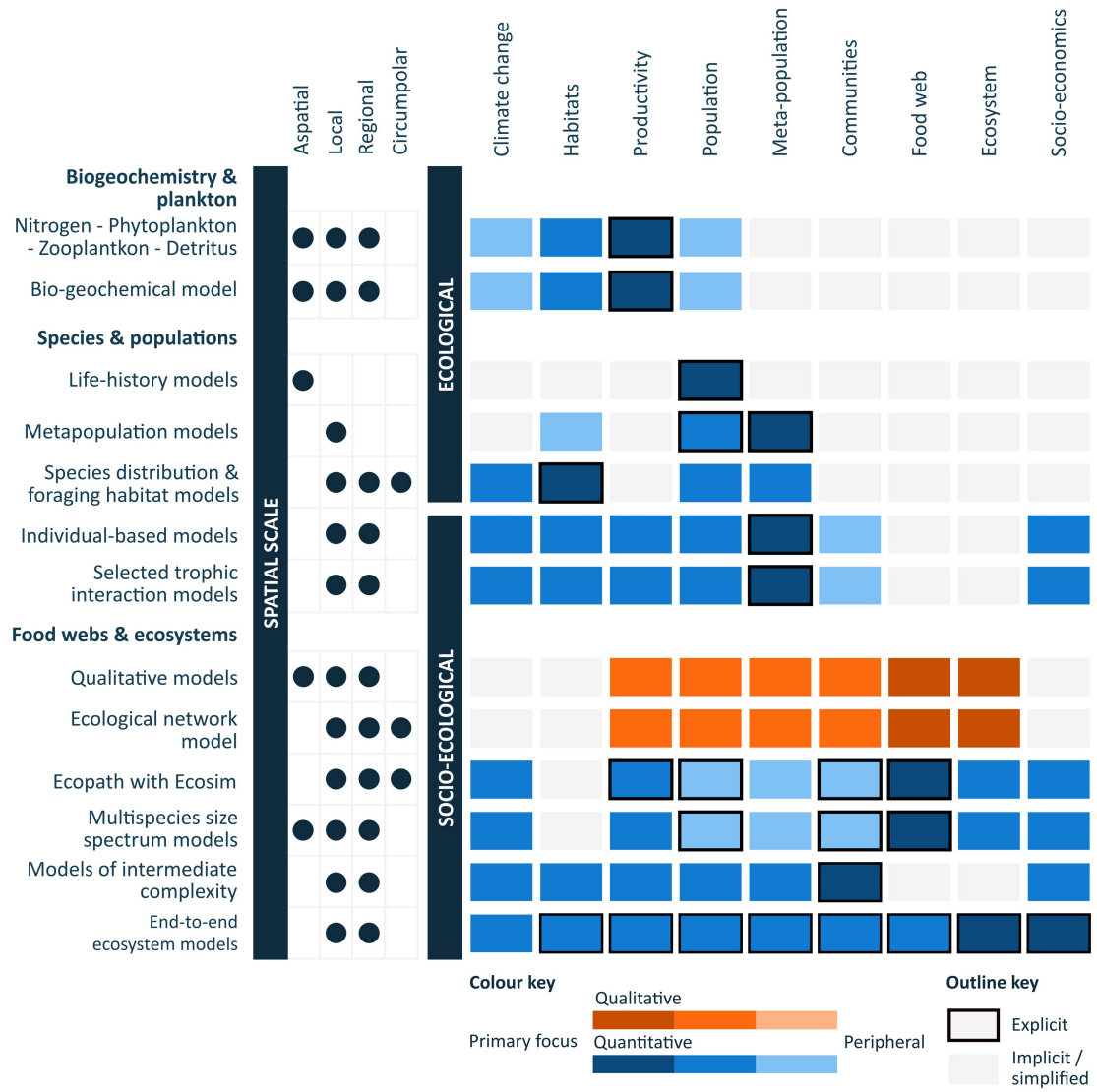


FIGURE 3 | Summary of various ecological modelling approaches and the associated spatial and socio-ecological scales at which they can be applied (concept visualisation based on Fulton and Link, 2014; Melbourne-Thomas et al., 2017). Coloured rectangles indicate the inclusion and level of focus (i.e., dark—primary focus, light—peripheral) of each of the components for the summarised qualitative (orange) and quantitative (blue) models. Reference to spatial scales relate to Southern Ocean applications.

In **Table 2** we assess the spatial coverage of Southern Ocean focussed models published since the last assessment of Southern Ocean food webs in 2012 (see Murphy et al., 2012), with respect to each MEASO sector (**Figure 1**). **Table 2** also distinguishes between the following classes of models, all of which can be used to inform the development of food web models and/or to validate them:

i) habitat models (including species distribution models, niche models and foraging habitat models) that might influence interpretation of food web models i.e., "where might a particular species do best";
ii) population dynamics models, including both non-spatial (life-history modelling) and spatial (metapopulation) approaches e.g., matrix models and stock assessment models; and
iii) trophic models (including predator-prey models and Models of Intermediate Complexity (MICE; Plagányi et al., 2014) that focus on a particular species and represent a subset of the food web.

Bridging the gap between single-species assessment models and more comprehensive ecosystem models are those that consider system operation and change based on a subset of the ecosystem and key processes, i.e., selected trophic interaction models (such as predator–prey models) and MICE models (**Figure 3**). These models have a long history of use in the Southern Ocean, particularly for evaluating the nature and

TABLE 2 | Examples of published models (since 2012) for the Southern Ocean which capture habitat, population and trophic interactions for key species (not fully comprehensive).

MEASO sector	Model domain/region	Modelling approach	Model purpose	Focus taxa	Reference
Circumpolar	Circumpolar	Population dynamics	Project climate	Emperor penguins	Jenouvrier et al., 2014
Circumpolar	Circumpolar (Global)	Trophic (foodweb sub-set)	Biogeochemistry (WOMBAT)	Phyto-plankton	Oke et al., 2013
Circumpolar	Circumpolar (aspatial)	Trophic (foodweb sub-set)	Nutrient recycling through trophic interactions	Phyto-plankton, krill, whales	Ratnarajah et al., 2015
Circumpolar	Circumpolar	Trophic (foodweb sub-set)	Harvesting impacts	Baleen whales	Tulloch et al., 2017
Circumpolar	Circumpolar	Habitat (growth rate)	Krill growth potential and impacts of change	Krill	Murphy et al., 2017
Circumpolar	Circumpolar	Trophic (Trophic MICE model with NPZD model)	Climate change impacts	Baleen whales, krill	Tulloch et al., 2019
Circumpolar	Circumpolar	Niche model	Estimate present and future distribution of Myctophids	Myctophids	Freer et al., 2019
Circumpolar	Circumpolar (spatial)	Habitat	Climate change impacts on growth potential	Antarctic krill	Veytia et al., 2020
Circumpolar	Circumpolar	Individual-based model	Metazoan biology	Salps	Henschke et al., 2018
Circumpolar	Circumpolar	Habitat	Krill spawning habitat quality to understand source and sink areas	Antarctic krill	Green et al., 2021
Atlantic	West Antarctic Peninsula	Population dynamics	Spatial population dynamcis	Salps	Groeneveld et al., 2020
Atlantic	West Antarctic Peninsula	Habitat	Advection pathways	Krill	Piñones et al., 2013
Atlantic	West Antarctic Peninsula	Foraging habitat model	Project future foraging habitat for Southern Ocean predator	Crabeater seal, Antarctic krill	Hückstädt et al., 2020
Atlantic	Scotia Sea	Trophic (foodweb sub-set)	Feedback management	Krill, predators, fishery	Hill and Cannon, 2013
Atlantic	Scotia Sea, southern Drake Passage	Trophic (foodweb sub-set)	Sensitivity analysis	Krill, predators, fishery	Hill and Matthews, 2013
Atlantic	Scotia Sea	Habitat	Climate change impacts	Krill	Hill et al., 2013
Atlantic	Scotia Sea	Trophic (foodweb sub-set)	Risk assessment	Krill, predators, fishery	Plagányi and Butterworth, 2012
Atlantic	Scotia Sea and southern Drake Passage	Trophic (foodweb sub-set)	Risk assessment	Krill, predators, fishery	Watters et al., 2013
Atlantic	Scotia Sea	Habitat Trophic (foodweb sub-set)	Climate change impacts	Krill, predators, fishery	Klein et al., 2018
Central Indian	Aspatial but fit to Indian sector	Trophic (foodweb sub-set)	NPZD	Plankton	Melbourne-Thomas et al., 2013b
Central Indian	Kerguelen Plateau and surrounding area (spatial)	Foraging behaviour	Simulated prey fields (micronekton) as a predictor for predator foraging behaviour	Southern elephant seal, mesopelagic prey	Green et al., 2020
Central Indian	East Indian	Foraging behaviour	Simulate energy use and life history of a Southern Ocean predator	Southern elephant seal (females)	Goedegebuure et al., 2018
West Pacific	Ross Sea	Population dynamics	Stock assessment	Antarctic toothfish	Mormede et al., 2014a
West Pacific	Ross Sea	Population dynamics	Spatial population dynamics	Antarctic toothfish	Mormede et al., 2014b
West Pacific	Ross Sea	Trophic (foodweb sub-set)	Mesopredator release	Antarctic toothfish, silverfish, Adelie penguins	Pinkerton et al., 2016

The colour of each row corresponds to the MEASO sectors in ***Figure 1****.*

impact of fishing on predators that share a fished resource. Beginning with the work of May (1979) and the subsequent agreement for the Convention on the Conservation of Marine Living Resources (CCAMLR), explicit acknowledgement of the importance of maintaining the integrity of food webs to support dependent species was developed, laying the foundation for the input of modelled insights into management and policy decisions globally (Plagányi, 2007).

Historically, the nature and impact of fishing on predators that share a fished resource has been an important consideration

in ecosystem-based fisheries management (Constable, 2001). In the Antarctic, predator–prey modelling procedures have been used to assess the impacts of Antarctic krill harvesting on krill predator populations and to inform subsequent recommendations for setting annual krill catch levels. For example, initial modelling estimated the level of krill harvesting that would reduce the availability of krill and hence impact predator populations (Thomson et al., 2000). More recently, modelling procedures have been developed to consider these krill predation issues and advise on the spatial allocation of krill catches (e.g., in the Scotia Sea; Plagányi and Butterworth, 2012). Watters et al. (2013) developed a dynamic model of Antarctic krill, its predators and fishery, to explore potential krill fisheries impacts in the Southwest Atlantic. Klein et al. (2018) modified the model to simulate ocean warming impacts on krill growth by incorporating the results of Hill et al. (2013). These results suggested spatial disconnect between the strongest potential impacts of krill biomass and those on the abundance of its predators.

Whilst there is a general acceptance that parameter estimates for krill are often highly uncertain and subject to spatial, seasonal and interannual variability (Hill et al., 2006; Atkinson et al., 2012a), many models have developed innovative methods for dealing with such uncertainty (Hill et al., 2012; Watters et al., 2013). For example, Plagányi and Butterworth (2012) used models that are composed of alternative combinations of parameters to bound the uncertainty. Nevertheless, better understanding of the fine-scale interactions between both predators and fisheries with krill in relation to fishing operations and foraging trips (Cresswell et al., 2008; Waluda et al., 2010) will help refine some of these uncertainties along with identifying critical gaps in representations of krill in food-web models (Atkinson et al., 2012a).

Whole-of-Food Web Models

Ecopath with Ecosim (EwE) (Christensen and Walters, 2004) has been one of the most widely applied modelling frameworks for assessing the impacts of fishing and environmental change on Southern Ocean food webs. Indeed, there are only a few examples of whole-of-food web models for the Southern Ocean that use modelling approaches other than EwE (see **Table 3**), and there are no published whole-of-ecosystem models for any region of the Southern Ocean. There are many approaches to evaluating how change propagates through modelled networks using EwE including manipulation of specific ecosystem components, analytical methods (e.g., metrics built into the EwE software) and more intensive methods such as the forcing of parameters in dynamic *Ecosim* models to represent the direct impacts of a specified driver.

Based on mass-balance constraints, *Ecopath* describes food webs in terms of the biomass, consumption, production and diets of species or life stages, which can be aggregated into functional groups according to trophic similarity and/or data availability. Applications of *Ecopath* in the Southern Ocean (see **Table 3**) have contributed significantly to our understanding of food web characteristics and emerging patterns following change across multiple regions and latitudes. Commonly characterised as a top-down model (i.e., trophic interactions are represented in relation to predator diets), *Ecopath* can be inverted to represent interactions in terms of the fate of prey biomass (Steele and Ruzicka, 2011). This simplified calculation can help tease apart the response of higher trophic levels to changes exhibited by lower trophic levels. Ballerini et al. (2014) used this approach to explore five scenarios of change in an Ecopath dataset representing an area adjacent to the western Antarctic Peninsula. The simulated changes included reduction in the size of unicellular phytoplankton, which predicted a reduced production of Antarctic krill and the top predators that feed on it.

An alternative approach is to manipulate the biomass of functional groups within an Ecopath dataset and to introduce compensatory changes elsewhere in the food web during the balancing process (Hill et al., 2012). McCormack et al. (2019b) and Saunders et al. (2019) used this approach to examine the consequences of reduced krill biomass for other trophic pathways in the Scotia Sea and Prydz Bay. Whereas the krill pathway remained dominant in the former, pathways involving squid and fish became dominant in the latter area. Similarly, the Mixed Trophic Impact (MTI) metric built into the EwE software provides an indication of the effect of a change in the biomass of one functional group on another (Libralato et al., 2006; Christensen et al., 2008). Subramaniam et al. (2020a) used this method to explore the direct and indirect impacts of the Patagonian toothfish (*Dissostichus eleginoides*) and mackeral icefish (*Champsocephalus gunnari*) fisheries activities (catch and by-catch) on trophic interactions on the Kerguelen Plateau. This identified the functional groups that frequently interact with fishery target species, and the importance of fished species in the transfer of energy through the food web.

Several studies have used *Ecosim* to explore the time-dynamic variations of Southern Ocean food webs (Surma et al., 2014; Suprenand and Ainsworth, 2017; Dahood et al., 2019; Subramaniam et al., 2020b). This approach fits models from *Ecopath* to time-series and/or fisheries data for functional groups (Christensen et al., 2008). Most models are fitted to the data by manipulating how consumption is influenced by changes in predator and prey biomass (vulnerability parameter; Christensen et al., 2008) while others also use forcing functions (e.g., Dahood et al., 2019). Since 2012, *Ecosim* has been used to explore the effects of whaling and bottom-up forcing, concluding that they may have had counteracting impacts on krill biomass (Surma et al., 2014). Suprenand and Ainsworth (2017) explored potential future change, with most scenarios resulting in reduced biodiversity and increased trophic level. Dahood et al. (2019) evaluated changes to sea-ice cover as an environmental driver of predator–prey interactions, finding that the sea-ice regime was needed to recreate observed biomass trends and Subramaniam et al. (2020b) correlated time-dynamic food web interactions with environmental variables, highlighting sea surface temperature, zonal wind, and the Southern Annular Mode as important drivers of ecosystem change.

An additional component of EwE is *Ecospace*, which simulates *Ecosim* models over a two-dimensional grid using habitat maps and movement rates (see Christensen et al., 2014). Ecospace

TABLE 3 | Examples of Southern Ocean EwE and whole-of-food web models published since 2012 (not fully comprehensive).

MEASO sector	Model domain/region	Modelling approach	Model purpose (year/s represented)	Reference
Circumpolar	Circumpolar	Ecopath with Ecosim	Food web exploration (Ecopath 1900; Ecosim 1900–2008)	Surma et al., 2014
Circumpolar	Nearshore (shelf); Circumpolar (aspatial)	Conservative normal food web	Parameter refinement	Bates et al., 2015
Circumpolar	Circum-Antarctic	Ecopath	Food web exploration, iron balance (1900, 2008)	Maldonado et al., 2016
East Pacific	West Antarctic Peninsula	Inverse food web	Carbon flux	Sailley et al., 2013
East Pacific	West Antarctic Peninsula	Ecopath	Food web exploration (2001, 2002)	Ballerini et al., 2014
East Pacific	West Antarctic Peninsula	Inverse food web	Biogeochemical fluxes	Ducklow et al., 2015
East Pacific	West Antarctic Peninsula	Ecopath with Ecosim	Climate change impacts (Ecopath 1992–2002; Ecosim 1996–2012)	Dahood et al., 2019
East Pacific	Antarctic Peninsula	Ecopath with Ecosim	Food web exploration (Ecopath 1978, 2010; Ecosim scenarios 2010–2050)	Suprenand and Ainsworth, 2017 (see also Hoover et al., 2012)
Central Indian	Prince Edward Islands	Ecopath	Food web exploration (1960s, 1980s, 2000s)	Gurney et al., 2014
Central Indian	Prince Edward Islands	ECOTRAN	Food web exploration	Treasure et al., 2015
Central Indian	Prince Edward Islands	ECOTRAN	Food web exploration	Treasure et al., 2019
Central Indian	Prydz Bay	Ecopath	Explore alternative energy pathways (2010s)	McCormack et al., 2019b
Central Indian	Kerguelen Plateau	Ecopath with Ecosim	Food web exploration, harvesting impacts and environmental drivers of ecosystem change (Ecopath average state 2008–2018; Ecosim 1986–2018)	Subramaniam et al., 2020a,b
West Pacific	Ross Sea	RSTM/Ecopath	Harvesting impacts	Pinkerton et al., 2010

The colour of each row corresponds to the MEASO sectors illustrated in ***Figure 1****.*

presents an advantage and incentive to build EwE models as food web models that incorporate spatial information are few in the Southern Ocean. One published spatially explicit food web model currently exists for the Southern Ocean, exploring scenarios relating to ecosystem-based fisheries management (Dahood et al., 2020). The model evaluated scenarios regarding the designation of marine protected areas and future changes in sea ice and krill fishing effort. Results from the study indicate that establishing marine protected areas in the right locations could be important for mitigating the negative effects of climate change.

Steps toward addressing model reliability and parameter uncertainty have resulted in additional tools, guides, and improvements to the EwE software. Heymans et al. (2016) provide guidelines for testing and reviewing EwE models for management, detailing pre-balancing diagnostics and thermodynamic and ecological rules for balancing models. Ainsworth and Walters (2015) outline the top ten mistakes made by EwE modellers to help new users side-step pitfalls. Current tools address uncertainties for management strategy evaluation (Steenbeek et al., 2016) and find best statistical fits to *Ecosim* input (stepwise fitting procedure, Scott et al., 2016). A new development addresses EwE-wide parameter uncertainty by recording alternate mass-balanced parameter sets in the Monte Carlo routine (Ecosampler; Steenbeek et al., 2018). These guidelines and improvements to the software provide a path forward for developing reliable models for ecosystem-based management, including multi-model ensemble approaches to predict ecosystem response to change (Heymans et al., 2016; Hill et al., 2021).

Although the suite of regional food web models has expanded since 2012, the only attempt at a circumpolar food web model (de Santana et al., 2013) is based on a simple interrogation of the Southern Ocean Diet and Energetics Database (Scientific Committee on Antarctic Research, 2020). This is a static network model (see section "Ecological Network Models") that considers only the links between species, with no possibilities to compensate for the significant spatial heterogeneity in sampling effort. As suggested previously a significant improvement for this model would be to consider weights for the links based on the probability of interactions due to species distributions (Poisot et al., 2015). Most Southern Ocean food web models consider relatively small scales whereas the dynamic models often consider regional (>1 million km^2) or circumpolar (>10 million km^2) scales. The food web models predominantly consider continental shelf ecosystems. This reflects data availability: intensive ecosystem studies across multiple trophic scales tend to be localised within the area of interest of particular Antarctic operators, which in turn tends to be associated with land-based research stations. The SCAR Southern Ocean Diet and Energetics Database, collated by the SCAR Expert Groups on Antarctic Biodiversity Informatics (EG-ABI) and Birds and Marine Mammals (EG-BAMM), provides data related to diet and energy flow from conventional (e.g., gut content) and modern (e.g., molecular) studies, stable isotopes, fatty acids, and energetic

TABLE 4 | Summary of progress in the development of Southern Ocean food web models to meet three different approaches to informing policy makers and supporting decision making—testing outcomes of future scenarios, support of decision-making, and assessment of risks.

	Aspects of need	Progress	Requirements to meet each aspect of need
Testing outcomes of scenarios	Regional coverage	● ● ● ○ ○	Requires adequate coverage of food web models across all Southern Ocean regions. Currently, three out of five of the MEASO sectors have models, and coverage is skewed to Atlantic sector (see **Tables 2**, **3** for current coverage)
	Whole of ecosystem representation	● ● ○ ○ ○	Requires whole of ecosystem models to be available. Better representation of pathways alternative to the krill pathway is needed. There are currently no published whole-of-ecosystem models (that incorporate physics, chemistry, and the entire food web, either coupled or through end-to-end modelling)
	Representation of realistic future scenarios	● ○ ○ ○ ○	Requires agreed scenarios and available forcing data (e.g., see Cavanagh et al., 2017), specifically require improved earth system modelling for the Southern Ocean and means to downscale to appropriate ecological scales
	Enabling assessments of spatial variation	● ● ○ ○ ○	Requires spatially structured models allowing reasonable representation of spatial dependencies of predators and prey and their covariation (e.g., see McCormack et al., 2020)
Support for decision making	Ability to test food web performance in management systems	● ● ○ ○ ○	Requires models in which predator and prey dynamics are realistic in their co-dependency and covariation, despite that these may operate at different spatial and temporal scales
	Climate change context considered	● ○ ○ ○ ○	Requires available models to test the sensitivity of food webs to decision rules under climate change scenarios
	Relevant scales for decision-making	● ● ○ ○ ○	Requires that the spatial resolution and overall spatial scale of models is suitable for scales of decision-making
Assessment of risks	Capacity to address uncertainty in evaluation of risks	● ○ ○ ○ ○	Requires model uncertainty to be characterised and translated in evaluation of risk
	Capacity to evaluate spatial risk	● ○ ○ ○ ○	Requires representation of spatial connectivity (and down-stream/up-stream effects)
	Capacity to evaluate ecosystem-level risk	● ○ ○ ○ ○	Requires whole of ecosystem models + methods to consider ecosystem-level risk
General model suitability	Validation	● ○ ○ ○ ○	Requires models to have their behaviour shown to be satisfactorily for the task for the right reasons. If they are intended to represent a known period of time or a known region then their behaviour needs to be assessed against observations from that time and place
	Verification	● ● ○ ○ ○	Requires model code to be verified to be operating in the manner expected, particularly relevant for models that are not widely used

Progress is indicated by a dot scale-bar (1 filled dot, minimal progress - 5 filled dots, significant progress). General requirements for assessing suitability of models are also presented.

content. At larger spatial scales, the available data are limited to remote sensed chlorophyll data and population or distribution estimates for high profile taxa including Antarctic krill, marine mammals, and penguins. Despite the higher level of detail at intensively studied sites, most Southern Ocean food web models incorporate parameter estimates which are not based on direct observation of the modelled site.

Building on Murphy et al. (2012, 2013), Murphy et al. (2016) suggest that development of a generic food web model approach (i.e., representative of all Southern Ocean regions) is both possible and useful in analyses of Southern Ocean food webs. A number of potential general model structures for food webs have been suggested, involving different sets of species or functional groups or alternative representations of groups of organisms and interactions (e.g., based on classifications of guilds or organism size) (Murphy et al., 2012, 2013, 2016). These provide a valuable basis for the development of generic computational models of Southern Ocean food webs. The aim of such an approach is to apply a single model throughout the Southern Ocean, and on the basis of a series of environmental constraints/drivers (physical and biogeochemical), identify the major structural form of regional food webs and the main species/groups involved in the major pathways of energy flow. Such an approach can be extended to include more complex representations of the food web if there is sufficient understanding and data to validate model outcomes.

While the on-going development of more complex food web models is providing greater understanding of Southern Ocean ecosystems, there is also a growing awareness, particularly from management, of the uncertainties of this approach. Given the complexity and associated uncertainty, ecosystem models face many challenges which are complicated further by the additional uncertainties associated with representing environmental and harvesting scenarios (Travers et al., 2007; Plagányi et al., 2011). General uncertainties include the lack of observational data, concerns on the ability of such models to capture the

underlying ecosystem dynamics and the ability to identify emergent behaviour, regime shifts and evolution of food web structure and function (Griffith and Fulton, 2014).

The interactions between species are generally defined by correlations. If the underlying dynamics are non-linear then mirage correlations can occur in which the causally connected interaction can be positive or negative or neutral over different periods of time (Fogarty et al., 2016). The "dynamical systems" perspective offers an alternative and complementary approach to viewing marine food webs (Griffith, 2020). It assumes that the food web results from the complex interplay between multiple processes. Viewing Southern Ocean food webs in this way allows us to leverage some powerful approaches from dynamical systems theory. These concepts are particularly useful in the Southern Ocean context where observing all the species that inhabit an ecosystem is near impossible, and knowledge of which of the observed variables are relevant and causally related is lacking. Rather than attempting to investigate system dynamics through complex equation-based models (e.g., *Ecopath* models) that explicitly account for each interaction, the "non-linear dynamic" perspective draws on the concept from state-space reconstruction which implies that any variable in a state-dependent dynamic system encodes the history of its interactions with other system variables (Munch et al., 2020). That is, the data itself provides the evidentiary portal to identifying the causal relationships in complex real-world system dynamics. Previously, this approach has been limited by requiring long-time series. Recent work shows that integrating an equation free non-linear approach with a Bayesian model can overcome the problem of short ecological time series (Johnson et al., 2020). To many in marine management, this concept is challenging despite recent work demonstrating the utility of this approach to a wide range of topics in marine ecology (Griffith, 2020). In future work, sensibly applied and complementary to existing Southern Ocean food web models, this approach may provide valuable insights into understanding and predicting causal food web interactions.

CONCLUDING REMARKS—ADDRESSING NEEDS OF POLICY MAKERS

Policy makers need information on how changing climate and environmental drivers (Henley et al., 2020; Morley et al., 2020) and local drivers, such as fisheries and pollution (Grant et al., 2021), will impact on the conservation and long-term maintenance of Southern Ocean species, biodiversity and productivity. Modelling to date has shown how these drivers have cascading effects through food webs and ecosystems. The parallel changes that are occurring through climate change, increasing ocean acidification, increasing krill fishing, and recovery of whales means that not only are individual species being affected but, also, the relative importance of different energy pathways may change (Trebilco et al., 2020). Policy makers will need to develop ecosystem-based strategies for achieving their conservation and sustainability objectives that take account of the changing ecosystems (Constable et al., 2017). A good example of this requirement is embedded in Article II of CCAMLR, such that fisheries must be managed in such a way to ensure.

"prevention of changes or minimisation of the risk of changes in the marine ecosystem which are not potentially reversible over two or three decades, taking into account the state of available knowledge of the direct and indirect impact of harvesting, the effect of the introduction of alien species, the effects of associated activities on the marine ecosystem and of the effects of environmental changes, with the aim of making possible the sustained conservation of Antarctic marine living resources."

Changing system productivity is naturally embedded in existing approaches to managing fisheries under CCAMLR (Constable, 2001, 2002). However, the potential for changing food web structures could lead to unwanted outcomes if they are not countenanced, not only in terms of shifting the relative importance of production of different fished species but also in the conservation of biodiversity generally (Constable et al., 2017). Food web and ecosystem models could be used to support policy makers at present but there is much room for improvement, particularly with respect to the challenges of climate change.

Based on our review here, we provide an expert synthesis to summarise the state of ecosystem models to support policy makers in **Table 4**. We also summarise the expected requirements of models that may be used in three different forms of advice. The use of food web and ecosystem models for testing specific scenarios is becoming common place, such as through FishMIP (Tittensor et al., 2018) or in specific circumstances (Holsman et al., 2019). Typically, future scenarios are from Earth System models. As a result, end-to-end modelling approaches are needed to simulate and predict changes in the state of marine ecosystems and remain to be developed for the Southern Ocean. Testing scenarios helps form hypotheses about, or frame, plausible futures for which management strategies need to be developed. End-to-end ecosystem models, or simpler versions of them, can be used to evaluate management strategies and for assessing risks of failing to meet objectives (Constable, 2002, 2011; Melbourne-Thomas et al., 2017; Plagányi and Fulton, 2017). A great challenge in these cases is to provide satisfactory representation but with computational economy in order to explore the many and varied uncertainties that plague decision-makers. Novel representations of the properties and dynamics of ecosystems can be very useful in these circumstances if they satisfactorily represent the decision environment and its relationship to the real world (Griffith, 2020).

Table 4 shows that considerable effort and resources remain to be invested in developing ecosystem and food web models that satisfactorily represent the whole of the ecosystem in a manner suitable for policy makers. A major advance since Murphy et al. (2012) has been better characterisation of food webs around the Southern Ocean. However, three critical challenges remain to be addressed by the scientific community and policy makers. First, end-to-end ecosystem models or food web models coupled to Earth System model outputs are urgently needed for developing future scenarios under climate change, and to frame the ecosystem issues for policy makers to address in the coming decades. A second challenge, and no less important,

is to establish sustained observations of food webs in more than just the Antarctic Peninsula and Scotia Arc (Newman et al., 2019). Without these observations, it will be very difficult to detect changes in food webs, validate ecosystem models of the region and support management in areas other than the south Atlantic and Antarctic Peninsula. The third challenge is to establish processes and procedures for validating ecosystem and food web models and for verifying that their behaviours are "right for the right reasons," a process that still challenges the Earth System modelling community (Russell et al., 2018). The importance of validation and verification cannot be overstated. Russell et al. (2018) articulates very well that fitting a model to data, while centrally important to the validation process, does not guarantee that the model will provide satisfactory projections into the future. Models need to also have behaviours of state variables as well as spatial and temporal correlations amongst variables that make sense when compared to known broader patterns, understanding, and theory. With appropriate validation and weighting of each model's utility for the task, ensembles of different models can help with understanding the impacts of model uncertainty on the conclusion about different scenarios.

Managers rely on models, heuristic or formal, to make decisions. Ecosystem models enable conversations about what processes are important, how species interact and where the greatest risks and vulnerability to ecosystem structure and function may lie. They also allow scientists and policy makers to frame the possible futures that we face. Earth System models point to the vulnerability and diminution of polar systems. At present, we can foresee how species will be affected by physical changes and what the consequent pathways of effects might be. In the absence of ecosystem models, we are unable to foresee what the system-level response will be for Southern Ocean ecosystems once climate recovery begins.

AUTHOR CONTRIBUTIONS

SM led the development and writing of the manuscript, figures, and tables. SM, JM-T, RT, and AC developed the approach. All authors contributed text to the manuscript and input to the figures and tables.

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Status, Change, and Futures of Zooplankton in the Southern Ocean

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In the Southern Ocean, several zooplankton taxonomic groups, euphausiids, copepods, salps and pteropods, are notable because of their biomass and abundance and their roles in maintaining food webs and ecosystem structure and function, including the provision of globally important ecosystem services. These groups are consumers of microbes, primary and secondary producers, and are prey for fishes, cephalopods, seabirds, and marine mammals. In providing the link between microbes, primary production, and higher trophic levels these taxa influence energy flows, biological production and biomass, biogeochemical cycles, carbon flux and food web interactions thereby modulating the structure and functioning of ecosystems. Additionally, Antarctic krill (*Euphausia superba*) and various fish species are harvested by international fisheries. Global and local drivers of change are expected to affect the dynamics of key zooplankton species, which may have potentially profound and wide-ranging implications for Southern Ocean ecosystems and the services they provide. Here

we assess the current understanding of the dominant metazoan zooplankton within the Southern Ocean, including Antarctic krill and other key euphausiid, copepod, salp and pteropod species. We provide a systematic overview of observed and potential future responses of these taxa to a changing Southern Ocean and the functional relationships by which drivers may impact them. To support future ecosystem assessments and conservation and management strategies, we also identify priorities for Southern Ocean zooplankton research.

Keywords: zooplankton, ecosystems, Southern Ocean, global change, projections, ecosystem services, management, conservation

INTRODUCTION

Metazoan zooplankton (hereafter zooplankton) are globally important. They are ubiquitous and abundant in the world's oceans (Bar-On et al., 2018; Chiba et al., 2018), playing a critical role in the structure and function (Odum, 1964, 1969) of marine ecosystems, including 'ecosystem services' that benefit humans (Millennium Ecosystem Assessment, 2005; Simcock, 2017; Bebianno et al., 2021a,b). Zooplankton are pivotal in the cycling of carbon and nutrients, regulating climate, supporting primary and secondary production, maintaining biodiversity, food web configurations and balance among trophic levels, and sustaining fisheries production, tourism, and human communities (Richardson, 2008; Keister et al., 2012; Pinkerton et al., 2020). Their central trophic position as grazers and prey means they directly affect biomass, structure of food webs, and modulate ecosystem functioning. In some regions, zooplankton are the major grazers and can influence the amount of production that reaches mid and higher trophic level consumers, including fish, squid, marine mammals, and birds. Through the regeneration of nitrogen, zooplankton enhance phytoplankton production (Richardson, 2008). Processes associated with feeding, vertical migration, and mortality also support microbial production and facilitate the transfer of organic matter to the deep ocean: contributing to benthic communities (Ruhl and Smith, 2004; Schnack-Schiel and Isla, 2005), carbon drawdown, storage and sequestration, dimethyl sulfide production (Daly and DiTullio, 1996) and hence a negative (mitigating) feedback on climate change (Jónasdóttir et al., 2015; Steinberg et al., 2017; Barnes et al., 2018).

Like all ecological communities, zooplankton communities are shaped by a combination of intrinsic biotic interactions (e.g., competition, food web interactions) and extrinsic abiotic interactions associated with the influence of environmental stressors (or drivers) on individual species. Several attributes of zooplankton, including poikilothermy, stenothermy, small size (20 μm to 20 mm in length in the case of micro- and mesozooplankton), short generation times and lifecycles (generally <1 year), and complex life histories (often passing through a range of ontogenic stages), render them very sensitive to environmental drivers (Hays et al., 2005; Richardson, 2008). This can be expressed as alterations in, for example, behavior, physiology, phenology, productivity, abundances and shifts in species ranges and distribution, all of which modify zooplankton populations and community dynamics (i.e., changes in population or community structure, dominance, and distribution patterns) and their trophic interactions with other taxa over a range of space and time scales. Through these alterations the structure and function of whole ecosystems can be modified (Doney et al., 2012; Malhi et al., 2020). Zooplankton are therefore not only susceptible to human-induced climate change and concurrent processes (a significant component of global change), but they also propagate climate signals through ecosystems and feedback to biogeochemical cycles, carbon sequestration, and the global climate system. As such they are considered good indicators of water mass types and environmental change (Chiba et al., 2018), and are integral to interpreting the responses of marine ecosystems to climate change, and developing adaptation and mitigation strategies. In addition to observed impacts of natural environmental variability, there are many diverse examples of the impacts of human-induced climate change and other anthropogenic stressors (e.g., pollutants, fisheries) on zooplankton that are having profound and complex ecosystem-level consequences (see Richardson, 2008; Doney et al., 2012; Murphy et al., 2016; Beaugrand and Kirby, 2018).

To enhance understanding and predictions of Earth System functioning and global change under the mounting pressures of the Anthropocene (IPCC, 2018, 2019), it is imperative that we understand the role of zooplankton within the world's oceans under present conditions, the potential impacts of future change and associated risks (Reid et al., 2003; Atkinson et al., 2012; Constable et al., 2014b; Pecuchet et al., 2020; Kohlbach et al., 2021), and adequately represent zooplankton dynamics in Earth System Models (ESMs) (Le Quéré et al., 2005, 2016; Buitenhuis et al., 2010). This requires specific knowledge of the complex interactions and mechanisms associated with zooplankton dynamics, their sensitivity to drivers of change, and the resultant effects on ecosystems and socioeconomics. Appreciation of these aspects at local, regional and oceanic scales are essential in underpinning decision-making for regulating human activities that impact ecosystems, conserving and managing ecosystems, and planning for the response to future change to promote the resilience and viability of marine ecosystems (Malhi et al., 2020).

Antarctica and the Southern Ocean are inherent to the Earth System. In addition to the perturbations that have already impacted the Southern Ocean, major changes in its habitats and ecosystems are expected over the coming years

in response to increased pressures from a range of global (see Morley et al., 2020) and local environmental drivers (see Grant et al., 2021), the majority of which have an anthropogenic component (Murphy et al., 2007b; Rogers et al., 2007; Clarke et al., 2012; Constable et al., 2014b; Gutt et al., 2015; Chown and Brooks, 2019; Kennicutt et al., 2019). Owing to the extensive physical, biogeochemical, and ecological connectivity between Southern Ocean ecosystems and the global ocean, future changes in the structure and functioning of these ecosystems will also have consequences throughout the Earth System (Henley et al., 2020; Murphy et al., 2021). To predict how Southern Ocean ecosystems will respond to global change and the implications for regional and Earth System functioning and decision-making, assessments of the sensitivity of Southern Ocean zooplankton to changes in these drivers are necessary (Constable et al., 2014a,b). Moreover, changes in zooplankton population and community dynamics and their relative importance in Southern Ocean food webs over time will reflect species-specific differences in vulnerability or resilience to these drivers. Together with a mechanistic understanding of the processes involved, this knowledge will enable the development of food web and ecosystem models that are needed for assessing different scenarios of change and projecting how Southern Ocean ecosystem structure and functioning may be impacted. Aside from Antarctic krill (*Euphausia superba*), which are comparatively well studied, zooplankton are considered to be less well understood but critical to the development of these models (Murphy et al., 2012a, 2016, 2018; McCormack et al., 2021).

Southern Ocean zooplankton comprise a diverse range of endemic and non-endemic species that collectively dominate the pelagic biomass. They vary in their body forms and sizes (e.g., from <100 μm copepod nauplii to >1 m jellyfish or salp chains), and in their life history traits and strategies, and occupy a range of habitats and environmental conditions (Atkinson et al., 2012). Many of the endemic species are uniquely adapted to Southern Ocean conditions, including the intense seasonality, sea ice, and low ocean temperatures (Murphy et al., 2016) associated with its cooling >24 mya and formation of the Antarctic Circumpolar Current (ACC) and Antarctic Polar Front (APF) (Clarke and Johnston, 2003; Lagabrielle et al., 2009; Clarke and Crame, 2010). These physical features are indeed fundamental drivers of natural processes, life history evolution, and ecological connectivity across the Southern Ocean (Clarke and Crame, 2010; Clarke et al., 2012; Murphy et al., 2012b, 2016; Varpe, 2017), signifying the vulnerability of Southern Ocean biota, including zooplankton, to climate change (Constable et al., 2014b).

A number of consistent and distinct zooplankton communities have been identified in the Southern Ocean, occupying the cold coastal regions and seasonally variable sea ice zone in the south, the open ocean, and the relatively warmer subantarctic areas in the north. Zooplankton abundance is highest in the epipelagic and upper mesopelagic layers (wherein many species undertake diel vertical migrations) though some species may extend to deeper waters during seasonal migrations and intermittent forays. These biogeographic regions are generally defined by sea and pack ice, bathymetry, and the series of oceanographic frontal zones across the Southern Ocean (Hosie et al., 2000; Hunt and Hosie, 2005, 2006; Pinkerton et al., 2010; Ward et al., 2012; Hosie et al., 2014; Steinberg et al., 2015). The associated zooplankton communities are dominated by a small number of metazoan taxa (including euphausiids, copepods, salps, and pteropods) and vary in their structure (i.e., species richness and diversity) and dominance patterns. Interannual variations in community dynamics also occur within and between these regions in relation to seasonal succession and transitions through key life history stages (Atkinson and Sinclair, 2000; Froneman et al., 2000; Pakhomov et al., 2000; Hunt and Hosie, 2006; Ducklow et al., 2012; Murphy et al., 2021). Additional temporal variations in community dynamics may also occur in relation to oceanographic and cryospheric processes. Future shifts in sea ice (Turner et al., 2020), fronts (Chapman et al., 2020) and related bio-physical oceanographic processes (e.g., Pinkerton et al., 2020) in association with human-induced climate change are projected to result in changes in zooplankton distributions (Constable et al., 2014b). There is also concern over the impacts of additional climate-related processes (e.g., atmospheric and oceanographic processes, including ocean acidification) and other direct and indirect anthropogenic drivers (e.g., dynamics of predator and prey populations, the recovery of previously harvested whale species, fisheries, invasive species, and pollution, etc.) on zooplankton and community dynamics and the implications for Southern Ocean ecosystems.

The review by Atkinson et al. (2012) provided an overview of the then-current understanding of the biology of dominant Southern Ocean metazoan zooplankton, focusing primarily on the data available for parameterizing models. In the intervening decade, understanding of the distribution, ecology, and response to change of these taxa has continued to advance concomitant with a greater diversity of research approaches. These advances have been facilitated in part by improved data availability as a result of new surveys and process studies (e.g., Meyer et al., 2017; Wallis, 2018; Wallis et al., 2019; Conroy et al., 2020; Yang et al., 2020), and extensive data rescue and compilation (e.g., Mackey et al., 2012; Atkinson et al., 2017; Tarling et al., 2018; Perry et al., 2019; Pinkerton et al., 2020; Takahashi et al., 2021). At the same time advances have been made in modelling across multiple taxa (e.g., Pinkerton et al., 2020) and of key species such as Antarctic krill (e.g., Constable and Kawaguchi, 2018; Veytia et al., 2020; Sylvester et al., 2021) and *Thysanoessa macrura* (e.g., Driscoll et al., 2015), and *Salpa thompsoni* (e.g., Henschke et al., 2018). There has also been progress in the understanding of the role of zooplankton in biogeochemical cycling, including the biological pump *via* grazing and vertical carbon flux (e.g., Alcaraz et al., 2014; Henschke et al., 2016; Belcher et al., 2019; Cavan et al., 2019; Manno et al., 2020) and their sensitivities to ocean acidification, including the additional synergistic effects of warming, temperature and deoxygenation (e.g., Kawaguchi et al., 2013; Manno et al., 2017, 2018; Ericson et al., 2018; Peck et al., 2018; Bednaršek et al., 2019; Saba et al., 2021). Some of these advances, especially for Antarctic krill, are captured in other reviews, which have generally focused on the ecological effects of climate change (Mackey et al., 2012; Hunt et al., 2016; Chown and Brooks, 2019; Siegert et al., 2019; Rogers et al., 2020) and/or the Antarctic krill fishery (e.g., Meyer et al., 2020; McBride et al., 2021). This contribution adds to this literature with an up-to-date systematic comparison of the major Southern Ocean zooplankton

taxa as detailed in the next paragraph. We stress, however, that limitations remain due to the paucity (and/or inaccessibility) of detailed qualitative and quantitative knowledge for many zooplankton species, populations and communities. In particular the underlying processes of their dynamics and causal links to drivers are often poorly understood; furthermore, projections of future changes in Southern Ocean zooplankton that can support policy decisions are limited.

The first Marine Ecosystem Assessment for the Southern Ocean (MEASO) is an international collaborative activity of the Integrating Climate and Ecosystem Dynamics in the Southern Ocean (ICED) programme. The primary aim of MEASO is to assess the status and trends of Southern Ocean habitats, species, and food webs, and the risks to these ecosystems and their services from drivers of change, particularly climate change and related processes. As a core MEASO contribution, this paper synthesizes the current state of knowledge of zooplankton, focusing on the dominant taxa that are understood to have an important role in ecosystem structure and functioning and are susceptible to global change, and for which sufficient data and knowledge are available. We provide an overview of key euphausiids, copepods, salps, and pteropods in terms of their ecology and roles, observed changes, and future prognoses across the Southern Ocean within the MEASO areas [which include protected areas and fishery reporting areas of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), **Figure 1**]. We synthesize available knowledge on their current circumpolar distributions, observed changes, and the key drivers and mechanisms involved. We also provide an analysis of environmental suitability (modelled abundance) for some of these taxa in the MEASO areas over the past two decades based on samples collected by the international Scientific Committee on Antarctic Research (SCAR) Southern Ocean Continuous Plankton Recorder Survey (SO-CPR). We undertake a qualitative assessment of potential future changes of these key taxa in response to anticipated changes in key physical, chemical, and ecological global and local drivers (**Figure 2**) that we consider important for these taxa. We also assess their potential resilience (*sensu* Oliver et al., 2015a) focusing on the mechanisms that may underpin resistance and recovery, which can either be expressed (or examined) at the individual or population level; an aspect that has not been widely explored for these taxa. We conclude by identifying current limitations and important directions for Southern Ocean zooplankton research to enhance marine ecosystem models for the region, develop robust projections of change, and improve understanding of Earth System functioning that will further support policy makers in developing conservation and management strategies.

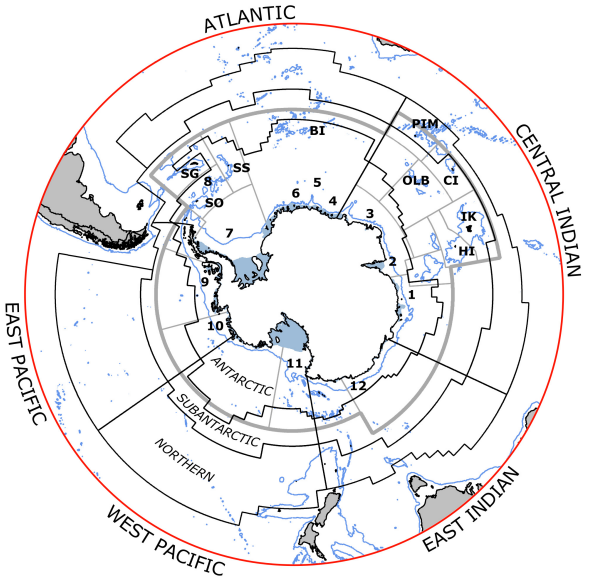

FIGURE 1 | Areas for assessing status and trends of dominant metazoan zooplankton in the Marine Ecosystem Assessment for the Southern Ocean (black lines). Sectors are divided meridionally: corresponding names of sectors are outside the circle. Zones extend from the coast to the Southern Antarctic Circumpolar Current Front (SACCF, Antarctic), to the Subantarctic Front (SAF, Subantarctic) and to the Subtropical Front (STF, Northern). Seas are marked in the Antarctic Zone as (1) Davis, (2) Cooperation, (3) Cosmonaut, (4) Riiser-Larsen, (5) Haakon VII, (6) Lazarev, (7) Weddell, (8) Scotia, (9) Bellingshausen, (10) Amundsen, (11) Ross, and (12) Dumont D'Urville. Islands in the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) area include Heard (HI), Isles Kerguelen (IK), Crozet (CI), Prince Edward-Marion (PEM), Bouvet (BI), South Sandwich (SS), South Georgia (SG), South Orkney (SO), Ob and Lena Banks (OLB), and South Shetlands (not initialed but found on the north-western side of Antarctic Peninsula). Gray lines indicate the CCAMLR reporting areas (Subareas and Divisions). NB: The Southern Boundary (not shown) and the STF mark the southern and northern limits of the intense eastward flowing Antarctic Circumpolar Current (ACC, not shown), which reaches up to 2000 km wide and extends from surface waters to 2000–4000 m. The Antarctic Polar Front, APF (not shown) lies between the SACCF and SAF and represents an important ecological boundary. It marks the northern extent of ice-influenced surface waters, and the transition between the cold surface waters to the south and the warmer waters to the north. Within the ACC, the SACCF, APF, and SAF delimit boundaries between different water masses with distinct and relatively homogeneous physical and chemical characteristics. These also coincide with intense narrow currents jets that dominate the ACC (see Orsi et al., 1995; Rintoul, 2018; Park et al., 2019; Chapman et al., 2020).

KEY TAXA IN SOUTHERN OCEAN ZOOPLANKTON COMMUNITIES

Four zooplankton taxa are notable for their biomass and abundance: euphausiids, copepods, salps, and pteropods (Atkinson et al., 2012). There is also increasing awareness and insight into their roles in maintaining Southern Ocean ecosystem structure and function, including locally and globally important ecosystem services (Grant et al., 2013; Rogers et al., 2020; Trebilco et al., 2020; Cavanagh et al., 2021), and their susceptibility to global change. Members of these taxa have evolved distinct and complex life histories, habitat, and environmental preferences which define their spatial and temporal distributions, and form part of the key zooplankton communities described above with varying degrees of dominance and support regional pelagic food webs (**Figures 3**, **4**) across the MEASO areas (see **Supplementary Table 1**; Bestley et al., 2020; Pinkerton et al., 2020; Brasier et al., 2021; Caccavo et al., 2021; McCormack et al., 2021).

The euphausiids have similar morphological, reproductive, and behavioral (i.e., swarming, migrating) traits, and trophic niches but they vary substantially in their adult size, life

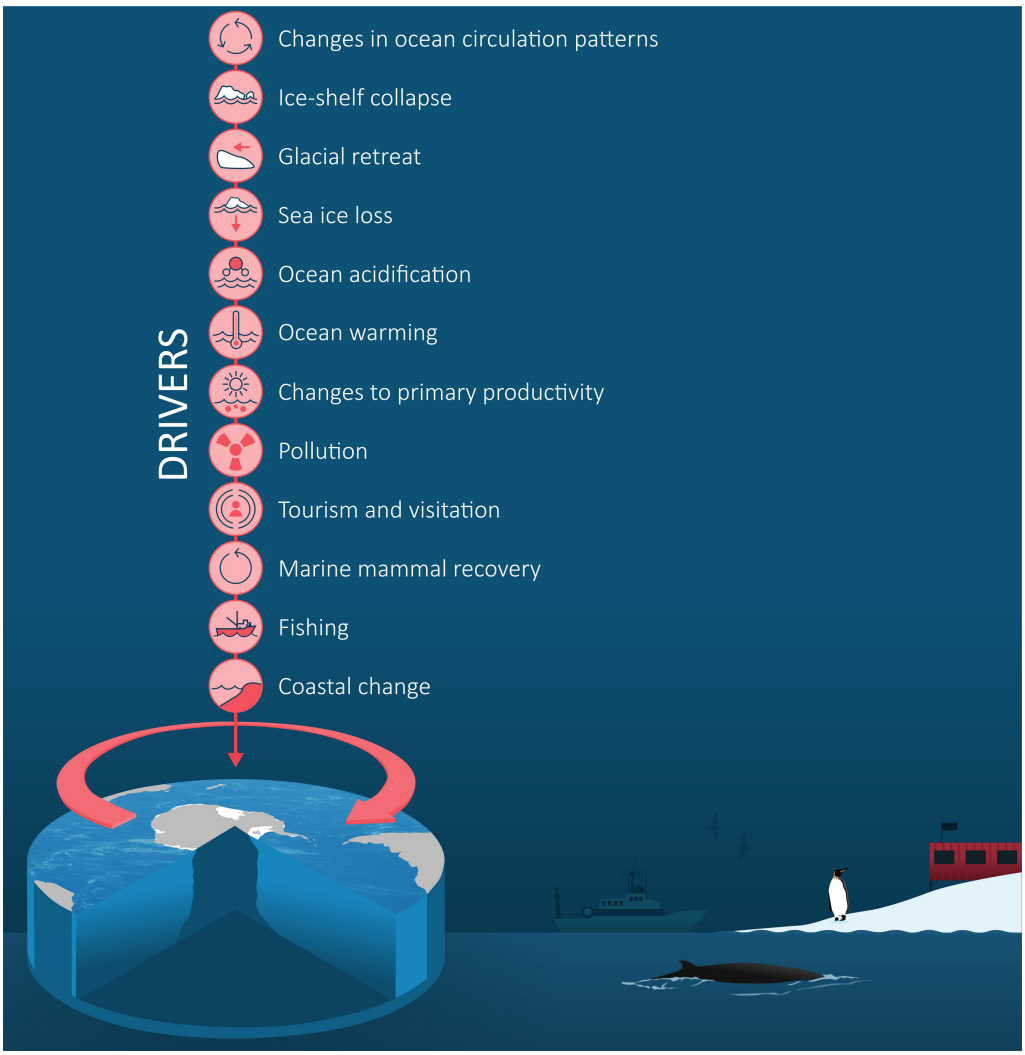

FIGURE 2 | Key drivers of change in metazoan zooplankton taxa within the Southern Ocean. For a complete description of global and local drivers of change in Southern Ocean ecosystems see Morley et al. (2020) and Grant et al. (2021).

span and adaptations to/associations with ocean temperatures (Cuzin-Roudy et al., 2014; Siegel, 2016). The dominant euphausiids include three endemic species. Antarctic krill is considered a keystone species and is the best studied secondary producer. It is the largest and longest-lived euphausiid in the Southern Ocean and a dominant zooplankton omnivore, capable of forming extensive dense swarms (up to several kilometers in length and tens of meters in depth), and channels substantial primary production directly to higher trophic level predators (Siegel, 2000, 2016). Whilst it has a circumpolar distribution and wide latitudinal range in the cool waters south of the APF, its biomass is concentrated in the iron-enriched waters of the southwest Atlantic sector where phytoplankton blooms are common (a region referred to as high nutrient, high chlorophyll, HNHC). Here Antarctic krill is the target of an international fishery (CCAMLR, 2018; Grant et al., 2021) and supports large populations of fish, marine mammals and seabirds, underpinning wildlife tourism and commercially exploited fish species (Antarctic toothfish, *Dissostichus mawsoni*, Patagonian toothfish, *D. eleginoides*, and mackerel icefish, *Champsocephalus gunnari*). At higher latitudes, the endemic congener *E. crystallorophias* (ice or crystal krill), becomes more common, being restricted to cold (<0°C) shallow coastal waters associated with sea ice and in polynyas. *Thysanoessa macrura* is perhaps the most numerically abundant Southern Ocean euphausiid, with a cosmopolitan distribution, contributing to zooplankton communities across a much wider (and more northerly) latitudinal range than *E. superba* and *E. crystallorophias*.

In high nutrient, low chlorophyll (HNLC) regions of the Southern Ocean, copepods dominate the zooplankton fauna with a similar biomass but greater total production than Antarctic krill (Atkinson et al., 2012). Across this group, there is considerable diversity in life history traits and strategies, particularly in their

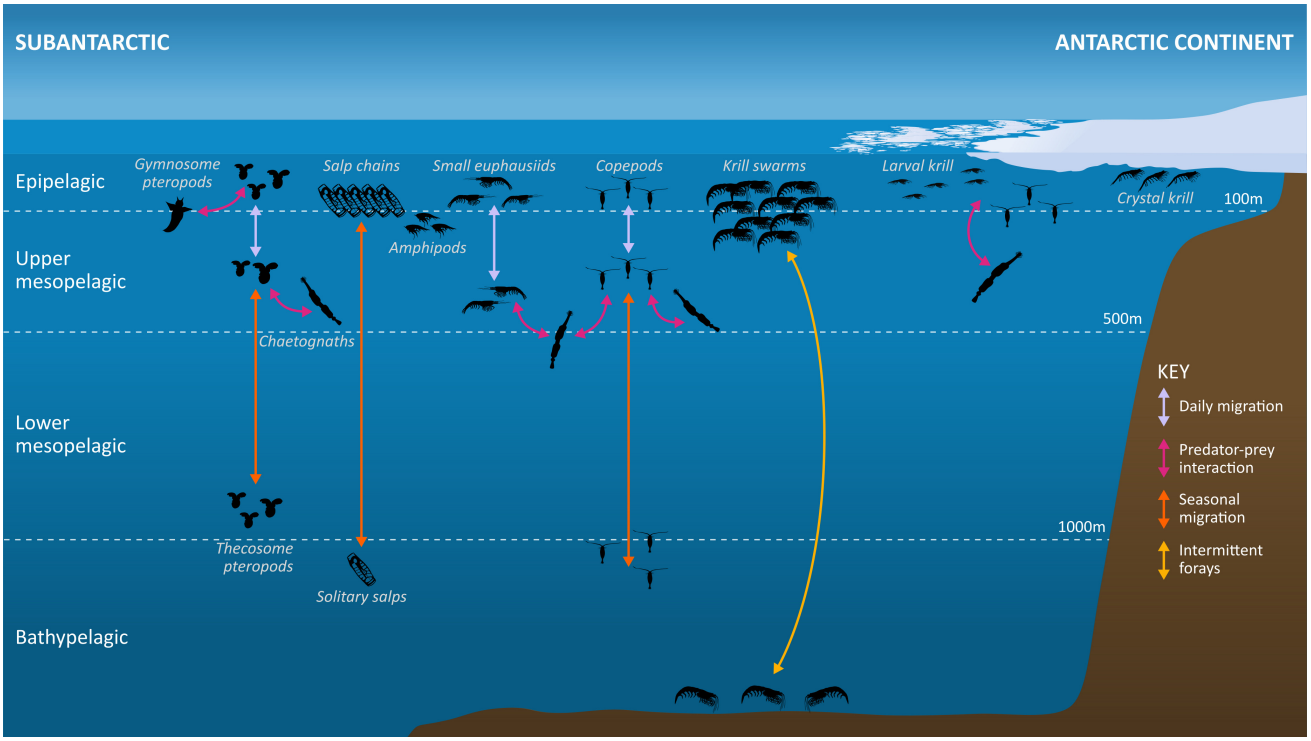

FIGURE 3 | Metazoan zooplankton occupy a range of habitats throughout the Southern Ocean, from the continent to the subantarctic islands, from the surface waters to the deep ocean, and in association with sea ice. They migrate vertically over daily and/or seasonal timescales. Several species of euphausiids, copepods, salps and pteropods are notable for their biomass and importance in maintaining Southern Ocean food webs and ecosystem structure and functioning, including as key consumers and prey items in supporting benthic communities and predator populations, and in biogeochemical cycles and carbon budgets. A number are also important in the diets of fish, marine mammals and seabirds that underpin wildlife tourism and commercially exploited fish species (Antarctic toothfish, Patagonian toothfish, and mackerel icefish), while Antarctic krill (*Euphausia superba*) is the direct target of harvesting operations. Not illustrated (for clarity) are a variety of other detritivorous or carnivorous groups, for example ostracods, cnidarians, appendicularians, polychaetes, decapods, etc., whose predominance increases with depth. We have illustrated chaetognaths as a major predator of the key taxa illustrated here, although many other taxa such as cnidarians and decapods also perform this function. Intermittent forays: performed by Antarctic krill to the seabed are carried out over a range of timescales from daily to seasonal.

morphological, reproductive, and behavioral traits, and dietary preferences, ranging from the small (1 mm) egg brooding, opportunistic omnivorous *Oithona similis* to the large (∼10 mm) free spawning and primarily herbivorous *Rhincalanus gigas*. The deep winter diapause (or less active) stage of the endemic *Calanoides acutus* and some of the larger species, such as *R. gigas*, integrate energy rich lipid production from phytoplankton across space and time, which fuels upper trophic levels (Schnack-Schiel and Hagen, 1995; Atkinson, 1998; Pasternak and Schnack-Schiel, 2001) and may contribute to a significant, but yet poorly known, proportion of Southern Ocean carbon sequestration *via* mortality and the "lipid pump"(Shreeve et al., 2005; Jónasdóttir et al., 2015).

Salps (particularly *Salpa thompsoni* and *Ihlea racovitzai*), together with euphausiids and copepods, comprise the bulk of the zooplankton both in terms of absolute numbers and biomass (Pakhomov et al., 2002; Pakhomov, 2004; Siegel, 2016). These large gelatinous pelagic tunicates can form seasonally high densities. South of the APF, they are major grazers of smaller phytoplankton, and their importance and spatio-temporal variability in food web linkages, particularly those with higher trophic levels, and vertical carbon flux, is becoming increasingly realized (Kelly et al., 2020; Henschke et al., 2021). Whilst *I. racovitzai* occurs in cold ice-covered regions close to the Antarctic continent, *S. thompsoni* occupies a wider latitudinal range, preferring warmer waters of the APF. These temperature preferences generally result in spatial segregation from *E. superba,* although co-occurrence is also observed. Although the relative role of euphausiids, copepods and salps in carbon and biogeochemical cycling is still poorly resolved despite decades of research, the extensive abundances and biomass of the euphausiids, copepods and salps imply their potential significance in driving biogeochemical cycling and feedback processes across the circumpolar ocean (see Henley et al., 2020).

Pteropods are another important member of the Southern Ocean zooplankton, and some of the highest population densities in the global distribution of this taxa are estimated to occur in this region (Hunt et al., 2008; Roberts et al., 2014). Although they account for a lower biomass and energy flow than euphausiids, copepods, and salps the information on the species typical of the Southern Ocean (representative of the shelled Thecosomata and non-shelled Gymnosomata) has increased in recent years in response to concerns about

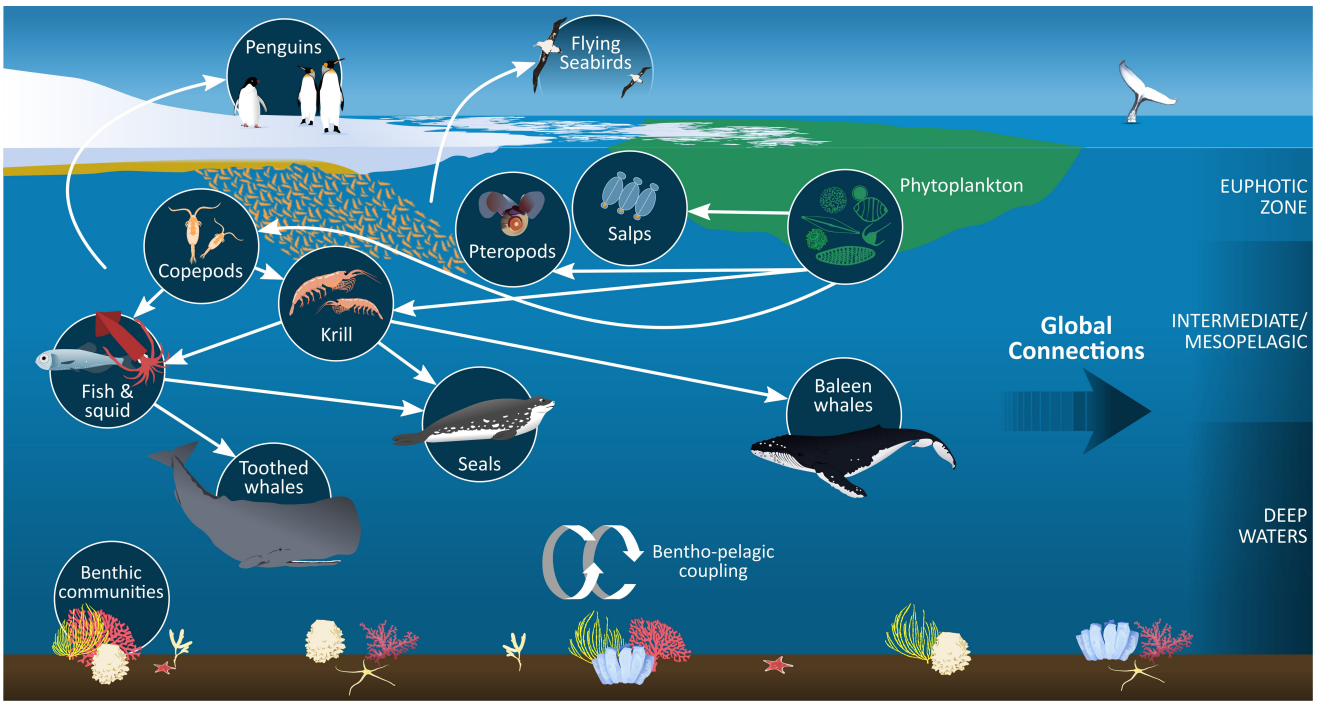

FIGURE 4 | Metazoan zooplankton form integral components of food webs across a range of spatial and temporal scales within the Southern Ocean, providing a link between air breathing predators (including seabirds, seals, and whales), pelagic and benthic communities. Food web connections between these communities are partially determined by feeding strategies and migration patterns/intermittent forays of each zooplankton taxa. Processes associated with zooplankton feeding, vertical migrations and forays, and mortality also contribute to vertical carbon flux, linking productive surface waters with deeper layers and the sediments.

the impacts of ocean warming and aragonite undersaturation resulting from ocean acidification. This has revealed high ingestion rates and distinct trophic roles of these orders, as well as the potential importance of the thecosomes in carbon flux and their vulnerability to ocean acidification (see Figuerola et al., 2021). Pteropod community structure differs north and south of the APF and their biomass is concentrated between 70 and 80°S and in HNHC regions generally. They are considered consistent and ocassionally dominant components of zooplankton communities, collectively contributing to between 5 and 63% of zooplankton abundance in some locations. There are also important food web dynamics among pteropods communities as gymnosomes are preferential predators on the predominantly herbivorous thecosomes (Weldrick et al., 2019).

Given the apparent importance of euphausiids, copepods, salps, and pteropods it follows that, depending on their response to direct and indirect changes in environmental drivers, they have the potential to modify food webs and the structure and functioning of whole ecosystems across various spatial and temporal scales within the Southern Ocean. A focus on these taxa is therefore integral to understanding, predicting and managing the consequences of the impacts of anthropogenically driven change on Southern Ocean ecosystems. There are of course additional species within these taxa, as well as a range of other taxonomic groups within Southern Ocean zooplankton communities. These include amphipods, chaetognaths, and other detritivorous or carnivorous groups whose predominance increases with depth, such as formanifera, ostracods, cnidarians, appendicularians, polychaetes, and decapods. Unfortunately, lack of knowledge and data on their ecological dynamics and roles in the structure and functioning of Southern Ocean ecosystems precludes them from being considered in the present assessment.

EUPHAUSIIDS (FAMILY EUPHAUSIIDAE)

Antarctic krill

Antarctic krill (hereafter krill) is the most studied Southern Ocean zooplankton species (Siegel, 2016). Their high biomass (Siegel and Watkins, 2016), relatively large size (up to >60 mm, Tarling et al., 2016a) and ability to feed on a wide range of prey (e.g., phytoplankton, micro- and mesozooplankton, and detritus) (Pakhomov, 2000; Schmidt et al., 2014, 2018) mean that they have a significant influence on the structure and functioning of Southern Ocean ecosystems. Where krill are abundant, they support large populations of predators (Trathan and Hill, 2016) ranging in size from mesopelagic fish (length c. 0.1 m, including commercially harvested fish species) to baleen whales (length up to c. 25 m). Krill therefore play an important role in regulating the flow of nutrients to mid and higher trophic levels (Atkinson et al., 2001; Whitehouse et al., 2008; Schmidt et al., 2011; Hill et al., 2012). Many krill predators are non-specialists and can adapt to short-term fluctuations in krill abundance by feeding on alternative prey such as copepods, amphipods and fish (Croxall et al., 1999; Waluda et al., 2012). However, the availability of these alternative prey, their own dependence on krill and relative

nutrient value, and the flexibility of predator diets will all play a role in determining how changes in the distribution and biomass of krill affects dependent predators and the wider ecosystem (Ducklow et al., 2007; Murphy et al., 2007a, 2012a; Staniland et al., 2007; Collins et al., 2008; Shreeve et al., 2009; Hill et al., 2012; Watters et al., 2013; Klein et al., 2018; Saunders et al., 2019). Krill also play a potentially important, but largely unquantified, role in ocean biogeochemical cycles (Cavan et al., 2019) with locally intense feeding, egestion and molting conveying megatons of carbon per year from surface to deep waters. In the marginal ice zone fecal pellet flux has been estimated to be 0.04 G tons C year^{-1} (Belcher et al., 2019) and in the north Scotia Sea the flux due to molted exoskeletons matches that due to fecal pellets (Manno et al., 2020). Conversely, there is little evidence that krill exert significant top-down control on primary production (Atkinson et al., 2014) although at smaller scales predation impacts may be intense and their nutrient excretion can promote phytoplankton turnover rates. Krill is also the target of the largest Southern Ocean fishery, which currently removes >400 k ton year^{-1} (CCAMLR, 2020, see also **Figure 5**).

The importance of krill to the Southern Ocean ecosystem and as a fisheries resource is reflected in a number of dedicated reviews (Everson, 2000; Atkinson et al., 2012; Flores et al., 2012a; Hill et al., 2016; Siegel, 2016; Kawaguchi and Nicol, 2020; Meyer et al., 2020; McBride et al., 2021) and specific sections in more general reviews (Constable et al., 2014b; Hunt et al., 2016; Cavan et al., 2019; Saunders et al., 2019; Rogers et al., 2020; Cavanagh et al., 2021) which consider its population status and response to recent climate change. Despite this attention, current understanding is based on a limited suite of observations primarily from the Antarctic Peninsula and Scotia Sea regions (hereafter the southwest Atlantic), with the majority of sampling targeting the epipelagic zone (<200 m) (Atkinson et al., 2012). Consequently, significant knowledge gaps and uncertainties remain (Meyer et al., 2020).

Current Distribution

Siegel and Watkins (2016) provide a detailed review of the distribution of krill. Although models (Cuzin-Roudy et al., 2014) suggest that most of the 32 million km^2 marine area south of the APF constitutes suitable habitat (but see Murphy et al., 2017), the species has only been observed in about 60% of this area (Atkinson et al., 2008) with significant concentrations observed mainly in shelf areas of the southwest Atlantic and the Indian sectors (Mackintosh, 1973; Atkinson et al., 2008; Siegel, 2016). Knowledge about krill distribution is limited in some locales such as the ice-covered western Weddell Sea and eastern Ross Sea, which remain largely inaccessible to sampling. The horizontal distribution of krill is patchy at the regional scale (>1,000,000 km^2) and there are between-regional differences in its association with key habitat variables, including bathymetry and sea ice, and in the influence of ocean currents (Nicol et al., 2000a; Hofmann and Murphy, 2004; Atkinson et al., 2008; Jarvis et al., 2010; Silk et al., 2016; Davis et al., 2017). For example, high densities in the Indian sector occur primarily within the seasonal ice zone whereas high densities in the southwest Atlantic can also occur in ice free areas (Murphy et al., 2007a; Atkinson et al., 2008, 2019).

Using data spanning 1926 to 2004, Atkinson et al. (2008) estimated that 70% of the circumpolar krill stock was concentrated in the sector between 0° and 90°W (the southwest Atlantic); however, several independent data sources suggest that the circumpolar krill stock is now more evenly distributed with average densities in the Atlantic sector being about twice those seen in other sectors (Siegel and Watkins, 2016; Yang et al., 2020). At finer spatial scales (<1000 km), krill can be highly aggregated, with the majority of individuals occurring in large swarms (over >300 m^2) during summer (Murphy et al., 2004a,b; Thorpe et al., 2007; Tarling et al., 2009; Meyer et al., 2017). The degree of aggregation varies temporally and spatially, possibly associated with food availability and predation risk.

Krill aggregation characteristics are also dependent on demography. This is a long-lived species (potentially surviving >5 years), which spends 1 year in its larval and juvenile stages. Females and males reach maturity at approximately 2 and 3 years, respectively (Reiss et al., 2017). Distributions of the different size, age or maturity categories appear to be dependent on the spatially restricted habitats which support successful spawning and first winter larval survival (Piñones and Fedorov, 2016; Siegel and Watkins, 2016; Meyer et al., 2017; Murphy et al., 2017; Perry et al., 2019; Thorpe et al., 2019). North of the Antarctic Peninsula adults appear to migrate offshore in late spring/early summer to spawn in waters deep enough (1000 m) to allow the developmental decent-ascent cycle, followed by onshore migration for overwintering (Siegel, 1988; Trathan et al., 1993; Reiss et al., 2017; Thorpe et al., 2019; Meyer et al., 2020). Krill are also reported to undergo episodic dispersal in ocean currents which might connect populations over large scales (>1000 km) (Hofmann and Murphy, 2004; Thorpe et al., 2007; Atkinson et al., 2008; Young et al., 2014).

In ice-free conditions krill is more abundant in epipelagic waters (Marr, 1962; Lascara et al., 1999; Jarvis et al., 2010) but the species also occurs in the mesopelagic zone (200 to 1000 m) and has been observed in the bathypelagic zone (>1000 m). It also associates with the seabed in both shallow and deep waters where it feeds on phytodetritus (Schmidt et al., 2011). In ice-covered waters, specialized sampling methods indicate that a large part of the population is in the upper water column, with some proportion of it concentrated at the ice-water interface (Daly and Macaulay, 1988; Marschall, 1988; Daly and Macaulay, 1991; Brierley et al., 2002; Flores et al., 2012a).

Evidence of Past Change

Genetic evidence suggests that krill populations underwent a significant increase over the past 100,000 years, a period that was largely glacial (Goodall-Copestake et al., 2010). More recent changes in population size, demographic structure and distribution have primarily been documented for the southwest Atlantic where regular monitoring was initiated in the early 1990s. However, this monitoring covers only a small proportion (<5%) of the species' habitat (Hill et al., 2016). There is also a composite dataset, KRILLBASE, which compiles all available circumpolar net sampling data for most years since 1976 as well as

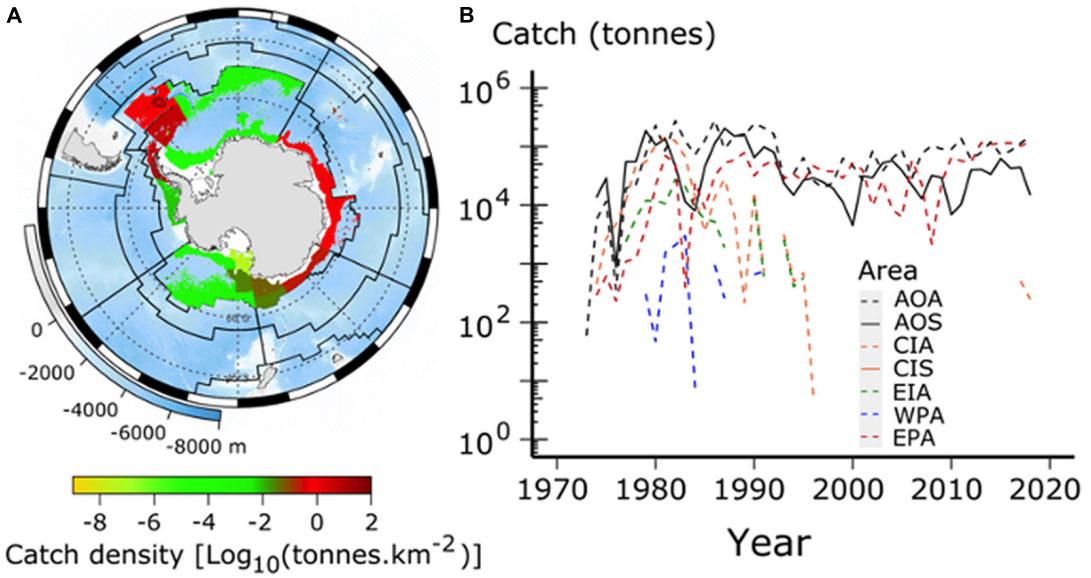

FIGURE 5 | Catches of Antarctic krill (*Euphausia superba*) from 1970 to 2018, derived from the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Statistical Bulletin 2019. **(A)** Shows total accumulated catch density over this period as log10 (catch density in tons.km^{-2}) (see colour ramp at bottom). Background is ocean depth in meters (bottom left legend on map). Black lines show boundaries of Marine Ecosystem Assessment for the Southern Ocean (MEASO) areas as depicted in **Figure 1**. Grey lines show a graticule (see Grant et al., 2021). **(B)** Shows time series of catches of Antarctic krill in each of the MEASO areas (log10 transformed *Y*-axis). Legend embedded in plot indicates line types for each area, where acronyms relate to MEASO sectors (first two letters) and zones (last letter). Sectors are Atlantic (AO), Central Indian (CI), East Indian (EI), West Pacific (WP), and East Pacific (EA). Zones are Antarctic (A), Subantarctic (S), and Northern (N).

some years in the 1920s, 1930s, and 1950s (Atkinson et al., 2017). Regional scale krill biomass in the southwest Atlantic sector has only been surveyed twice, in 2000 and 2019. These two surveys of an area of c. 2 M km^2 provided similar biomass estimates (60.3 and 62.6 Mt, respectively) (SC-CCAMLR, 2010; Krafft et al., 2021).

Various indices have been used to examine variability and change in krill population size in the southwest Atlantic over the past several decades. These indices include mesoscale (<125,000 km^2) biomass estimates (Fielding et al., 2014; Kinzey et al., 2018), estimates of numerical density (number per unit sea surface area) at various spatial scales (Loeb et al., 1997; Atkinson et al., 2004, 2019; Saba et al., 2014; Loeb and Santora, 2015), and indices derived from time series of predator performance (Watters et al., 2020), predator diets (Forcada and Hoffman, 2014) and isotope signatures (Huang et al., 2011), and anecdotal evidence based on personal field experience (Watters et al., 2013). Some studies indicate a declining trend in krill population size (Loeb et al., 1997; Atkinson et al., 2004, 2019; Huang et al., 2011; Trivelpiece et al., 2011; Forcada and Hoffman, 2014; Loeb and Santora, 2015; Yang et al., 2020) while other studies suggest a more stable trajectory in this sector (Fielding et al., 2014; Saba et al., 2014; Kinzey et al., 2015, 2018; Cox et al., 2018).

Several studies have identified environmental correlates of krill distribution, recruitment, and population size indices (Loeb et al., 1997; Atkinson et al., 2004, 2019; Huang et al., 2011; Trivelpiece et al., 2011; Fielding et al., 2014; Forcada and Hoffman, 2014). These correlates include sea ice in both the southwest Atlantic and Indian Ocean sectors (Loeb et al., 1997; Nicol et al., 2000a,b; Atkinson et al., 2004; Braithwaite et al., 2015) and two broad indicators of ocean circulation and climate variability (El Niño Southern Oscillation, ENSO, and Southern Annular Mode, SAM) in the former (Saba et al., 2014; Loeb and Santora, 2015; Atkinson et al., 2019). Some studies suggest mechanisms by which climate fluctuations propagate through the ecosystem; first affecting regional physics which in turn affect krill recruitment and dispersal, driving population dynamics and hence abundance and biomass (Murphy et al., 1998; Murphy et al., 2007a,b; Thorpe et al., 2007; Saba et al., 2014). These relationships suggest that population changes might be driven, in part, by climate change (Atkinson et al., 2004, 2019; Huang et al., 2011; Trivelpiece et al., 2011; Forcada and Hoffman, 2014).

Limited sampling in the Indian Ocean sectors has not provided any evidence of a trend in that location (Nicol et al., 2000a; Atkinson et al., 2004; Jarvis et al., 2010). Yang et al. (2020) conducted a circumpolar analysis of the available data. They concluded that a detectable decline in krill numerical density (number per m^2) was specific to the Atlantic sector, whereas densities in the other sectors changed little over time, resulting in a krill population that is now more evenly distributed around the continent than it was in the past.

Resolving the uncertainty in conclusions about population trajectories, and the influence of spatial scale, time series length and index type (i.e., different indices based on biomass, abundance, population structure of predators) on these conclusions, is a current key research priority

(Meyer et al., 2020). It is clear that any reported trend applies only to the time period analyzed and additional evidence is necessary to distinguish it from variability operating over longer timescales (Loeb and Santora, 2015). It is also clear that, even in the southwest Atlantic sector, there are spatial differences in observed patterns of krill variability and change (Atkinson et al., 2004, 2019; Hill et al., 2016; Cox et al., 2018). A recent study suggests some coherence in these patterns, indicating that the krill distribution within this sector has contracted southwards since the 1970s, with a decline in numerical density near their northern limit, and more stability in southern shelf areas (Atkinson et al., 2019).

Response to Drivers

Several important perturbations have affected the Southern Ocean ecosystem over the past two centuries. These include the sequential depletion of krill predators, which began with Antarctic fur seals in the late 18th century and progressed to baleen whales and several finfish stocks in the 20th century (Croxall and Nicol, 2004; Grant et al., 2021). They also include a prolonged period of warming and sea ice loss that occurred in the southwest Atlantic sector in the 20th century (Whitehouse et al., 2008; Stammerjohn et al., 2012; Maksym, 2019; Meredith et al., 2019), albeit with a hiatus over the last two decades (see Morley et al., 2020). Also, commercial harvesting of krill began in the 1970s and gradually became concentrated in the southwest Atlantic sector, moving further south and becoming more winter focused over time (Kawaguchi and Nicol, 2020; Meyer et al., 2020). Of these changes, krill fishing probably had the least impact on krill populations at the circumpolar and regional scales. Catches (circumpolar maximum 528 kt y^{-1}) have always been <1% of available biomass estimates at both of these scales (Hill et al., 2016; Nicol and Foster, 2016; Siegel and Watkins, 2016). Nonetheless, recent studies suggest that fishing can impact the density of krill at small scales (<10 km) and that these effects can propagate through to their predators (Santa Cruz et al., 2018; Krüger et al., 2020; Watters et al., 2020).

The ecosystem effects of predator depletion are potentially complex as recovery occurs at different rates which can alter the balance of predators over long timescales (Murphy, 1995; Croxall and Nicol, 2004). While there is a long-established expectation that increased predation negatively impacts krill populations (Laws, 1977), there is also a hypothesized positive feedback between baleen whale and krill populations. This states that pre-exploitation whale and krill populations may have consumed and recycled larger quantities of iron thereby enhancing overall ocean productivity and the production of krill (Smetacek, 2008; Nicol et al., 2010; Henley et al., 2020). Changes to predator populations as a result of past perturbation are still ongoing (Branch et al., 2007; Branch, 2011; Zerbini et al., 2019) and the full implications of these changes for krill populations remain to be explored.

The most reliable environmental predictor of krill biomass and numerical density discovered to date is sea floor bathymetry (Atkinson et al., 2008; Hill et al., 2009; Silk et al., 2016). Densities are generally highest over island shelves and shelf breaks and decrease offshore, although the lower densities offshore occupy a greater area and constitute most (up to 80%) of the observed biomass (Atkinson et al., 2008; Hill et al., 2009; Silk et al., 2016). However, distribution and abundance are also influenced by a suite of complex associations with other environmental characteristics, including water temperature, ocean acidification (OA), food availability, frontal activity, and the presence of sea ice. Changes in any of these variables have implications for krill populations which are discussed below.

Adult krill, within their optimal thermal range (0–3°C Atkinson et al., 2006; Tarling et al., 2006), are able to grow and reproduce if metabolic demand is met by food intake (Atkinson et al., 2006; Flores et al., 2012a; Hill et al., 2013), but their performance is likely to decrease at temperatures >3°C due to thermal stress (Constable and Kawaguchi, 2018). Larval and juvenile krill, with lower energy reserves compared to adults, are more vulnerable to extended periods of starvation (Hagen et al., 2001; Yoshida et al., 2009). Temperatures >3°C also negatively impact embryo development causing a rapid decline in egg hatching rate and increasing malformation (Perry et al., 2019, 2020).

The reported relationships between krill numerical density and sea ice extent in the southwest Atlantic sector (Atkinson et al., 2004, 2019) and between the circumpolar distributions of both krill and sea ice (Brierley et al., 2002) suggest that population status is closely linked to sea ice conditions. Systematic observations of krill's association with sea ice began in the late 20th century (e.g., O'Brien, 1987; Daly and Macaulay, 1988; Marschall, 1988; Stretch et al., 1988; Daly and Macaulay, 1991). These studies have revealed a rich variety of contrasting behaviors at different life history stages, in different locations, and at different times of the year, which indicates a high degree of plasticity. In a region of the Lazarev Sea with persistent sea ice cover, the horizontal distribution of krill is related to ice thickness and a large part of the population remains in the upper two meters of the water column throughout the year (Flores et al., 2012a, 2014). Elsewhere, in the Scotia-Weddell seas and the Antarctic Peninsula, typically only a proportion of larval and juvenile stages are observed on the under-surface of sea ice, while the rest of the population is distributed throughout the water column (Daly and Macaulay, 1991; Lancraft et al., 1991; Quetin and Ross, 1991; Daly and Zimmerman, 2004; Meyer et al., 2017).

Overwintering larval survival is a critical bottleneck which can affect recruitment and population size (Daly, 1990; Flores et al., 2012b). Cracks and crevices in sea ice provide a refuge from predation, which enhances krill survival (Meyer et al., 2009, 2010, 2017; Schaafsma et al., 2017). Survival is also enhanced by sea ice biota which are a key food source for krill larvae which, unlike adults, lack the lipid reserves to survive winter without feeding (Quetin et al., 1994; Meyer et al., 2002; Meyer, 2012). In the spring melting sea ice promotes phytoplankton production and releases ice algae into the water column, thereby enhancing the food supply available to krill in open water (Schmidt et al., 2018). Ice-conditioned spring phytoplankton blooms fuel the growth and maturation of early life stages, as well as adult nutrition essential for gonadal development and egg production. Consequently, this productivity supports enhanced larval survival and adult reproductive output (Schmidt

et al., 2012; Kohlbach et al., 2019). Nonetheless while sea ice is important it is not always essential for first winter survival. Walsh et al. (2020) found that extensive sea ice does not guarantee a strong recruitment and that in the absence of sea ice larval krill can still survive in the water column.

Future Prognoses

Flores et al. (2012b), Murphy et al. (2018), and McBride et al. (2021) provide detailed reviews of potential direct and indirect effects of climate change on krill. These include the negative impacts of OA on the embryonic and post-larval stages (Kawaguchi et al., 2013; Ericson et al., 2018) and of decreased duration and extent of the seasonal sea ice refugia and feeding grounds (Meyer, 2012; Kohlbach et al., 2017; Meyer et al., 2017; Schaafsma et al., 2017). They also include changes to population size and the quality of krill habitats resulting from ocean warming and changes in both their predators and food sources (Wiedenmann et al., 2008; Hill et al., 2013; Saba et al., 2014; Piñones and Fedorov, 2016; Murphy et al., 2017; Klein et al., 2018; Tulloch et al., 2018; Veytia et al., 2020). Such changes might be modified by concurrent changes in predator populations or fishery catch.

The effects of future OA on krill biology are unclear. Embryonic development and hatching are negatively affected by CO_2 at near future levels pCO_2 >1000 μatm (Kawaguchi et al., 2013). Conversely adult krill are resilient to these levels and can actively maintain the acid-base balance of their body fluids at pCO_2 >1000 μatm (Ericson et al., 2018). The only study on combined impacts of acidification and increased temperature to date suggests shorter-term (48 h) effects were primarily pH driven whereas longer-term (21 days) effects on growth and survival were strongly driven by temperature with little to no pH effect (Saba et al., 2021).

Mechanistic understanding of the interaction between the larval and juvenile stages and ice is still limited (Meyer, 2012; Kohlbach et al., 2017; Meyer et al., 2017; Schaafsma et al., 2017), and therefore the implications of ice loss for larval survival, recruitment and krill population size and distribution are not clearly understood (Murphy et al., 2018). Melbourne-Thomas et al. (2016) suggest that increased instability in sea ice will benefit krill by increasing the availability of larval overwintering habitat. Conversely, sea ice decline may impact phytoplankton community structure, reducing the contribution of large lipid-rich diatoms relative to smaller, less easily filtered and less nutritious taxa (e.g., cryptophytes Deppeler and Davidson, 2017; Pinkerton et al., 2020) and potentially reducing krill feeding efficiency, recruitment, and population size (Saba et al., 2014). Groeneveld et al. (2015) suggest that reductions in sea ice extent could lead to a poleward contraction of the krill population.

Several studies have examined the potential direct effects of ocean warming on krill habitat quality, suggesting that habitat contraction is likely as the temperatures at the northern fringes of their range exceed physiological limits (Wiedenmann et al., 2008; Hill et al., 2013; Murphy et al., 2017; Klein et al., 2018; Veytia et al., 2020). Spatial variability in warming and the possibility of localized increases in primary production could enhance habitat quality in some restricted regions, but these enhancements are unlikely to offset degradation elsewhere (Hill et al., 2013; Murphy et al., 2017; Veytia et al., 2020). Climate change impacts are also likely to reduce the availability of reproductive habitat (Piñones and Fedorov, 2016).

The physiological cycle of adult krill is tightly synchronized with photoperiod (Höring et al., 2018; Piccolin et al., 2018) such that reproduction and larval development coincide with the seasonal cycles of food availability (Kawaguchi et al., 2007; Kawaguchi, 2016). Model projections suggest that the timing and duration of such events could shift with future climate change and thus negatively impact krill population size across its current distributional range (Quetin et al., 2007; Veytia et al., 2020).

The populations of several baleen whale species dependent on krill in Southern Ocean feeding grounds are recovering (Branch et al., 2007; Branch, 2011; Zerbini et al., 2019). Model-based projection studies suggest that climate change could delay their recovery due to reduced krill availability (Klein et al., 2018; Tulloch et al., 2019). However, the hypothesized positive feedback loop whereby nutrient recycling by increased whale populations could enhance primary production and support increased krill stocks (Smetacek, 2008; Lavery et al., 2010; Nicol et al., 2010) may counteract this impact.

Thus the prognosis for krill is highly uncertain but the majority of studies suggest that climate change is likely to increase the physiological stress on both early life stages and adult krill. These effects may be compounded by loss and fragmentation of spawning and overwintering habitat. In the worst case, krill may eventually become restricted to a limited number of areas suitable for successful spawning, survival and recruitment (i.e., those with sufficient sea ice cover and reliable seasonal productivity cycles, see Hofmann and Hüsrevoğlu, 2003; Kawaguchi et al., 2007; Kawaguchi, 2016; Thorpe et al., 2019). Reductions in krill biomass and distribution are also likely to impact krill predator populations (Hill et al., 2013; Klein et al., 2018). In projection studies the severity of the impacts on krill and its predators generally increases with the severity of climate change (e.g., Hill et al., 2013; Kawaguchi et al., 2013; Klein et al., 2018).

Resilience

Krill is well known for its behavioral plasticity and variations in life history strategies that have allowed it to flourish in the highly variable Southern Ocean environment and to adapt its pattern of habitat use according to seasonally localized food availability. This plasticity is demonstrated by the high levels of variability in krill's association with and apparent dependence on sea ice (Meyer et al., 2017) and by rapid acclimation of individuals to the effects of reduced pH (Saba et al., 2021). Adults are able to survive long periods without food using a combination of lipid reserves and reductions in body size (Quetin et al., 1994; Tarling et al., 2016b). Krill have successfully colonized a range of habitats from the ocean surface to abyssal depths, and from continental ice shelves to the APF (Atkinson et al., 2008). This plasticity confers considerable resilience and is likely to ensure the survival of krill as a species. Current understanding of resilience in krill is based primarily on observations of the diversity of krill behaviors and habitats or experiments on individuals. Understanding of the consequences for krill populations is limited. For example,

feeding on phytodetritus on the seabed (Schmidt et al., 2011) might allow individuals to avoid adverse conditions closer to the surface. Whether this is sufficient to sustain the current krill population depends on many factors, including the availability and nutritional value of the novel food source and connectivity to other life history critical habitats, which remain to be explored.

Other Euphausiids

Aside from the Antarctic krill, there are twelve other euphausiid species in the Southern Ocean (Cuzin-Roudy et al., 2014). For most of these species there is extremely limited data on their biomass relative to Antarctic krill but their biomass are potentially orders of magnitude lower (however, see Wallis et al., 2020). Two species, *E. crystallorophias* and *Thysanoessa macrura*, are the most common taxa among this group, and are abundant and ecologically important as prey for upper trophic levels (Ainley et al., 2004). Others are common members of the pelagic community (*E. frigida*, *E. triacantha, E. vallentini*, and *T. vicina*) and may play important but unknown ecological roles in some regions of Antarctica near or south of the APF (e.g., *E. triacantha*, Liszka et al., 2021), or the broader sub-Antarctic region (e.g., *T. vicina*). The patterns of occurrence of these euphausiids are generally defined by the latitudinal and bathymetric features of the Southern Ocean, from the neritic environments of the high Antarctic to the pelagic areas north of the APF (Cuzin-Roudy et al., 2014). Many of these taxa undergo large diel migrations, from deep waters during the day to shallower waters during the night (Taki and Hayashi, 2005; Ono et al., 2011; Liszka et al., 2021). Additionally, these taxa vary in their life history strategy and their degree of omnivory. For example, *T. macrura* has adaptations including a pair of elongated second legs (thoracic legs) that can be used to catch zooplankton, while *E. crystallorophias* eat sea ice algae and sea ice microbiota. The variety of feeding strategies suggests that food web interactions amongst these taxa and the broader Antarctic ecosystem will vary greatly with climate change. Owing to their biomass some of these euphausiid species also undoubtedly play an important role in biogeochemical cycling (Guglielmo et al., 2009), however, this has yet to be quantified. Here we focus on the most common and best understood of these other euphausiid taxa, *E. crystallorophias* and *T. macrura*.

Euphausia crystallorophias

Crystal krill is smaller than Antarctic krill, reaching a maximum length of ∼40 mm over its 4 to 5-year lifespan (Siegel, 1987). The species typically feeds on small particles in the water column, including phytoplankton, microzooplankton (Kohlbach et al., 2019) and small zooplankton (O'Brien, 1987; Pakhomov and McQuaid, 1996). In addition, juveniles and adults have been observed on the sea floor feeding on phytodetritus (Deibel and Daly, 2007). Crystal krill is also an important prey item for upper trophic levels in the coastal environments of the high Antarctic (Thomas and Green, 1988; Pakhomov, 1997; Ainley et al., 2004).

Current Distribution

Crystal krill is a circumpolar high Antarctic species that replaces Antarctic krill in shallow (<500 m) neritic environments (Thomas and Green, 1988; Pakhomov, 1997; Ainley et al., 2004) covered by sea ice or in open water areas such as polynyas. It has been found as far north as the northern Antarctic Peninsula (Loeb et al., 2009), but has its greatest densities farther south than about 70° (Mauchline, 1969). It is common around the coastal areas of east Antarctica, and the Amundsen Sea (La et al., 2015) and is also abundant on the shelves of the Weddell (Boysen-Ennen and Piatkowski, 1988; Boysen-Ennen et al., 1991) and Ross Seas (Sala et al., 2002; Murase et al., 2006; Davis et al., 2017). Like other euphausiids, *E crystallorophias* undergoes diel vertical migrations (Conroy et al., 2020) that may deepen in winter, or in the presence of krill predators (Ainley et al., 2015).

Because the oceanography of coastal environments varies greatly around the Antarctic continent, crystal krill populations are largely self-contained, and some modelling studies have shown that population structure may be effectively aided by the currents in the areas of spawning (Piñones et al., 2016) or retained in areas because of the physical processes unique to the coastal ecosystems around the continent. However, genetic studies have shown that the genetic structure is not solely a function of distance between populations, suggesting that small scale processes are also important in the population structure in different parts of the Antarctic (Jarman et al., 2002).

The neritic nature of crystal krill ties reproduction and population dynamics to the seasonal coastal sea ice conditions including the opening of polynyas. Spawning starts under fast ice but peaks during coastal polynya breakout (Pakhomov and Perissinotto, 1996). Crystal krill eggs are neutrally buoyant and concentrate in the surface layers and larvae are associated with sea ice but appear to have a different vertical distribution (either shallower or deeper) than *E. superba* larvae (Pakhomov and Perissinotto, 1996; Daly and Zimmerman, 2004; Wiebe et al., 2011), which may reduce bottom predation of eggs by shelf benthos and grazing competition between these morphologically similar species, in areas where they overlap. The larvae are also abundant in inshore waters where they develop over the summer and into the following winter, taking about twice as long as *E. superba* to reach stage furcilia CIV (Kirkwood, 1996) and recruit to juvenile stages in spring (Pakhomov and Perissinotto, 1996; Daly and Zimmerman, 2004).

The biomass of crystal krill can be high in some areas around the Antarctic. For example, La et al. (2015) measured ice krill biomass in the Amundsen Sea polynya and found mean biomasses of 16 g fresh mass m^{-2}, an order of magnitude higher than those found in the Ross Sea (Sala et al., 2002) and of more similar magnitude to those reported for Antarctic krill. Other regions also had high biomass (Boysen-Ennen et al., 1991). In some cases, the regional peculiarities that make some polynyas important for crystal krill consequently make this species more abundant and these areas important for high latitude food webs (Pakhomov and Perissinotto, 1996).

Evidence of Past Change

From an evolutionary perspective *E. crystallorophias* is highly adapted to the high Antarctic ecosystem and may be constrained in a warming future owing to some genetic adaptations. Between 40 and 400 kya, *E. crystallorophias* underwent a population crash or directional selection to cold adaptation over time owing to periods of glaciation and deglaciation that resulted in the loss of the genetic diversity in its heat shock proteins. The diversity of

heat shock proteins is thought to provide phenotypic plasticity to species to tolerate and adapt to changing environments (Cascella et al., 2015; Papot et al., 2016).

There are few long-term studies of crystal krill with which to draw conclusions about past changes. Along the northern Antarctic Peninsula, where the U.S. Antarctic Marine Living Resources (AMLR) Program has sampled since the early 1990s, crystal krill are sporadically found around the South Shetland Islands and also on the west side of the peninsula but the data are not sufficient to build a time series to examine changes in their temporal abundance (U.S. AMLR unpublished data). Further west along the Antarctic Peninsula, there is some evidence for variability in crystal krill populations, in conjunction with variability in other ice-dependent taxa like silverfish (Ross et al., 2014). A 30 year time-series, from 1990 through to 2019, shows an increase in crystal krill abundance in the southern part of that study area, and is attributed to an increase in primary production or more favorable timing of spring sea ice retreat for larvae (Steinberg et al., 2015). Along other coastal regions of the Southern Ocean, patterns of distribution are similar over time, reflecting the neritic, polynya, and ice-covered waters that have shaped the life history of this important species. In the Prydz Bay region of the East Antarctic (Pakhomov and Perissinotto, 1996; Yang et al., 2011) and in the Ross Sea, surveys of crystal krill distribution conducted over the last several decades are not sufficient to document changes in abundance or biomass but do show considerable variability.

Response to Drivers

The high Antarctic, neritic nature of crystal krill suggests that its productivity and response to environmental drivers is tied to ecological adaptations associated with the oscillating regime of shelf environments and may be strongly influenced by the dynamics of coastal polynyas (Pakhomov and Perissinotto, 1996).

Future Prognoses

There have been few assessments of the likely trajectory for *E. crystallorophias* under different climate change scenarios. However, because crystal krill is a high Antarctic species, and has a narrow thermal habitat constrained to waters $\leq$2°C (Guglielmo et al., 2009), this makes crystal krill stocks vulnerable to climate change. Given their lower diversity of heat shock protein systems, *E. crystallorophias* may be physiologically less resilient to thermal shocks, so in geographic areas where ocean surface and subsurface areas are warming it could be more vulnerable to climatic change compared to Antarctic krill (Cascella et al., 2015; Papot et al., 2016).

Changes in sea ice extent and duration, especially at the northern limits of its range, are likely to negatively impact its preferred habitat greatly. Declines in the extent and duration of sea ice (Stammerjohn et al., 2008, 2012) or the timing of closing of polynyas will impact both larval and juveniles stages that rely on seasonal primary production in their first year of life, and will impact post-larvae perhaps by limiting their ability to accumulate lipids necessary for reproduction.

Simulations of future changes in sea ice concentrations suggest that the extreme loss of spawning habitat might greatly diminish the reproductive success of crystal krill (Smith et al., 2014). In some areas, simulations of future temperature, ice and vertical mixing depths on the Ross Sea continental shelf suggested that stratification will increase and favor diatoms, which likely would allow for enhanced ingestion by crystal krill, but due to the loss of ice (and spawning habitat) in the next 100 years, populations would decrease significantly (Smith et al., 2014). Further simulations suggested that the seasonal structure of phytoplankton production may change, with a shift toward *Phaeocystis antarctica,* a colonial haptophyte, but that this production would be largely unavailable to crystal krill (Kaufman et al., 2017). Both future scenarios suggest a mechanism for the decline in crystal krill success.

Changes in sea ice dynamics along the coast and warming of waters would, in general, create additional stresses on this thermally constrained taxon directly by affecting its habitat but also indirectly as increased water temperatures could make some environments more hospitable to other species like Antarctic krill or *T. macrura*. Interactions with these and other species (e.g., silverfish) are unknown. Continued study of the biology and ecology of crystal krill is warranted, and the establishment of monitoring programme in selected high Antarctic environments could provide data to better constrain projections about the future status and trends of this species and the animals that are dependent on it.

Resilience

The limited (thermal and geographical) range of crystal krill (Guglielmo et al., 2009) and the genetic adaptations that made it successful during periods of increased glaciation are likely to negatively impact this species in the future (Cascella et al., 2015; Papot et al., 2016). The capacity to move to other areas is undoubtedly low, and its neritic nature means that this taxon is not likely to be resilient to directional climate change as the quality of physical habitat at lower latitudes it occupies declines over the foreseeable future (Mackey et al., 2012; Steinberg et al., 2015). Areas in the high Southern Ocean (Pakhomov and Perissinotto, 1996), such as in the Ross Sea, the Amundsen Sea (La et al., 2015) or the southern most parts of the Weddell Sea, where reproductive polynyas may open earlier, may provide refugia for some populations of crystal krill, but lower latitude areas at the limits of its range may result in local extinction of some populations.

Thysanoessa macrura

T. macrura is likely the most numerically abundant euphausiid species in the Southern Ocean, although its circumpolar biomass is unknown (Nordhausen, 1992). It is smaller than Antarctic krill and has a maximum size similar to crystal krill (~42 mm) but with a shorter lifespan (<4 years) (Siegel, 2000; Haraldsson and Siegel, 2014; Driscoll et al., 2015). *T. macrura* is omnivorous but more predatory than *E. superba* (Hagen and Kattner, 1998), feeding on phytoplankton, microzooplankton, and copepods, as well as Antarctic krill larvae (Hopkins, 1985; Hopkins and Torres, 1989; Driscoll, 2019). Through its omnivorous diet, it can receive significant parts of its carbon budget from ice algae (Kohlbach et al., 2019). *T. macrura* is also an important prey item for upper trophic levels, including both midwater and demersal fish, marine

mammals and seabirds. *T. macrura's* position as a grazer, predator and prey means that the species' trophic position contributes significantly to various energetic pathways.

Current Distribution

In contrast to the thermally constrained and high Antarctic life history of crystal krill, *T. macrura* is a substantially more cosmopolitan taxon (Cuzin-Roudy et al., 2014; Pinkerton et al., 2020). *T. macrura* is by far the most-identified euphausiid species in Southern Ocean Continuous Plankton Recorder (SO-CPR) survey (Pinkerton et al., 2020). It is found in pelagic and coastal waters across a wide thermal gradient, from near freezing water (−1.8°C) to warm waters (10°C) in the northern latitudes where it overlaps with its congener *T. vicina* (Hempel and Marschoff, 1980). *T. macrura* is ubiquitous and relatively abundant throughout its range, without the concentration in the Atlantic sector that is evident in *E. superba* (McLeod et al., 2010; Yang et al., 2020). In some areas its average abundance can be higher than that of Antarctic krill (Loeb and Santora, 2015; Steinberg et al., 2015). Few zooplankton surveys conduct net tows below 200 m, however, those that have found that *T. macrura* has a deeper median depth distribution than Antarctic krill (Lancraft et al., 1989; Taki et al., 2008; Marrari et al., 2011) suggesting that most estimates of *T. macrura* abundance, especially near surface methods such as CPR, are generally biased low. *T. macrura* also tends to be form less dense and more spatially distributed aggregations during winter, rather than forming dense aggregations and concentrating inshore like *E. superba* (Nordhausen, 1994; Loeb and Santora, 2015; Driscoll, 2019).

Evidence of Past Change

Like most other zooplankton taxa that are not directly targeted for long-term studies, the temporal patterns in *T. macrura* abundance are less well defined than the spatial patterns of its distribution. In the Prydz Bay Region (Yang et al., 2011) and along the Antarctic Peninsula temporal patterns in abundance showed considerable variability over the past three decades (1992–2013) (Loeb and Santora, 2015; Steinberg et al., 2015; Driscoll, 2019) but do not show any trends indicative of changing population size. There is some indication that their abundance along the Peninsula may be related to changing climate drivers because growth has been correlated with temperature; however, the drivers of variability in the population are unknown. Pinkerton et al. (2020) found evidence of small (∼0.2%/year) increasing trends of habitat suitability for *T. macrura* between 1997 and 2018 (see also Section "Past Changes in Zooplankton: A Modelled Example Using Continuous Plankton Recorder Data").

Response to Drivers

T. macrura's wide latitudinal distribution suggests it may be more adaptable to changes in its environment, particularly increasing ocean temperature, than other Southern Ocean euphausiids. *T. macrura* has shown temperature dependent growth, with slower growth in colder Weddell Sea influenced waters compared to warmer Antarctic Circumpolar Current (ACC) waters (Driscoll et al., 2015). In contrast to *E. superba's* dependence on summer primary production for reproductive success, *T. macrura* spawn in winter and early spring using wax ester lipids to support egg development (Hagen and Kattner, 1998; Wallis et al., 2017). This life history strategy decouples production from the spring bloom which is required for gonad development in *E. superba*. *T. macrura* also have a faster larval development rate than the *Euphausia* species (Nordhausen, 1992; Haraldsson and Siegel, 2014; Wallis, 2018) where later stage larvae are found during summer (Makarov, 1979) and recruitment to juvenile stages has been observed by autumn, suggesting changes in abundance are likely to be driven by direct forcing on the populations (Marrari et al., 2011). Loeb and Santora (2015) also found that postlarval *T. macrura* abundances near the north Antarctic Peninsula were correlated with lagged ENSO conditions.

Future Prognoses

Temperature dependent growth models for *T. macrura* indicate increased growth under future climate change scenarios (Driscoll et al., 2015; Richerson et al., 2015). These models also indicate that the biomass per recruit may increase in the future and surpass that of *E. superba* in some areas (Richerson et al., 2015). Habitat suitability modelling for euphausiids sampled by the CPR, in which catches are dominated by *T. macrura* (Pinkerton et al., 2020) suggested that increasing environmental suitability between the APF and the northern annual limit of sea ice were related to surface warming and to deepening of the mixed layer depth, whereas predicted decreases in the Pacific sectors were related to shallowing mixed layer depths. Further north, increases in euphausiid environmental suitability were primarily correlated to increased primary production.

Resilience

Thysanoessa macrura may be relatively resilient to the climatic changes and future environments in the Southern Ocean over the next 50 to 100 years (Richerson et al., 2018). This resilience may be driven by several factors: its wide thermal tolerance (Driscoll et al., 2015), its omnivorous diet (Phleger et al., 2002), its highly flexible life cycle, and its independence from the spring bloom and sea ice cycle for reproductive success (Hagen and Kattner, 1998; Haraldsson and Siegel, 2014; Wallis, 2018). However, future climate-influenced changes in prey communities, predators, competitors, and other biotic conditions still may have the potential to impact this species in ways that are difficult to predict. Because of its relatively cosmopolitan distribution, flexible life history and high abundance, future studies should focus on *T. macrura*'s role in shunting energy around the short and generic phytoplankton-krill-predator food chain model, especially in open ocean environments in the northern extent of its range.

COPEPODS (SUBCLASS COPEPODA)

At the Southern Ocean scale, copepods have a biomass at least equivalent to that of Antarctic krill, with a total production far exceeding that of krill (Conover and Huntley, 1991; Voronina, 1998; Shreeve et al., 2005). Their biomass is dominated by large species of the genera *Calanoides*, *Calanus, Rhincalanus,* and *Metridia*, which perform varying degrees of seasonal vertical migration between summer feeding grounds in the epipelagic zone and overwintering depths below 200 m. The numerically

dominant smaller species have a diversity of life history strategies, including the small, egg-brooding, epipelagic cyclopoid *Oithona similis* (Cornils et al., 2017), seasonal migrants such as *Ctenocalanus citer* (Schnack-Schiel and Mizdalski, 1994) and sea ice dependent genera such as *Drescheriella, Paralabidocera*, and *Stephos* (Schnack-Schiel et al., 1995; Tanimura et al., 1996; Swadling et al., 2004). As a group, copepods provide food for a diversity of both invertebrate and vertebrate predators. Invertebrates are thought to be particularly important copepod predators (Hill et al., 2012), including chaetognaths, amphipods, euphausiids, and cnidarians. Among the vertebrate predators, smaller myctophid fish are particularly important predators of the larger copepods (Collins et al., 2008; Shreeve et al., 2009; Saunders et al., 2019), but also among the air-breathing predators, small petrels include an important component of copepods in their diet. Commensurate with their high circumpolar biomass and production relative to krill and salps, their grazing impacts are also substantial (Hill et al., 2012). In generalizing about the trophic roles of whole taxonomic groups such as copepods, it is important to emphasize the large diversity in size and feeding modes. The major size increase of each species through its ontogeny will expand this overall size range even further. Thus, large predatory groups including species such as *Paraeuchaeta antarctica*, feed on other copepods, and intraguild predation among the copepods is likely to be important (Hopkins, 1985; Hopkins and Torres, 1989). In addition to the raptorial feeding displayed by *P. antarctica*, copepod species use suspension and ambush feeding modes, with variations in the contribution of motile cells, non-motile cells, and detrital particles in the diet.

Current Distribution

Copepods typically have circumpolar distributions, similar to other Antarctic zooplankton groups. Latitudinally, a series of circumpolar fronts mark water mass discontinuities and help to define their thermal envelopes. The circumpolar distributions of the dominant copepods were first charted by the *Discovery Expeditions* of the 1920s and 1930s (Ommanney, 1936; Andrews, 1966) and then by the extensive Soviet expeditions (e.g., Voronina, 1972) with large scale coverage recently provided by the SCAR SO-CPR survey that began in 1991 (Hosie et al., 2003; McLeod et al., 2010; Takahashi et al., 2011; Pinkerton et al., 2020). These distributions have been further resolved by national survey programmes (e.g., Pakhomov and Froneman, 2000; Ward et al., 2006, 2012; Swadling et al., 2010). However, despite the high degree of collaboration over many areas of the Southern Ocean (e.g., the Pacific sectors), many remain under-studied due to their inaccessibility or lack of regular voyages (McLeod et al., 2010). Based on SO-CPR measurements, habitat suitability modelling has been used to "fill in" these spatial sampling gaps and provide insights into seasonal and long-term variability of copepods in the Southern Ocean (Pinkerton et al., 2010, 2020) (see also Section "Past Changes in Zooplankton: A Modelled Example Using Continuous Plankton Recorder Data").

Evidence of Past Change

There are few copepod time series of sufficient length in the Southern Ocean from which we can document and understand climate change effects over multiple decades. One of the longest, the U.S. AMLR time series, focused on the tip of the Antarctic Peninsula, shows ENSO influences on copepod abundance, acting through the translation of frontal systems and associated high and low phytoplankton concentrations across their study area (Loeb et al., 2010; Zhang et al., 2020).

However, longer timescales of observation are provided by a series of comparisons of distributions between the *Discovery* and the modern eras, with these comparisons needing to adjust for sampling differences (Vuorinen et al., 1997; Ward et al., 2008). Having standardized sampling methods, Ward et al. (2018) found that the biomass-dominant species *Calanoides acutus*, *Rhincalanus gigas,* and *Calanus simillimus* have increased in abundance in the last 70 years by 20–55%. Further, Tarling et al. (2018) found that the main copepods in the southwest Atlantic sector of the Southern Ocean had broadly conserved their spatial distributions despite a mean ∼0.74°C surface warming. In other words, they are nowadays inhabiting warmer surface temperatures than they were 80 years ago. This is an important result as it is the exception to the general expectations of range shifts (generally polewards to cooler waters) under warming scenarios (Beaugrand et al., 2009). Indeed, Antarctic range shifts have been found in the Atlantic sector, both for *E. superba* and salps (Pakhomov et al., 2002; Atkinson et al., 2004, 2019), in keeping with those found for aquatic and terrestrial ectotherms more generally (Parmesan and Yohe, 2003). Positive trends for 1997–2018 in modelled environmental suitability for copepods by Pinkerton et al. (2020) were found between the northern extent of seasonal sea ice and the southern limit of the ACC, with linear trends predicted to be highest in the Atlantic and Indian sectors and to exceed 6%/year in some places (see also Section "Past Changes in Zooplankton: A Modelled Example Using Continuous Plankton Recorder Data").

Response to Drivers

Copepods comprise numerous species with differing vertical and horizontal distributions and life histories (Atkinson, 1998). This means that responses to drivers may differ over time and space. Likewise, drivers can be direct, for example warmer temperatures increasing physiological rates, or indirect, for example climate affecting food sources (Moline et al., 2004; Montes-Hugo et al., 2009) which in turn affect the copepods.

Three "universal" responses to rapid warming have been described for ectotherms. Copepods may shift (1) in geographical range (i.e., polewards range shifts Beaugrand et al., 2009), (2) in phenology (i.e., earlier when warmer Mackas et al., 2012), and (3) in body size (i.e., smaller species', life stages or adult sizes in warmer environments Daufresne et al., 2009; Horne et al., 2016). The relative degree of expression of these responses is poorly known for zooplankton generally; it is certainly not known for Antarctic copepods. Due to the lack of seasonal coverage over multiple years we have particularly poor understanding of their phenological responses, for example to the rapid changes in sea ice duration along the Western West Antarctic Peninsula (WAP) (Stammerjohn et al., 2012; Henley et al., 2019).

While polar ectotherms are known generally for their stenothermy, the physiology of Southern Ocean copepods is still not well understood. Acclimation has a key role in governing responses to stress, so short term experiments measuring acute stress responses (for example to temperature or OA) are hard to interpret in the context of long-term climate change. For this reason, growth and egg production rate experiments on freshly collected copepods are, arguably, the best indicator of how the natural present-day variation in both food and temperature dictate copepod performance. This allows at least a glimpse of how they may fare in a changing world. Using this method on the ubiquitous, albeit, colder water cyclopoid, *Oithona similis,* the balance between fecundity and mortality was found to be sensitive to low temperatures, suggesting that increasing temperatures in the Scotia Sea may result in increased abundances (Ward and Hirst, 2007). Likewise, Ward and Shreeve (1998) demonstrated extension of large calanoid egg hatching times with colder temperatures. Shreeve et al. (2002) found changes in egg production rates, carbon mass and abundance of copepod populations at South Georgia were all strongly dependent on food concentrations, saturating only at high ($>3\mu$g Chl $a\,L^{-1}$) values. This suggests the importance of food limitation in most Southern Ocean environments. This result is consistent with habitat modelling of copepods in the Southern Ocean (Pinkerton et al., 2020) which found that although copepod abundances were related to sea surface temperature (SST) at the large scale, changes to their abundance at a given location were most strongly related to changes in phytoplankton biomass.

Effects from the gradual increase in OA are hard to determine experimentally, but in an acute response microcosm experiment, Tarling et al. (2016b) found that copepods show a stronger preference for dinoflagellates when in elevated pCO_2 conditions, demonstrating that changes in food quality and altered grazing selectivity may be a major consequence of OA (Tarling et al., 2016b).

Future Prognoses

An increase in small copepod species has been suggested as a possible future scenario in a warmer Southern Ocean (Murphy et al., 2016), and an Ecopath model experiment of krill or copepod dominance showed that copepod dominance would have major implications for the higher trophic levels that can be supported (Hill et al., 2012). Likewise, commonly made projections include general poleward range shifts of biota and increases in open water blooms over high latitude shelves formerly covered with ice (Constable et al., 2014b; McBride et al., 2014).

While an increasing number of studies are making large scale projections, this review has highlighted the paucity of basic knowledge needed to predict how copepods will respond to future changes in temperature, sea ice, food quantity and quality, and OA. The data obtained so far suggest that we should be very cautious in applying climatic envelope modelling of the type applied successfully to *Calanus* in the northern hemisphere (Helaouët and Beaugrand, 2007). In fact, north Atlantic *Calanus* may be an exception rather than the rule, since copepods in that region have showed widely divergent shifts over the last 60 years, with no evidence that their distributions tracked the shifting isotherms (Chivers et al., 2017). In addition to a suite of model-specific issues (Brun et al., 2016), the species may show resilience in maintaining a fixed geographical distribution (Tarling et al., 2018).

Some knowledge of how distributions have changed over past decades is, in our view, essential to generate informed projections for the future of copepods (and all zooplankton taxa examined here). For copepods there is much scope for progress in this area, given the wealth of data on this group that have been collected in Antarctica since the *Discovery Expeditions*, from a wide variety of nations working across the Southern Ocean. Efforts to retrieve and compile Antarctic krill and salp data have already shown their worth (Atkinson et al., 2017) and national historical data sets on copepods have already been compiled (O'Brien et al., 2017; Cornils et al., 2018). The SO-CPR will yield increasingly valuable insights into both phenology and long-term change (McLeod et al., 2010; Takahashi et al., 2011; Mackey et al., 2012), and these various data sources need to be combined to provide the spatio-temporal coverage needed to examine climate change responses.

Resilience

The traditional view is that future warming rates will be too fast to allow genetic-level adaptation to respond in time (reviewed in Ji et al., 2010; Beaugrand and Kirby, 2018). However, this view has been challenged (Dam, 2013; Peijnenburg and Goetze, 2013), and there is debate over the extent to which species can adapt genetically *in situ*, adjust phenotypically (e.g., changes in body size, behavior) or otherwise compensate by changes in their phenology, or spatial distribution (Chivers et al., 2017). The importance of adaptation has been suggested (Dam, 2013) and in this context the observations of cryptic speciation in two major copepod species *Oithona similis* in the Southern Ocean is noteworthy (Cornils et al., 2017).

Efforts have been made to define the thermal niches of Antarctic copepods (McGinty et al., 2018) and then to project their distributions in a warmer environment based on the assumption of a fixed thermal niche (Mackey et al., 2012). However, Tarling et al. (2018) found that spatial distributions of copepods within the southwest Atlantic sector did not change, despite over 70 years of warming. This result therefore questions the common assumptions underlying range shift projections. Several candidate explanations for this resilience to distribution shifts need to be investigated. For example, one possibility is that the distributions of species are partially "anchored" by suitable food concentrations. These are related to fixed areas of elevated topography that promote iron fertilization, leading to locally elevated phytoplankton and thus copepod densities. Likewise, the marginal ice zone and sea ice is known to promote feeding conditions in both winter (Kohlbach et al., 2018) and by pre-conditioning effects after ice retreat (Schmidt et al., 2018). Again, this could help to weaken the direct link from temperature to copepod abundance. Another mechanism may be adaptation at a genetic level, or phenotypically, for instance with a reduction in body size (see above).

To understand how climatic drivers affect copepods, we need to study their effects in tandem, for example how food

and temperature interact to driving copepod performance. This is achievable through egg production or somatic growth experiments on freshly collected copepods (Shreeve et al., 2002, 2005). Longer term incubations (involving realistic OA doses and acclimated copepods) have now shown that, in general, copepods appear to be fairly resilient to end of century projections of OA, but the degree of resilience to more local, but potentially acute effects such as increased glacial flour from glacial melt is poorly known (Garcia et al., 2019). Notwithstanding these uncertainties, the degree of resilience of copepods to climate change is central to understanding how food webs work and the higher predator species that may benefit, for example from a krill or a copepod-dominated food web.

SALPS (ORDER SALPIDA)

Salps are gelatinous pelagic tunicates with individuals usually ranging between 2 and 4 cm long but reaching 16 cm in length in the Southern Ocean. Seven species are recorded south of the Subtropical Convergence, although only two (*Salpa thompsoni* and *Ihlea racovitzai*) are documented south of the APF (Foxton, 1961). Salps are major contributors to the total wet mass of three major metazoans (salps, copepods, euphausiids) and rank third in terms of dry or carbon mass after copepods and krill (Voronina, 1998). Salps are non-selective feeders, with a highly effective filter capable of capturing a wide range of prey sizes, although they are most suited to digesting small flagellates and, to some degree, diatoms (von Harbou et al., 2011; Pakhomov et al., 2019). As major grazers, salps are important mediators of vertical carbon flux (Pakhomov et al., 2002; Pakhomov, 2004; Bernard et al., 2012; Alcaraz et al., 2014). Despite their gelatinous nature, the perception that salps are a "trophic cul-de-sac" is changing, with increasing evidence of the importance of salps in the diets of various groups of Antarctic animals (Pakhomov et al., 2002; Gili et al., 2006; Jarman et al., 2013). Here we concentrate on *Salpa thompsoni* and *Ihlea racovitzai.*

Current Distribution

Salpa thompsoni is by far the most numerous and widely distributed Southern Ocean salp species, with the highest densities observed in the warmer mid-latitude waters of the Southern Ocean within the Antarctic Polar Frontal Zone (Foxton, 1966; Pakhomov et al., 2002). *S. thompsoni* is a flexible species able to tolerate a range of habitats, with potentially significant implications for the food web. While *S. thompsoni* can be sampled over a broad thermal range (−1.5 to 9°C), it primarily occurs in warmer waters of 2 to 5°C, possibly because cooler temperatures may reduce their reproductive fitness through failed embryo development (Henschke and Pakhomov, 2019). *Ihlea racovitzai* is a smaller, cold-water, much less studied counterpart of *S. thompsoni* only found in low numbers in the ice-covered regions closer to the Antarctic continent (Foxton, 1966).

Evidence of Past Change

Observations from 1926 to 2003 suggest that salps have undergone a general increase in densities and a circum-Antarctic southward expansion in their distribution (Pakhomov et al., 2002; Atkinson et al., 2004). Despite extreme patchiness in their distribution and large inter-annual variability in abundance, during recent decades, local salp populations have shifted significantly southward, intruding into areas generally dominated by Antarctic krill (Pakhomov et al., 2011; Steinberg et al., 2015; Henschke and Pakhomov, 2019). This was demonstrated by empirical observations in the Prydz Bay Region during the 1990s (Pakhomov, 2000). Similar trends were observed over four decades from the 1970s in the Scotia Sea and around the Antarctic Peninsula (Loeb et al., 1997; Steinberg et al., 2015). The historic increase in salps was also captured in the ecosystem models of Hoover et al. (2012) around Antarctic Peninsula.

Response to Drivers

Salps have a unique life cycle, with alternating sexual and asexual reproduction (Foxton, 1966). The 1-year conceptual model of the *S. thompsoni* life cycle described by Foxton (1966) has recently been challenged. Empirical observations of growth rates and modelling currently support a notion that *S. thompsoni* asexual forms could live for as long as 2 years (Loeb and Santora, 2012), although this species may complete its entire life cycle, i.e., from egg to egg, passing through both the sexual and asexual stages, in as little as 3 months (Pakhomov and Hunt, 2017; Henschke et al., 2018; Groeneveld et al., 2020). This allows salps under certain water temperatures and food concentrations to sustain localized rapid population increases (blooms), mostly through asexual reproduction (Pakhomov et al., 2002). Currently, salp responses to temperature, food composition and concentrations as well as other environmental parameters are not well understood (Pakhomov et al., 2002; von Harbou et al., 2011; Pakhomov and Hunt, 2017). The most recent modelling studies indicate that salp development is sensitive to food concentrations (Henschke et al., 2018; Groeneveld et al., 2020) and salps have a preference for picoplankton (Pakhomov et al., 2019). At the same time, *S. thompsoni* distribution strongly correlates negatively with the ice cover and positively with the warm water intrusions into high Antarctic regions (Pakhomov, 2000; Pakhomov et al., 2002, 2011; Rogers et al., 2020). Furthermore, following a reanalysis of multi-year data sets on salp biology, Henschke and Pakhomov (2019) postulated that temperature strongly drives *S. thompsoni* population dynamics.

Future Prognoses

Model-based projections (based on proposed changes in primary production regimes) indicate the potential for replacement of Antarctic krill by pelagic tunicates in the regions around the Antarctic Peninsula (Suprenand and Ainsworth, 2017). Recent observations (1970s to present) suggest a general increase in salp densities and a southward expansion in their distribution (Pakhomov et al., 2002; Atkinson et al., 2004). Antarctic krill and *S. thompsoni* habitats seem to show little overlap on thousands of km and meters to km scales, while both species often co-occur at mesoscales (10s to 100s km) (Loeb et al., 1997; Nicol et al., 2000b). The suggested interspecies interactions

between krill and salps range from avoidance through to competition to predation, but these are not well understood (Le Fèvre et al., 1998; Pakhomov and Froneman, 2004). It seems that *S. thompsoni* cannot establish persistent populations in the high Antarctic and its occurrence at high latitudes is likely sustained by advection of warm waters (Pakhomov et al., 2011). This may change in a warmer Southern Ocean, although the consequences of higher salp numbers for the ecology of the Southern Ocean are hard to predict. An enhancement in the interactions between krill and salps, for instance, will have major effects on both the planktonic food web and the contributions of krill and salps to the carbon sink (Atkinson et al., 2012).

Salps are important mediators of the vertical carbon flux (Pakhomov et al., 2002; Pakhomov and Froneman, 2004; Alcaraz et al., 2014). Tunicates produce large, fast sinking (>1000 m day^{-1}) and carbon-rich (up to 40% dry weight) fecal pellets, increasing the speed and efficiency of transfer of nutrients and carbon from surface waters (Bruland and Silver, 1981; Perissinotto and Pakhomov, 1998b). Even in areas where salps do not dominate plankton biomass (e.g., the Scotia Sea), their pellets contribute significantly to downward carbon flux (Manno et al., 2015). Furthermore, they perform migrations between the surface and 300–500 m during summer and reside at depths of 500–1000 m during winter, actively enhancing carbon flux into deep water (Manno et al., 2015). Therefore, the downward flux of carbon could significantly increase in the future due to an increase in salp biomass and range expansion (Ducklow et al., 2012; Rogers et al., 2020). However, the rate of fragmentation of salp fecal pellets through coprophagy may be as high as 80% in the upper water layer (Iversen et al., 2017), increasing uncertainty in the above predictions.

The importance of salps in Southern Ocean food webs and biogeochemical processes is now widely recognized and reflected in recent modelling studies. For the Antarctic Peninsula, the model of Hoover et al. (2012) recreated the historic decline in krill and increase in salps, while that of Suprenand and Ainsworth (2017) suggested a further decline in krill biomass, and an increase in salp biomass by 2050. With the current and expected future increase in salp biomass, their inclusion in biogeochemical models is becoming increasingly recognized as important to realistically parameterize the Southern Ocean carbon cycle (Henschke et al., 2016). Their contribution to iron recycling within the Southern Ocean has also been highlighted (Maldonado et al., 2016; Cabanes et al., 2017). A key limitation to further advancement of biogeochemical models is the paucity of data on physiological requirements and limitations, feeding preferences, and of biomass observations for model parameterization and validation (Le Quéré et al., 2016).

The response of salps to future climate change will have a variety of implications for predators, fisheries and biogeochemical cycling. To understand the impacts of change in these ecosystems there is a need to improve assessments of the distribution and abundance of salps in the Southern Ocean, salp interactions with other major metazoan grazers (particularly krill), and the factors (both abiotic and biotic) that drive their population dynamics

Resilience

Salp genetic studies are in their infancy but it appears that salps possess fast-evolving genes, potentially pointing to a faster turnover rate of the population and an enhanced selection for new life cycle traits (Jue et al., 2016; Batta-Lona et al., 2017; Goodall-Copestake, 2017, 2018). It may be hypothesized that salps have a higher capacity to adapt to abrupt shifts in the environment (Bucklin et al., 2018; Bitter et al., 2019). A combination of fast population turnover rates (Henschke et al., 2018; Groeneveld et al., 2020) and an ability to repeatedly produce chains of hundreds of genetically identical individuals during asexual reproduction would enhance chances of finding an environmental match, thus maintaining salp genetic diversity and resilience in the changing environment (Bucklin et al., 2018).

PTEROPODS (ORDER PTEROPODA)

Pteropods are pelagic gastropod molluscs with a global distribution, represented by six species in the Southern Ocean. They can be divided into two orders: the shelled thecosomes (Thecosomata), comprising *Limacina helicina antarctica*, *L. retroversa australis*, *Clio pyramidata*, and *C. piatkowskii*, and the shell-less gymnosomes (Gymnosomata), comprising *Spongiobranchaea australis* and *Clione limacina antarctica. Limacina spp.* are mesozooplankton typically in the 1–5 mm size range, while *Clio* spp. and gymnosomes are macrozooplankton typically in the 10–20 mm size range. Time series show a mean pteropod contribution to zooplankton abundance of $\sim$ 11% in the vicinity of the Prince Edward Islands and South Georgia, 14% in the WAP, and <5% in the East Antarctic; however, their contribution can periodically exceed 85% (Hunt et al., 2008; Steinberg et al., 2015). Thecosomes can be highly abundant and are important trophically as grazers and prey. A detailed review on the ecological role of pteropods in the Southern Ocean can be found in Hunt et al. (2008). From a biogeochemical point of view, pteropods play an important role in the direct export of carbon and sequestration to the deep ocean through the sinking of dead individuals and fecal pellets (Manno et al., 2010, 2018). Their calcification also contributes to the carbonate counter pump which releases CO_2 back into surface waters (Manno et al., 2018). Thecosome pteropods produce shells from aragonite, a metastable and relatively soluble form of biogenic calcium carbonate ($CaCO_3$) (Mucci, 1983) and are regarded as sensitive indicators of OA (Fabry et al., 2008; Bednaršek et al., 2017a; Manno et al., 2017). This is particularly relevant in the polar regions where ocean uptake of anthropogenic CO_2 and the undersaturation of carbonate ions resulting from OA is progressing most rapidly (Orr et al., 2005).

Current Distribution

Pteropods occur throughout Antarctic and sub-Antarctic waters but species composition differs north and south of the APF reflecting distinct temperature tolerances (van der Spoel et al., 1999; Hunt et al., 2008; McLeod et al., 2010). Globally,

the highest average pteropod biomass is estimated to occur within the 70–80°S latitudinal band of the Southern Ocean (39.71 ± 93 mg C m^{-3} Bednaršek et al., 2012a). Hot spots of pteropod occurrence in the Southern Ocean include in the vicinity of islands and the Ross Sea. Densities exceeding 1000 ind.m^{-3} have been recorded from around South Georgia, the APF, and in the Ross Sea (Pane et al., 2004; Hunt et al., 2008). All Southern Ocean pteropod species are predominantly epipelagic (Hunt et al., 2008; Akiha et al., 2017) with the exception of *C. piatkowskii*, which is mesopelagic (van der Spoel et al., 1999). Both diel and seasonal migration occurs, with most species occurring deeper in the water column (to 1000 m) during winter (Hunt et al., 2008; Flores et al., 2014).

Evidence of Past Change

The longest published pteropod time series is from the Palmer Long Term Ecological Research (PLTER) area off the WAP (Steinberg et al., 2015). Summer surveys have been conducted continuously since 1993, in the form of a north-south grid that spans the coast, shelf and continental slope. Over the time series, pteropod abundance has shown large interannual variability and while gymnosome abundance increased up to 2017, thecosomes have shown no long-term trend throughout the WAP (Thibodeau et al., 2019). Sub-regionally, *L. h. antarctica* abundance has increased in the slope region, while *C. pyramidata* abundance has increased in the south. The overall pattern is dominated by an alternation between high and low abundance that is negatively correlated with the Multivariate ENSO Index, and positively correlated with SST, sea ice, and primary production (Steinberg et al., 2015). Gymnosome abundance tracks thecosome abundance, reflecting their trophic dependency. Similar trends in pteropod abundance were observed by the U.S. AMLR Program time series in the northern Antarctic Peninsula region (Loeb and Santora, 2013). The other significant pteropod time series comes from the SO-CPR surveys (1997 to present), which has mainly focused on the Pacific sectors thus far (McLeod et al., 2010). Although a detailed analysis of the time series has yet to be conducted, the combined data have been used to model the abundance of major groups with respect to chlorophyll-*a* concentration, net primary productivity, SST, mixed layer depth, sea ice and the spatial gradient of SST (Pinkerton et al., 2020). Based on the relationship between pteropod abundance and these environmental parameters, that study suggested a significant increase in environmental suitability for pteropods in many areas south of the APF in the last 20 years, but a significant decrease over the Ross Sea Shelf (see also Section "Past Changes in Zooplankton: A Modelled Example Using Continuous Plankton Recorder Data"). A caveat with these model results is that they do not include a representation of OA or oxygenation state.

Response to Drivers

Pteropod abundance is strongly positively correlated with primary production (chlorphyll-*a* biomass) (Seibel and Dierssen, 2003; Hunt et al., 2008; Steinberg et al., 2015; Pinkerton et al., 2020), and environmental forcing of primary production is therefore expected to be an important driver of pteropod change. Global time series indicate that, to date, temperature and productivity have been the dominant drivers of change in pteropod species composition and abundance (Mackas and Galbraith, 2012; Beaugrand et al., 2013). The vulnerability of thecosome pteropods to OA, specifically aragonite saturation state (Ωar, for which 1 is generally considered the vulnerability threshold), makes this another potentially important driver of change (Comeau et al., 2010; Bednaršek et al., 2012a; Lischka and Riebesell, 2012; Bednaršek et al., 2014; Thabet et al., 2015; Manno et al., 2017; Mekkes et al., 2021). The magnitude of their sub-lethal and lethal responses to OA depends on life-stage, with larvae and juveniles being substantially more affected by Ωar than adults (Bednaršek et al., 2019). Maternal and embryonic OA stress was demonstrated to reduce the percentage of *L. h. antarctica* eggs successfully reaching the organogenesis stage by 80% (Manno et al., 2016). Numerous studies have demonstrated synergistic effects, leading to outcomes that are nonlinear and sometimes severe (Bednaršek et al., 2016). Experiments combining OA with warming, deoxygenation, freshening or increased stratification have demonstrated synergistic effects among drivers of change leading to increased mortality (Lischka et al., 2011), reduced calcification (Comeau et al., 2010), shell degradation and malformation (Lischka and Riebesell, 2012; Gardner et al., 2018), altered metabolic rates (Maas et al., 2011, 2016) and changes to swimming performance and behavior (Manno et al., 2012; Bednaršek and Ohman, 2015). Further, *in situ* observations along the California Current System, have demonstrated the negative impact of OA in combination with warming and deoxygenation on pteropod population (Bednaršek et al., 2018). The majority of these studies were not carried out on Southern Ocean species, and it has been shown that responses in the same, or closely related, species can vary between environments (Maas et al., 2016). Nevertheless, some Antarctic studies have been performed. Gardner et al. (2018) found that early life stages of *L. h. antarctica* in the Scotia Sea exhibited shell malformation and dissolution when exposed to warming and OA, with mortality reaching up to 39%. Meanwhile, Hoshijima et al. (2017) found that metabolic rates increased at low pH and that this increase was amplified at higher temperatures in the same species in the Ross Sea.

Future Prognoses

Southern Ocean warming is expected to result in a change in pteropod species distribution, specifically a southward shift in sub-Antarctic taxa (Gardner et al., 2018). Evidence also suggests that ongoing warming, sea ice loss, and increased productivity will favor increased pteropod abundance (Seibel and Dierssen, 2003; Steinberg et al., 2015). Projections for future Southern Ocean productivity are spatially variable, with productivity forecast to decrease in the sub-Antarctic and increase toward the Antarctic continental shelf (Deppeler and Davidson, 2017; Pinkerton et al., 2021). While productivity may favor pteropods in southern regions, they may be increasingly negatively impacted by OA (Manno et al., 2007; Bednaršek et al., 2012a). Southern Ocean surface waters are expected to start becoming undersaturated with respect to aragonite as early as 2030 (McNeil and Matear, 2008), affecting ∼ 30%

of surface waters by 2060 and >70% by 2100 (Hauri et al., 2016). Aragonite undersaturation will affect southern waters first, progressively moving northwards. Furthermore, both shell dissolution and survival in aragonite undersaturated conditions may be exacerbated by concurrent warming (Bednaršek et al., 2019). The development of predictive models of pteropods responses to environmental change requires further research into the effect of stressors, particularly the synergistic effects of multiple drivers. Future research will benefit from the application of new molecular tools, e.g., transcriptomics, in measuring the physiological response of pteropods to stressors (Johnson and Hofmann, 2016; Johnson et al., 2019).

Resilience

While a number of studies have documented the effect of OA on pteropod physiology and shell condition, the importance of carbonate chemistry as a control on pteropod populations in the Southern Ocean has yet to be demonstrated. No relationship was found between Ωar and pteropod abundance in the WAP time series (Thibodeau et al., 2019). The fact that Ωar has yet to become undersaturated across most Southern Ocean surface waters may explain the lack of any population relationship with carbonate chemistry. However, it should be noted that Southern Ocean pteropods do already experience Ωar undersaturated conditions on a seasonal basis through winter occupancy of Ωar depleted waters (Hunt et al., 2008; Jiang et al., 2015; Manno et al., 2016). Arctic *L. helicina* experience greater exposure to aragonite undersaturated conditions, with Ωar <1 occurring in surface waters of the Beaufort Sea (Yamamoto-Kawai et al., 2009) and Amundson Gulf (Niemi et al., 2021). *In situ* studies of the Arctic *L. helicina* showed that the periostracum of this species was an effective barrier to exposure to Ωar undersaturated waters (over 4 days of incubation), and that dissolution to the inner shell only occurred when this was breached by previous physical damage (Peck et al., 2016a,b). However, other studies (Bednaršek et al., 2016, 2021; León et al., 2019; Niemi et al., 2021) do not agree that dissolution only occurred at the time of the periostracum breach. Furthermore, Peck et al. (2018) revealed that, despite losing the entire thickness of the original shell in localized areas, *L. helicina* can maintain shell integrity through thickening the inner shell wall. Nevertheless, this resilience is likely to come at a metabolic cost, which such organisms are unlikely to maintain over the longer term. In fact Niemi et al. (2021) found limited evidence for shell repair in the Amundson Gulf even when food was abundant, while Bednaršek et al. (2021) found reduced shell thickness as evidence of exposure.

PAST CHANGES IN ZOOPLANKTON: A MODELLED EXAMPLE USING CONTINUOUS PLANKTON RECORDER DATA

The SO-CPR survey was established in 1991 to map the spatial and temporal patterns of zooplankton through the Southern Ocean (Hosie et al., 2003). The CPR is towed behind a ship and collects samples of zooplankton from ∼10 m depth, which are preserved in formalin and subsequently morphologically identified in the laboratory. SO-CPR surveys continue to be carried out (Takahashi et al., 2021). At various stages this dataset has been analyzed to help understand spatial distributions and variation/change in zooplankton over time (e.g., Hunt and Hosie, 2005, 2006; McLeod et al., 2010; Pinkerton et al., 2010, 2020; Takahashi et al., 2011, 2021; Meilland et al., 2016). Pinkerton et al. (2020) combined SO-CPR data and oceanographic conditions (namely: chlorophyll-*a* concentration, net primary productivity, SST, mixed layer depth, sea ice concentration, and the spatial gradient of SST as an indicator of ocean fronts) to understand long-term trends in the environmental suitability for broad groups of zooplankton in the Southern Ocean. Using the relationship between zooplankton and environmental data collected by the CPR tows, the authors used statistical models to extrapolate information on the environmental suitability of zooplankton to unsampled areas. "Environmental suitability" was defined as the expected abundance of a species or group of zooplankton at a given location and time based on environmental properties and used as a measure of ecological niche.

Six key taxonomic groups of zooplankton were considered by Pinkerton et al. (2020)[1]: Copepoda (Calanoida), Euphausiidae (numerically dominated in SO-CPR data by *Thysanoessa macrura*, 64%; *E. superba* comprised only 9%), *Oithona similis*, and pteropods, Foraminifera and *Fritillaria* spp. Salps were rarely identified in the CPR samples. Analysis using Boosted Regression Tree (BRT) models provided insights into the patterns of and changes in environmental suitabilities for these broad zooplankton groups over the period 1997–2018. Analysis was also carried out for all these groups combined (total abundance). See Pinkerton et al. (2020) for a spatial plot of CPR samples, which are predominantly from East Antarctica and the Ross Sea region.

The modelling of Pinkerton et al. (2020) suggested higher environmental suitability for all zooplankton between the SAF and the Southern limit of the ACC and lower suitability to the north and south. Lower abundances of euphausiids were predicted south of the APF and higher abundances of copepods were predicted between the APF and the SAF. Modelled environmental suitability for pteropods was highest over the Ross Sea shelf.

For the key groups presented in this study (i.e., Euphausiidae, Copepoda (Calanoida and *Oithona similis*), and pteropods) we replotted the absolute-values of mean and long-term linear trends in environmental suitability from Pinkerton et al. (2020) (**Supplementary Figures 1,2**). Based on data from Pinkerton et al. (2020), time series of change in environmental suitability for total abundance over the past two decades were calculated for MEASO Sectors, Zones and Areas [**Figures 6** and **7** (Sectors, Zones) and **Supplementary Figure 3** (Areas)]. Based on Pinkerton et al. (2020), the highest increase in modelled environmental suitability for zooplankton (combined) across all Zones and Sectors was in the MEASO sea ice zone (+2.1% per year on average). Our analysis also showed that changes environmental suitability for zooplankton total abundance were

[1]See Pinkerton et al. (2020) for assumptions, limitations, and caveats of the analyses.

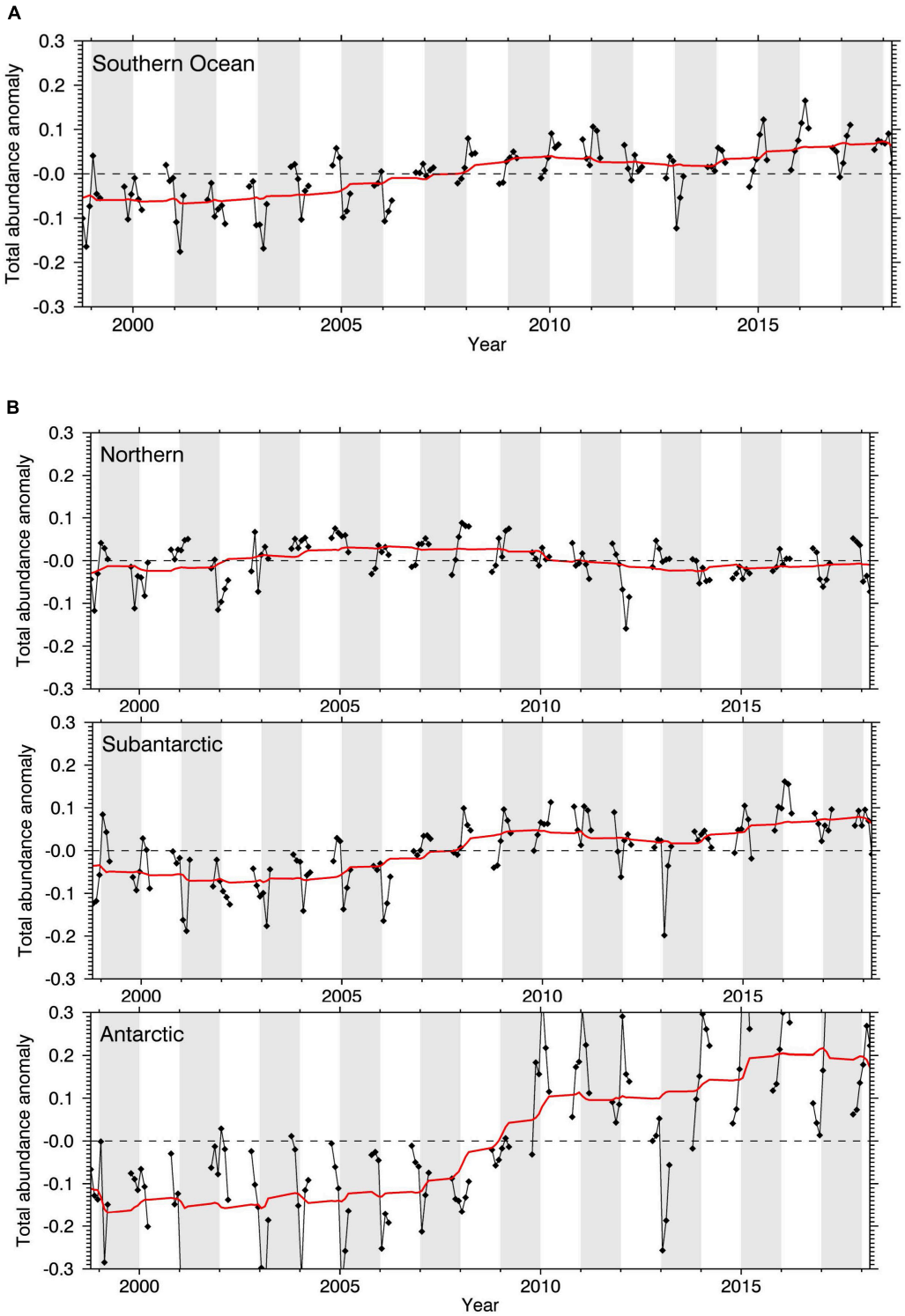

FIGURE 6 | Time series of change in environmental suitability for total zooplankton abundance, i.e., Euphausiidae, Copepoda (Calanoida and *Oithona similis*), and pteropods, from the combined Boosted Regression Tree model of Pinkerton et al. (2020) for the Southern Ocean Marine Ecosystem Assessment for the Southern Ocean (MEASO) **(A)** study area, **(B)** Sectors. Time Series change for each individual MEASO Zones and Area are given in **Figure 7** and **Supplementary Figure 3**, respectively. The environmental suitability anomaly (difference from the monthly climatological value) is shown for each month over period 1998–2018. Gray shading indicates calendar years. Black points and lines are monthly anomalies (differences from long-term monthly means). Red lines are smoothed changes (4-year running median).

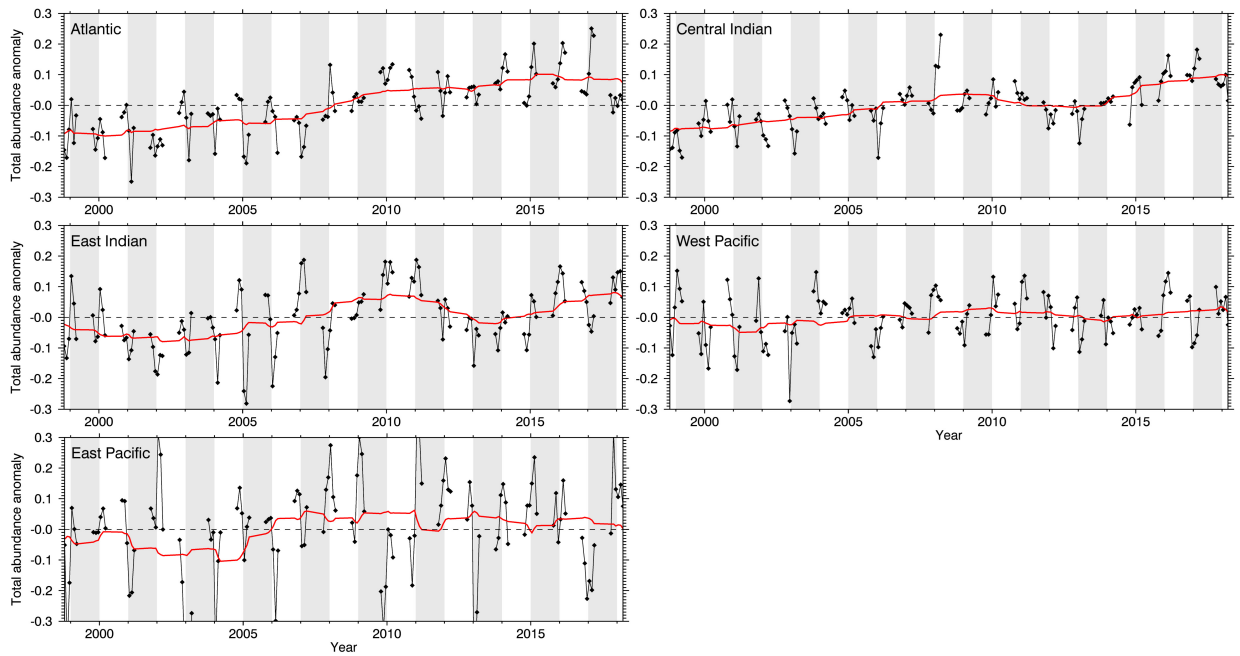

FIGURE 7 | Time series of change in environmental suitability for total zooplankton abundance, i.e., Euphausiidae, Copepoda (Calanoida and *Oithona similis*), and pteropods, from the combined Boosted Regression Tree model of Pinkerton et al. (2020) for Southern Ocean MEASO Zones. Time Series change for each individual MEASO Area are given in **Supplementary Figure 3**. The environmental suitability anomaly (difference from the monthly climatological value) is shown for each month over period 1998–2018. Gray shading indicates calendar years. Black points and lines are monthly anomalies (differences from long-term monthly means). Red lines are smoothed changes (4-year running median).

higher in the Atlantic Sector (1.1% per year) and Central Indian Sector (0.8% per year) than in the other MEASO Sectors, and statistically significant (p <0.05). For comparison, at the scale of the Southern Ocean, Pinkerton et al. (2020) reported that the average annual trend in environmental suitability for total zooplankton abundance over the same period was just 0.6%. Pinkerton et al. (2020) showed that changes in environmental suitability for zooplankton total abundance were predominantly driven by improving conditions for copepods (cyclopoid and calanoid trends of 0.6% per year on average), foraminifera (0.85% per year) and Fritillaria (0.8% per year); for euphausiids, the average annual trend was only 0.2%, and for pteropods there was no significant trend in modelled environmental suitability at the scale of the Southern Ocean.

Although environmental suitability modelling such as Pinkerton et al. (2020) can provide information on changes to amenable conditions for zooplankton, the analysis should be considered hypothetical in that it is not certain that zooplankton abundances actually change in response to these oceanographic drivers. In other words, ecological niches may expand, but populations size may not respond proportionately. Some evidence for this resilience of distribution was provided in the Atlantic sector, where Tarling et al. (2018) found that distribution centers of copepods had not shifted south over the last century to keep track with the warming thermal regime. Another caveat is that environmental conditions used to define the zooplankton habitat niche are necessarily limited to those for which information are available, and these are predominantly physical in nature. Unobserved ecological feedbacks can thus be missed. This, and small-scale issues, are reasons why only approximately half (at best) of observed variability in zooplankton abundances can be described by environmental-statistical models. Better understanding of the life histories and environmental and ecological dependencies of Southern Ocean zooplankton are as crucial as ever.

Additionally, broad groupings of zooplankton were used in Pinkerton et al. (2020) to avoid issues arising from difficulties in identifying some developmental stages of some species in CPR data. In particular, euphausiids are fragile with respect to the CPR collection process making their identification challenging. Genetic and image-analysis methods are under development for CPR data to address these identification issues (Pinkerton, unpublished data).

SUMMARIES AND ASSESSMENTS

A summary of the current role of these zooplankton taxa in the Southern Ocean, based on the information detailed in Sections Euphausiids (Family Euphausiidae), Copepods (Subclass Copepoda), Salps (Order Salpida), and Pteropods (Order Pteropoda) is presented in **Supplementary Table 1**. A summary of environmental tolerances of these taxa (based on recent empirical studies) are also presented in **Supplementary Table 2**.

An assessment of the influence of anticipated changes in key physical, chemical, and ecological drivers on the

TABLE 1 | Assessment* of the potential impacts of key physical and chemical drivers of change on the distribution and abundance of key Southern Ocean zooplankton taxa (based on information provided in Sections "Euphausiids (Family Euphausiidae), Copepods (Subclass Copepoda), Salps (Order Salpida), Pteropods (Order Pteropoda), and Past Changes in Zooplankton: A Modelled Example Using Continuous Plankton Recorder Data", including references cited therein). See **Supplementary Table 3** for a more detailed assessment of the potential future changes in these taxa (in response to some of these drivers) and their potential capacity for resilience.

Taxa	Wind	Sea ice	Sea surface temperature	Ocean circulation	Ocean stratification	Mixed layer depth	Ocean acidification	Extreme climate-related events	Climate indices
Antarctic krill	U	H	H	M	U	L	L	U	H
Other euphausiids	U	H	H	M	U	M	L	U	H
Copepods	U	U	U	U	U	U	U	U	U
Salps	M	M	H	H	M	M	L	H	H
Pteropods	U	M	H	U	M	M	H	U	H

Drivers may be direct or indirect and may not have an influence across all areas of the Southern Ocean, seasons, or life history stages. U = unknown/influence varies greatly according to species, L (blue) = low influence, M (orange) = medium influence, H (red) = high influence.
**This assessment represents the authors' expert consensus as explained in Section "Summaries and Assessments".*
*See **Supplementary Table 1** for a summary of the current role of these taxa in Southern Ocean ecosystems and **Supplementary Table 2** for environmental tolerances.*
NB: This is not a complete list of drivers. Extreme (high impact) climate-related events = e.g., upwelling events, very high air or sea temperatures events, or rapid loss of sea ice and/or intense storms that can collapse ice shelves or destroy habitat. Climate indices = e.g., ENSO, SAM.

distribution and abundance of these taxa is summarized in **Tables 1**, **2**. This assessment represents the authors' (unweighted) expert consensus based on current understanding and information detailed in Sections Euphausiids (Family Euphausiidae), Copepods (Subclass Copepoda), Salps (Order Salpida), Pteropods (Order Pteropoda) and Past Changes in Zooplankton: A modelled example using Continuous Plankton Recorder Data (including references cited therein). A qualitative assessment of the potential future changes in zooplankton in response to these drivers and their potential capacity for resilience is presented in **Supplementary Table 3** as a series of statements. This also represents the authors' (unweighted) expert consensus based on current understanding and information detailed in the Sections listed above (including references cited therein).

CONCLUDING COMMENTS

Understanding the processes by which key global and local drivers of change impact the habitat features, biodiversity, structure, functioning and variability of marine ecosystems across a range of spatial, temporal, and organizational scales is crucial to developing conservation and sustainable management strategies that can anticipate and respond to global change impacts. Zooplankton form an integral part of Southern Ocean marine ecosystems which are extensively connected to the global ocean (Murphy et al., 2021). Their inclusion in regional and circumpolar assessments is therefore vital to understanding present and future change in this globally important ocean and the ramifications for Earth System functioning (Murphy et al., 2008; Hofmann, 2016). Although a number of studies have recently assessed the potential future responses of these marine ecosystems to a changing Southern Ocean, few have provided detailed syntheses on the expected changes in zooplankton (Mackey et al., 2012; Hunt et al., 2016; Chown and Brooks, 2019; Siegert et al., 2019; Rogers et al., 2020).

This overview provides a synthesis of the current understanding of four key metazoan zooplankton taxa, euphausiids, copepods, salps and pteropods, which are important members of zooplankton communities and food webs across the Southern Ocean. It illustrates the range of life history strategies, habitat, and environmental associations and observed and modelled changes in their distribution and abundance across the circumpolar ocean. It has also highlighted their varied responses to physical, chemical, and ecological drivers and some of the mechanisms involved. Moreover, it has emphasized that despite the extensive research on Southern Ocean zooplankton (dating back to the 1872-6 HMS Challenger expedition Hosie et al., 2000), and growing awareness of the role of these taxa in modulating ecosystem structure and function, there are major gaps in our current understanding of their physiology, life history strategies and processes, population dynamics, distribution and abundance, food web and competitive interactions across a range of spatial and temporal scales. There are also gaps in our understanding of their roles in biogeochemical cycling and roles underpinning fisheries and wildlife tourism. Many of the limitations and uncertainties in this understanding (across a range of spatial, temporal, and organizational scales) can be attributed to the status of field, process and modelling studies of these taxa, including insights into their capacity for biological

TABLE 2 | Assessment* of the potential impacts of key ecological drivers of change on the distribution and abundance of key Southern Ocean zooplankton taxa (based in information in Sections "Euphausiids (Family Euphausiidae), Copepods (Subclass Copepoda), Salps (Order Salpida), Pteropods (Order Pteropoda), and Past Changes in Zooplankton: A Modelled Example Using Continuous Plankton Recorder Data", including references cited therein). See **Supplementary Table 3** for a more detailed assessment of the potential future changes in these taxa (in response to some of these drivers) and their potential capacity for resilience.

Taxa	Prey populations		Predator populations		Fisheries
	Microbiota (sea ice and sea floor)	Primary production	Predator populations	Recovery of historically harvested species (e.g., whales, seals)	
Antarctic krill	M	H	H	H	L
Other euphausiids	H	H	H	H	L
Copepods	U	H	M	U	L
Salps	U	H	U	U	U
Pteropods	U	H	U	U	U

Drivers may be direct or indirect and may not have an influence across all areas of the Southern Ocean, seasons, or life history stages. U = unknown/influence varies greatly according to species, L (blue) = low influence, M (orange) = medium influence, H (red) = high influence.
**This assessment represents the auhors' expert consensus as explained in Section "Summaries and Assessments".*
*See **Supplementary Table 1** for a summary of the current role of these taxa in Southern Ocean ecosystems and **Supplementary Table 2** for environmental tolerances.*

resilience. These reflect the difficulties in studying these taxa under laboratory conditions and sampling and observing them *in situ* across a range of spatio-temporal scales, particularly over large parts of the open ocean, within the sea ice zone, at depth, and during seasonal transitions and the winter months. There is also a paucity of multidecadal biological time series of sufficient duration to quantify the variability and rates of changes of relevant oceanic variables and zooplankton species or be definitive about the causal mechanisms (O'Brien et al., 2017; Cornils et al., 2018). Furthermore, the Southern Ocean is characterized by high natural spatial and temporal variability and has experienced ecosystem-level changes through the historical exploitation of marine living resources (Clarke et al., 2012). Observed changes in zooplankton are therefore currently difficult to attribute to specific climate or ecological processes.

Future Prognoses

Many current scenarios of future changes in key physical, chemical, and ecological drivers that are relevant to zooplankton distribution and abundance are highly uncertain. This can be attributed in part to the current suite of projections of physical and chemical drivers (based on current global climate models – i.e., CMIP5, available at the time of writing) that are poorly constrained and highly uncertain. These models are either not at the appropriate spatial or temporal scales or do not resolve key processes (e.g., primary production, sea ice and oceanic processes- except for the position of the APF, see Morley et al., 2020) to enable the interpretation of biological change in the Southern Ocean (Murphy et al., 2018). In addition, scenarios of other key local drivers (e.g., fisheries, predator impacts, whale recovery, tourism, pollution, and invasive species) also remain uncertain (see also Grant et al., 2021). The limitations and uncertainties surrounding the fundamental understanding of these taxa (as discussed above) together with the status of these scenarios, means that there is insufficient data to provide comprehensive prognoses for future changes in zooplankton with definitive levels of confidence (sensu Intergovernmental Panel on Climate Change, IPCC, e.g., Mastrandrea et al., 2010) either within each of the MEASO areas or at specific time and space scales relevant to the needs of conservation and management (see **Box 1**). Future prognoses with attached levels of confidence have, however, been made for Southern Ocean zooplankton within the IPCC's Working Group 2 reports (e.g., IPCC, 2014) and Special Report on the Ocean and Cryosphere in a Changing Climate (IPCC, 2019). McBride et al. (2021) have considered the impacts of climate-driven environmental change on Antarctic krill in the context of CCAMLR fisheries management. The potential impacts of change on Antarctic krill within CCAMLR statistical Area 48 have also been considered by Murphy et al. (2018) and serve as a model for other species and regions (see also future work below). The future prognoses presented here represent the authors' consensus view based on expert knowledge and the best available published evidence. Indications are that the response of these zooplankton to future change will be complex and vary across both life history stages and scales of space, time, and ecological organization, against a backdrop of natural variability. Their response to multiple drivers (including their variability over space and time and their additive, synergistic, or antagonistic effects) and their potential for biological resilience (Murphy et al., 2016; Gruber et al., 2021) will further add to this complexity but remain largely unexplored.

Population Level Changes

Based on our current understanding of the key zooplankton taxa, observed changes and the mechanisms involved, anticipated

BOX 1 | Research gaps and priorities: Current limitations to projections of future zooplankton change.

To develop robust future projections of changes in the distribution and abundance of zooplankton communities within the MEASO assessment areas requires a number of elements. These include (1) scenarios of key physical, chemical and ecological drivers within a given assessment area (based on Representative Concentration Pathway emissions scenarios where relevant), (2) mechanistic understanding of the impacts of key drivers on zooplankton within a given assessment area, and (3) development of zooplankton (and ecosystem) models that can be coupled with scenarios of key drivers to project qualitative or quantitative changes in zooplankton populations or communities within a given area. Development of these elements, together with clarification of the uncertainties and caveats involved, will facilitate conservation and management options for Southern Ocean ecosystems. Key limitations currently include:

Fundamental understanding of zooplankton ecology over a range of spatio-temporal and organizational scales (from local to circumpolar, seasonal to multi-decadal, and species to ecosystems) and the mechanistic processes involved. These limitations reflect the difficulties in studying zooplankton in the laboratory and the field, and the lack of time series data essential for detecting long-term trends in key areas, e.g.,:

- Physiological (energy and nutrient demands, tolerance to environmental stressors, such as temperature, starvation, oxygen, and pH– see also drivers below), morphological and behavioral traits.
- Growth, development and reproduction, feeding and dietary preferences, food quality.
- Life histories, traits, and strategies (including behaviors during life history events such as foraging and reproductive strategies, migrations, seasonal development and overwintering, competitive/anti-predator behaviors) and phenology.
- Phenotypic plasticity.
- Role in food webs (trophic ecology including modes of feeding, strength and direction of predator-prey interactions, ingestion and egestion rates, energy transfer, top-down and bottom-up controls, competition), particularly during winter when phytoplankton production in water column and sea ice is limited.
- Role in biogeochemical cycling (i.e., particle export and sequestration of organic material and the chemical cycling of nutrients).
- Distribution (horizontal and vertical), abundance/biomass and production estimates, spatial population connectivity, demography and community composition.
- Hotspot locations for key ecological processes (e.g., spawning, larval development and recruitment, overwintering, migrations, feeding, population concentrations, connectivity and advection routes, biogeochemical cycling).
- Natural variability in zooplankton dynamics (across seasonal to multi-decadal timescales).
- Changes in zooplankton dynamics that represent deviations from assumed natural variability.
- Key natural environmental and anthropogenic drivers of zooplankton dynamics, variability and change. Mechanistic understanding of their impacts, including additive/synergistic/antagonistic effects of multiple drivers, e.g.,:
  - Sea ice dynamics, ocean warming, stratification, circulation, acidification, and climate oscillations.
  - Prey (e.g., phytoplankton biomass, species assemblages) and predator dynamics (e.g., predator biomass, species assemblages, recovery of cetaceans).
  - Current fisheries (including their impacts on different life cycle stages).
  - Other possible drivers (e.g., pollution, tourism, invasive species).
- Resilience of zooplankton to multiple drivers of change (including additive, synergistic, or antagonistic effects).

Ecosystem models that can enhance understanding of zooplankton dynamics, variability and change, ecosystem structure and function, and inform regional and global assessments, conservation, and management decisions. There is a paucity of models underpinned by (a) to conceptualize and quantify ecological processes relevant to zooplankton over a range of spatio-temporal and organizational scales, e.g.,:

- Individual species models (e.g., life history models representing life history traits and rates, life history strategies, physiological, morphological, and behavioral traits, biogeochemical cycling and simulating the effects of drivers on key life history stages and processes, i.e., life history models embedded in full 3D ocean physics models that include sea ice).
- Food web models (e.g., representing regional and temporal variations in zooplankton community composition, trophic links and alternative energy pathways to higher trophic levels).
- Biogeochemical models (e.g., representing the role of different zooplankton species).
- End-to-end ecosystem models that integrate physical, biogeochemical and biological processes across multiple species, trophic levels, and spatio-temporal scales.

Comprehensive standardized future scenarios of key physical, chemical, biological, and ecological drivers including:

- Scenarios for sea ice, ocean warming, stratification, circulation and acidification and phytoplankton change. The current suite of global climate model projections available [i.e., CMIP(5) at the time of writing] to develop scenarios of zooplankton drivers under different emission pathways are poorly constrained and highly uncertain. They are too low in spatial resolution (>100 km) to resolve many key processes relevant to these taxa (e.g., related to sea ice, ice shelves, upwelling, cross-shelf exchange, connectivity, and retention), which often occur over smaller spatial scales. Differentiating between patterns of natural internal variability versus global anthropogenic change in these drivers is also complex. Local modes of atmospheric variability (e.g., Southern Annular Mode, Amundsen Sea Low, El Niño events) and potential extreme climate-related events may further influence ocean, biogeochemical and sea ice processes.
- Scenarios for predator and prey dynamics, recovery of cetacean populations, and fisheries. Aside from those relevant to Antarctic krill within the Scotia Sea ecosystem, there are few available scenarios of changes in these ecological drivers.

Coupled physical, chemical, and biological models that can be forced by future scenarios of key drivers to generate qualitative and quantitative projections of future changes in zooplankton species, communities, and ecosystems across a range of spatio-temporal scales.

changes in sea ice, ocean warming, ocean circulation, mixed layer depth, primary production, and predators were considered here as important direct and indirect drivers of future change in these biotas. Whilst (the anticipated direction of) many of these drivers are expected to have an overall negative effect (e.g., decreased egg production rates, growth, food availability/suitability, feeding efficiency, availability of suitable habitat for spawning, reproduction and overwintering, population size and abundance, range contraction, and competition) on some species (e.g., *E. superba*, *E. crystallorophias*), other species may experience an overall positive effect. For example, increased growth rates, feeding efficiency, habitat availability, population size and abundance, and range expansion of *T. macrura*, salps, and pteropods. A potential positive feedback loop, generated by the recovery of whale populations in the short term (see McBride et al., 2021), on phytoplankton productivity may also result in increased abundance of *E. superba, E. crystallorophias*, and *T. macrura* (Schmidt et al., 2011; Ratnarajah et al., 2014). For some species and localities, however, the positive effects of some

drivers may be offset by the negative effects of other drivers – for example, enhanced feeding efficiency of *E. crystallorophias* in response to increased diatoms in phytoplankton communities may not be sufficient to counteract the impacts of sea ice loss on spawning habitat and reproductive success. Ocean acidification is expected to have negative consequences for the thecosome pteropods, starting in the higher latitudes first. It must be stressed however, that these drivers may not have an influence across all life stages of the taxa considered, or across all areas of their distribution. Competitive interactions brought about by driver impacts will also be important, but the nature of many of these are unknown. We also only considered the potential impacts of each driver in isolation and recognize that the additive, synergistic, or antagonistic impacts of multiple drivers on these taxa will be important and warrants further attention. Although we did not assess the impacts of some other global drivers, such as ocean deoxygenation, increased ultraviolet radiation, or recovery of the ozone hole over Antarctica and the Southern Ocean, or local drivers, such as pollution (e.g., microplastics), invasive species, parasites, or pathogens (see Grant et al., 2021), existing and emerging research suggests that these may also elicit future changes in zooplankton (Flores et al., 2012a; Rowlands et al., 2021). All of these will have important implications for the dynamics of zooplankton population dynamics and their spatial connectivity.

Community Level Changes

Although not considered explicitly in this assessment, predicting changes in zooplankton community dynamics will be key to predicting the resultant effects on regional food webs and ecosystem structure and functioning. As we have noted, the range of zooplankton communities that occupy different regions of the Southern Ocean are often represented by changes in the balance of taxa or in the abundance of species as opposed to fundamentally different faunas (see Murphy et al., 2021). Collectively, these communities support an array of biodiversity and energy pathways that enable the maintenance of ecosystem structure and functioning (Murphy et al., 2012a, 2016; Barnes and Pálinkó, 2017; Trebilco et al., 2020; McCormack et al., 2021). These include the classic short, efficient energy pathway from phytoplankton through to baleen whales *via* Antarctic krill. This was long viewed as the dominant food chain in the Antarctic marine ecosystem and in some areas, such as the southwest Atlantic sector, sustains large populations of higher trophic level predators (Clarke, 1985; Hill et al., 2006; Murphy et al., 2007a, 2012a; Siegel, 2016; Saunders et al., 2019). There are, however, alternative pathways that transfer energy to higher trophic levels and sustain other predators less dependent on krill including a range of seals, sea birds, icefish, toothfish and toothed whales. These pathways may be dominated for example, by copepods (Murphy et al., 2012a) or salps (Atkinson et al., 2004). Although understanding of the regional and temporal variations in these alternative pathways is emerging (Murphy et al., 2013; Hill et al., 2021) and such pathways may provide different links between pelagic-benthic and pelagic-mesopelagic communities, unless primary production changes they cannot support the same degree of predator demand as the phytoplankton-krill-predator pathway (Murphy et al., 2007a). This is because their increased complexity and concomitant trophic transfers are associated with greater energy loss (Murphy et al., 2012a, 2016). Changes in structure and dominance characteristics of zooplankton communities, the causal mechanisms, and the effects on spatio-temporal variations in these energy pathways (and interactions between them) will therefore be important in interpreting future changes in Southern Ocean ecosystems.

Of greatest concern south of the APF is a shift from Antarctic krill dominated communities in the HNHC waters of the Southwest Atlantic Sector, to communities dominated by salps and/or copepods in response to ocean warming and sea ice loss. Such a shift would have important consequences for food webs here, including species that rely on Antarctic krill as a food source, particularly higher trophic level predators (see Bestley et al., 2020). Disruption of the short, energetically efficient food chain afforded by Antarctic krill may not be sufficient to support current levels of predator populations in the region. Changes in grazing pressure under the dominance of salps and/or copepods (which favor smaller phytoplankton species than ingested by Antarctic krill) may also have a top down influence on primary producers and their community dynamics and dominance patterns (see Pinkerton et al., 2021). Crucially this shift would also affect the operation and success of the Antarctic krill fishery (see Trebilco et al., 2020), the mackerel icefish, Antarctic and Patagonian toothfish fisheries, and wildlife tourism (see Grant et al., 2021). Consequences for regional biogeochemical cycling and contributions to climate regulation would also ensue (see Henley et al., 2020). Similarly, a shift from *E. crystallorophias* dominated communities in the neritic regions and sea ice zone of the high Antarctic to ones dominated by Antarctic krill, *Thysanoessa macrura*, and/or salps in response to ocean warming and sea ice loss will have several consequences for food webs, including for predator populations that rely on *E. crystallorophias,* and for primary producers and their community dynamics. There will also be effects on wildlife tourism, regional biogeochemical cycling, and climate regulation associated with such shifts in dominance. Ocean warming may also generate a shift in open ocean communities which are currently dominated by copepods and indirectly support the Antarctic krill fishery, wildlife tourism and potentially contribute significantly to biogeochemical cycling and carbon sequestration. Although overall increases in salps in open ocean (and other zooplankton) communities may have negative consequences for ecosystems services, they could enhance the potential for carbon export and support benthic communities (Trebilco et al., 2020). The implications for the loss of pteropods from the various zooplankton communities discussed here and the food webs they are part of, in response to increased ocean acidification, are less clear (Hunt et al., 2008). These potential shifts highlight the urgent need for improved research into zooplankton species other than Antarctic krill[2].

[2]A Web of Science search (using appropriate terms to capture Southern Ocean research on the four taxa and key species examined in this study) reveals a prevalence of publications on krill and Antarctic krill over the past 10 years, compared with copepod, salps and pteropods.

The characterization of zooplankton communities in space and time across the Southern Ocean is challenging, especially given the vast scale and oceanographic complexity (Wiebe et al., 2017; Pinkerton et al., 2020), and relatively few studies have examined community dynamics and interactions. Nevertheless, an understanding of shifts in dominance at the community level will reveal important competitive and trophic interactions that may be missed if focusing solely on population level responses to change. A shift from autecological to synecological studies that examine life history traits and strategies, population and community dynamics is therefore required to facilitate more robust predictions of the cascading effects of global change through Southern Ocean food webs, and the associated top down and bottom up forcings.

Resilience

Just as some species may be vulnerable to drivers of future change, they may also be resilient (Keister et al., 2012; Murphy et al., 2016; Tarling et al., 2018). Resilience (sensu Oliver et al., 2015a) has gained increasing attention in interpreting change impacts on zooplankton and other marine species and for its application to ecosystem based management (Richardson, 2008; Watters et al., 2013; Constable et al., 2014a). There is also recognition that community dynamics may have potentially profound consequences for the resilience of ecosystem functions, including those upon which humans depend (Oliver et al., 2015b). Despite this, current projections of species and ecosystem change do not account for the capacity for resilience, for example the ability of communities to retain locations and distributional ranges (Angilletta, 2009; Tarling et al., 2018) and maintain processes that contribute to ecosystem function. Nor do they account for the negative impacts on biological resilence, particularly in response to multiple drivers of change.

Although we considered the potential resilience of zooplankton taxa to the impacts of key drivers, they are uncertain. Some of the taxa assessed here, including *E. superba*, *Thysanoessa macrura*, some copepods and salps, exhibit varying degrees of phenotypic plasticity and high variabilities in their life history strategies which confer their potential resilience to some drivers, at least up to a certain level. *E. crystallorophias*, however, has a limited thermal range and their genetic adaptation to past periods of increased glaciation imply that it is unlikely to be resilient to future climate change. The seasonal Ωar undersaturated conditions that thecosome pteropods already experience, together with an ability to maintain shell integrity may be indicative of a level of resilience. This, however, may come at a metabolic cost that is unlikely to be maintained over the long-term. A concerted effort to parameterize potential resilience and reduce associated uncertainties will enhance predictions of the distributional range of zooplankton species and communities (Tarling et al., 2018). Given that Southern Ocean zooplankton will be under the complex spatially and temporally variable influence of multiple drivers of change, further research into the individual as well as the additive, synergistic, or antagonistic effects of these on resilience is urgently required (Murphy et al., 2016; Gruber et al., 2021).

These zooplankton taxa dominate the mid trophic level of many Southern Ocean food webs, transferring energy from lower to higher trophic levels. The low functional redundancy (i.e., a small number of species performing the majority of core ecological functions) of Southern Ocean food webs at this key trophic level renders these ecosystems particularly sensitive to change (Atkinson et al., 2014; Murphy et al., 2016). Understanding the influence of community dynamics on the manifestation of alternative energy pathways (Ducklow et al., 2007; Ainley et al., 2015) and the resilience of ecosystem functions is therefore also integral to predicting change.

Consequences for Ecosystem Structure and Functioning

Given the current understanding of the role of dominant zooplankton taxa assessed here in Southern Ocean ecosystems, it is clear that future changes in their population and community dynamics will have potentially wide ranging and complex consequences for biodiversity and ecosystem structure and functioning, including ecosystem services. Future changes in these zooplankton communities may alter food web connections within regional ecosystems (see McCormack et al., 2021), with implications for biogeochemical cycling, carbon flux and sequestration (see Henley et al., 2020), population and community dynamics, and energy flows to benthic communities (see Brasier et al., 2021) and between primary producers (see Pinkerton et al., 2021) through to mid- (see Caccavo et al., 2021) and higher trophic level predators (see Bestley et al., 2020), fisheries production, and wildlife tourism (see Rogers et al., 2020; Trebilco et al., 2020; Cavanagh et al., 2021; Grant et al., 2021). These may have ramifications for the resilience of population-, community- and ecosystem-level structure and functioning, and the emergent properties of regional ecosystems across the Southern Ocean. In addition, these zooplankton may also be involved in feedback process that modify the physical and chemical conditions in the Southern Ocean and regional climate processes (see Henley et al., 2020). Before we can predict the resultant effects on whole ecosystems and socioeconomics with any level of confidence, however, we must address key knowledge gaps on the complex interactions and mechanisms associated with zooplankton dynamics, their functional roles, and their sensitivities to drivers of change.

Future Work: Moving Toward Robust Quantitative Projections

The current trajectory of global greenhouse gas emission pathways (IPCC, 2018, 2019, 2021) means that we may not be on track to limit global warming to 1.5°C above pre-industrial levels and so we must accept that future climate change will be rapid, large ecological changes will occur, and future research must hence be centered on providing options for conservation and management. Robust qualitative and quantitative projections of future changes in Southern Ocean zooplankton are therefore needed to support global

and regional assessments, and conservation and ecosystem-based management strategies that can anticipate or adapt to natural and anthropogenically driven change. As such, they must be focused on the appropriate species (and life history stages), processes, space, and timescales. Projections of the distributions and abundances of zooplankton populations and communities can be used to assess how these taxa may directly or indirectly influence the structure and functioning of Southern Ocean ecosystems, such as biodiversity, food webs, biogeochemical cycling and climate regulation, energy transfer to higher trophic level predators, and provisioning of fisheries and wildlife tourism. This requires three key areas of development. Firstly, a comprehensive understanding of zooplankton ecology, the internal and external drivers of zooplankton dynamics (e.g., ontogenic and species-specific physiology, morphology, behavior, dietary preferences and feeding strategies, life history strategies, populations, and community structure, distributions and dominance patterns, spatial connectivity and food web interactions, etc.) and seasonal development, past and present variability and change in zooplankton dynamics, attribution of the causes of zooplankton change to natural versus anthropogenic drivers, zooplankton resilience, and the mechanisms involved. Secondly, a suite of ecological models, including coupled physical, biogeochemical, and biological models, that can conceptualize and quantify these and relevant ecological processes. Thirdly, by driving these models with regionally appropriate scenarios of changes in key natural and anthropogenic drivers, robust projections of future changes in zooplankton can be made across a range of spatial, temporal, and organizational scales. Unfortunately, detailed knowledge (both qualitative and quantitative) for many zooplankton species, life history stages, populations and communities is limited to a few areas, and primarily during the austral spring/summer, and the underlying processes and causal mechanisms of their dynamics are poorly understood. Added to this scarcity, zooplankton data are not well centralized – they are dispersed across many storage platforms, in different formats, and in some cases are inaccessible. Whilst progress has been made in data synthesis and model development for some species (e.g., Antarctic krill) and scenarios and projections based on these, projections for zooplankton across the MEASO Areas and other key areas that can support policy decisions are restricted. Current key limitations are outlined in **Box 1**.

Given the mounting pressures of anthropogenic change, research resources need to be focused on the timely delivery of tailored information to policymakers that can support conservation and management options in the near-term. A coherent strategy that prioritizes Southern Ocean zooplankton research over the coming years to achieve this is therefore urgently required. Such a strategic approach (e.g., see **Box 2**) has already begun for Antarctic krill in the context of fisheries management through initiatives such as ICED and the SCAR Krill Action Group (SKAG) (Murphy et al., 2018; Meyer et al., 2020). An all-encompassing set of priorities for zooplankton is yet to be fully explored and consolidated, and will be a future collaborative activity of ICED.

BOX 2 | Research gaps and priorities: Improving projections of future zooplankton change.

Robust qualitative and quantitative projections of zooplankton change are urgently needed to undertake assessments of current and future risks and inform conservation and management options for Southern Ocean ecosystems over the coming decades. A strategy for zooplankton research that prioritizes aspects in **Box 1** to deliver these projections is therefore warranted. This must address knowledge gaps in fundamental (qualitative and quantitative) ecological understanding and facilitate model development by focusing on:

Key species and communities that are of importance to conservation and management and/or assumed or known to have important roles in ecosystem structure and functioning (including ecosystem services) either now or in the future.

Key regions and habitats that are of importance to the development of conservation and management strategies (this includes not only for, e.g., existing/planned Marine Protected Areas and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Statistical Areas, but other ecologically important areas or hotspots that influence zooplankton dynamics). This should also include regions and habitats (and seasons) that are poorly sampled.

Projections of zooplankton change over short timescales (and within key regions) that are relevant to conservation and management (e.g., the next 3, 5 to 10 years in addition to the next few decades) and consider, incorporate, and communicate the uncertainties underpinning them (e.g., in understanding of ecological processes and scenarios of key drivers, and hence model parameterization).

Examples of near-term (2–5 years) and longer-term (>5 years) research priorities (in addition to information on habitats) include:

<u>Near-term research priorities</u>

Synthesis of existing data on distribution and abundance: Mine, collate and synthesize existing circumpolar-scale information and data on the spatio-temporal distributions of key taxa across key regions and habitats (particularly sea ice environments).

Life history models: Develop life history models for key species (that incorporate phenotypic plasticity) can be used to estimate population dynamics across space and time scales. In combination with observational data, they can be used to explore the biological and environmental factors that impact critical life history processes/events and drive population dynamics, thus giving an indication of the vulnerabilities of species to changing conditions. They can also be used to explore species influence on ecosystem functioning including energy flows, nutrient cycling, climate regulation, and the provisioning of fisheries and wildlife tourism under changing conditions.

Biogeochemical roles: Improve understanding of the role of zooplankton in biogeochemical cycles, particularly in carbon budgets and particulate organic matter export and remineralization.

Communication of uncertainties and risks: Evaluate and communicate all sources of uncertainty (e.g., in ecological, physical, and chemical processes, observations, model formulations, parameter estimates, model evaluation, etc.) and their incorporation into projections of change. Explore ways of dealing with current uncertainties. E.g., approaches that evaluate risks (based on the magnitude and probability of change) and incorporate uncertainty rather than specific trajectories of zooplankton change under future scenarios.

Resolution of conflicting views: Resolve conflicting views in zooplankton ecology, e.g., of trends in distribution and abundances in Antarctic krill, poleward shifts, and resilience of zooplankton in response to multiple drivers of environmental change.

<u>Longer-term priorities</u>

Mechanistic understanding: Identifying the underlying mechanisms that control observed patterns of zooplankton dynamics is crucial to predicting how they will respond to future change. A focus on generating specifically defined rationales explaining observed patterns of zooplankton communities and environmental variables, particularly sea ice, ocean temperatures and ocean acidification is needed. These will be important for informing

(Continued)

BOX 2 | (Continued)
the development of ecological models, projections of change, and testing conservation and management approaches.
Life histories, traits, and strategies: These are fundamental determinants of zooplankton population dynamics and their responses to change. They also underpin conservation and ecosystem-based management decisions and stock assessments. A more complete understanding and quantification of these aspects can reveal many of the factors that constrain the success of different species across spatial and temporal scales. This forms the basis of predicting zooplankton responses to future change and improving conservation and management decisions.
Life history models: Refine life history models based on improved mechanistic understanding.
Community dynamics and interactions: Shift from autecological to synecological studies to improve understanding of community dynamics (i.e., changes in community structure, dominance, and distribution patterns), trophic interactions with other taxa, and the seasonal development of these processes.
Biogeochemical roles: Develop a more complete understanding of the role of zooplankton in biogeochemical cycling and feedbacks.
Uncertainties and risks: Continue to evaluate, refine, and communicate all sources of uncertainty and communicate associated risks.
Promote data availability and application: Continue to mine, collate, and synthesize data relevant to zooplankton habitats, distribution and abundance and promote open access.

Such a strategy must be developed by a broad range of relevant stakeholders including ecologists, physicists, biogeochemists, climate and conservation scientists, social scientists, environmental economists, fisheries managers, industry representatives, and relevant programmes and initiatives such as ICED, MEASO, SCAR (and relevant research programmes therein including SKAG, SCAR Plastic in polar environments Action Group, PLASTIC-AG, and the Southern Ocean Observing System, SOOS), the Antarctic Treaty System (including CCAMLR and the Committee for Environmental Protection, CEP), and international treaties and organizations (e.g., the International Whaling Commission, IWC, the Agreement on the Conservation of Albatrosses and Petrels, ACAP, the IPCC, and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, IPBES). This will also foster a shared understanding of the challenges involved and the nature of existing and new multi- and interdisciplinary research approaches needed to address them.

Whilst extensive future circumpolar field efforts can improve data coverage, offering much needed spatially and temporally comprehensive insight into population and community dynamics and ecological processes, they cannot yield near-term support for conservation and management. Likewise, many of the large international observational programmes that are underway or being developed to detect change in physical, chemical, and biological aspects of the Southern Ocean will take some years to fully develop. This means that our ability to be definitive about the attribution of zooplankton and wider ecological changes to natural and/or anthropogenic change in this highly variable ocean is limited. In the interim, focusing on research areas that can support model parameterization and development, particularly better mechanistic understanding, will be important. This will allow us to test and explore ecological processes based on the best available knowledge, while communicating assumptions and uncertainties. It will also allow us to constrain model projections of future zooplankton change, enabling assessments of the potential range of impacts of change together with the associated uncertainties and risks they entail.

A strategy for zooplankton research must therefore address knowledge gaps in the fundamental (qualitative and quantitative) ecological understanding and the model development required to generate robust projections of ecological change and undertake assessments of current and future risks. We still need very basic, circumpolar-scale information on the spatio-temporal distributions of key taxa across a range of habitats (particularly sea ice environments) throughout the Southern Ocean. The mining, collation and synthesis of the large volumes of existing data provides a tractable approach to address this primary priority issue (e.g., Cornils et al., 2018). However, knowledge of distribution, abundance, life history traits and strategies and the seasonal development of population dynamics, biogeochemical roles and food web interactions are also a priority. These aspects in turn underpin models and projections of responses to future change, which also need to incorporate detailed assessments of the underpinning model assumptions and various other sources of model uncertainty. Such an endeavor requires an international collaborative effort and will benefit from the support of national Antarctic research programmes and international research programmes and initiatives, such as the Southern Ocean focused ICED, SCAR, and the global Integrated Marine Biosphere Research project (IMBeR).

DATA AVAILABILITY STATEMENT

The data used in this study are available in the cited literature. Further details of methods and data and additional references are included in the **Supplementary Material**. The original contributions presented in this study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this article does not involve new or lab fieldwork.

AUTHOR CONTRIBUTIONS

NMJ, EJM, and AJC conceived the project. NMJ coordinated the project, leading and significantly contributing to the development, and writing and editing of the manuscript. EJM and AA contributed significantly to the development and writing of the manuscript. SLH, SK, CSR, RD, AA, KMS, EAP, BPVH, and GAT contributed significantly to writing the manuscript (particularly Sections 1–5). MHP, GAT, and AA contributed to

figure production. MHP provided analyses of SO-CPR data. All authors contributed to the writing of the manuscript, expert consenus assessments, and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.624692/full#supplementary-material

Supplementary Figure 1 | Modelled environmental suitability for **(A)** total zooplankton, i.e., Euphausiidae, Copepoda (Calanoida and *Oithona similis*), and pteropods, **(B)** Euphausiidae, **(C)** Copepoda (Calanoida), **(D)** *Oithona similis*, and **(E)** pteropod abundance from the combined Boosted Regression Tree model of Pinkerton et al. (2020) showing average modelled daily abundance (counts per 5 nautical mile CPR segment) over the 6 months (October to March) and years 1998–2018. No analysis was possible for areas shown in white, for example because environmental conditions were outside the observations. Black lines are nominal positions of (from north): Subantarctic Front, Antarctic Polar Front, average maximum northern extent of seasonal sea ice (dashed), and the Southern Boundary of the Antarctic Circumpolar Current.

Supplementary Figure 2 | Modelled environmental suitability for **(A)** total zooplankton, i.e., Euphausiidae, Copepoda (Calanoida and *Oithona similis*), and pteropods, **(B)** Euphausiidae, **(C)** Copepoda (Calanoida), **(D)** *Oithona similis*, and **(E)** pteropod abundance from the combined Boosted Regression Tree model of Pinkerton et al. (2020) showing long-term, linear trends in abundance (trend units are 1000 counts per 5 nautical miles of CPR segment per year). Sen slope values showing the changes in modelled abundance at each point. Colored vales are significant ($p < 0.05$). Warm colors indicate a positive (increasing) trend in the environmental suitability, and cold colors a negative (decreasing) trend. White areas have no significant trend. Areas shown gray have no data. Black lines are nominal positions of (from north): Subantarctic Front, Antarctic Polar Front, average maximum northern extent of seasonal sea ice (dashed), and the Southern Boundary of the Antarctic Circumpolar Current.

Supplementary Figure 3 | Time series of change in environmental suitability for total zooplankton abundance, i.e., Euphausiidae, Copepoda (Calanoida and *Oithona similis*), and pteropods, from the combined Boosted Regression Tree model of Pinkerton et al. (2020) for individual Marine Ecosystem Assessment for the Southern Ocean (MEASO) Areas. Imbedded three letter codes in figure relate to MEASO sectors (first two letters) and zones (last letter). Sectors are Atlantic (AO), Central Indian (CI), East Indian (EI), West Pacific (WP), and East Pacific (EA). Zones are Antarctic (A), Subantarctic (S), Northern (N). See also **Figure 1** in main paper. The environmental suitability anomaly (difference from the monthly climatological value) is shown for each month over period 1998–2018. Gray shading indicates calendar years. Black points and lines are monthly anomalies (differences from long-term monthly means). Red lines are smoothed changes (4-year running median).

Supplementary Table 1 | Current role of zooplankton in Southern Ocean ecosystems (based on information provided in taxonomic Sections Euphausiids (Family Euphausiidae), Copepods (Subclass Copepoda), Salps (Order Salpida), and Pteropods (Order Pteropoda)). Roles may vary across areas of the Southern Ocean, seasons, or with life history stages. See **Figure 1** for locations and key to MEASO areas. See **Supplementary Table 2** for environmental tolerances.

Supplementary Table 2 | Environmental tolerances of zooplankton in Southern Ocean ecosystems (based on empirical studies). n/a = data not available.

Supplementary Table 3 | Future prognoses* for Southern Ocean zooplankton in response to changes in key physical, chemical, and ecological drivers (based on information provided in Sections Euphausiids (Family Euphausiidae), Copepods (Subclass Copepoda), Salps (Order Salpida), Pteropods (Order Pteropoda), and Past Changes in Zooplankton: A modelled example using Continuous Plankton Recorder Data (including references cited therein)) and **Supplementary Tables 1, 2**. Prognoses may vary across areas of the Southern Ocean, seasons, or life history stages. See **Figure 1** for locations and key to MEASO areas.

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Using a risk assessment framework to spatially and temporally spread the fishery catch limit for Antarctic krill in the west Antarctic Peninsula: A template for krill fisheries elsewhere

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The west Antarctic Peninsula is an important breeding and foraging location for marine predators that consume Antarctic Krill (*Euphasia superba*). It is also an important focus for the commercial fishery for Antarctic krill, managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Aiming to minimise ecosystem risks from fishing, whilst enabling a sustainable fishery, CCAMLR has recently endorsed a new management framework that incorporates information about krill biomass estimates, sustainable harvest rates and a risk assessment to spatially and temporally distribute catch limits. We have applied a risk assessment framework to the west Antarctic Peninsula region (Subarea 48.1), with the aim of identifying the most appropriate management units by which to spatially and temporally distribute the local krill catch limit. We use the best data currently available for implementing the approach, recognising the framework is flexible and can accommodate new data, when available, to improve future estimates of risk. We evaluated 36 catch distribution scenarios for managing the fishery and provide advice about the scale at which the krill fishery can be managed. We show that the spatial distribution with which the fishery currently operates presents some of the highest risks of all scenarios evaluated. We highlight important issues that should be resolved, including data gaps, uncertainty and incorporating ecosystem dynamics. We emphasize that for the risk assessment to provide robust estimates of risk, it is important that the management units are at a similar scale to ecosystem function. Managing the fishery at small scales has the lowest risk but may necessitate a high level of management interaction. Our results offer advice to CCAMLR about near-term management and this approach could provide a template for the rest of the

southwest Atlantic (Area 48), or fisheries elsewhere. As each data layer influences the outcome of the risk assessment, we recommend that updated estimates of the distribution, abundance and consumption of krill, and estimates of available krill biomass will be key as CCAMLR moves forward to develop a longer-term management strategy.

KEYWORDS

fisheries management, predation pressure, ecosystem risk, Antarctica, Antarctic krill, CCAMLR

Introduction

The west Antarctic Peninsula provides critical breeding and foraging habitats for numerous marine predators that consume Antarctic krill (*Euphasia superba*; hereafter krill). Krill are a key component of the Antarctic marine ecosystem and provide an important food resource for many predators, including cetaceans, seabirds and fish (Tranter, 1982). Simultaneously, this region is an important area for the commercial krill fishery which has the potential to impact predators by removal or displacement of prey items and may have consequences on reproductive performance or adult survival (e.g. Croxall et al., 1999; Hinke et al., 2017; Watters et al., 2020). The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) manages the fishery with the objective of minimising risks associated with harvesting that may affect both the krill stock and dependent predator populations (CCAMLR, 2013, Article II).

In 2019, CCAMLR's Working Group on Ecosystem Monitoring and Management (WG-EMM) agreed a work programme to implement a revised management strategy for the krill fishery. This takes steps towards generating an integrated ecosystem view and requires analyses that incorporate contemporary information about different ecosystem components across a range of spatial and temporal scales. The strategy should facilitate moving towards a more dynamic management procedure, thereby improving the likelihood of achieving CCAMLR's conservation objective (CCAMLR, 2019, Annex 05, paragraph 2.59). Under the Convention (CAMLR Convention, Article IX) CCAMLR is required to develop catch limits based on the best available scientific evidence, and as such, the approach was also endorsed by the Commission (CCAMLR, 2019, paragraph 5.17 to 5.19).

In developing the new approach, WG-EMM prioritised (CCAMLR, 2019, Annex 05, paragraphs 2.18, 2.38 and 2.62) the need for:

i. Developing updated biomass estimates, initially at the Subarea scale, but potentially at multiple scales;
ii. Developing a stock assessment to estimate precautionary harvest rates; and
iii. Advancing the risk assessment framework to inform the spatial allocation of catch.

Fishery management strategies often use feedback loops that adjust measures (such as catch limits or closures) in response to information about the status of the fished stock (e.g. Constable, 2002). The requirement for a biomass estimate and harvest rate are therefore consistent with CCAMLR's general management practice. However, by endorsing the risk assessment as part of the new management strategy, CCAMLR has also recognised the need to incorporate information related to the structure and function of the wider krill-based ecosystem, including krill-dependent predator species, to identify options for ways that catch limits can be assigned in time and space.

The risk assessment extends prior work to provide advice on the spatial allocation of krill catches (Hewitt et al., 2004; Plagányi and Butterworth, 2012; Watters et al., 2013, see Constable et al. in review for detailed history). The implementation reported here also builds on earlier work by WG-EMM. As such, Constable (2016), Constable et al. (in review) developed a framework to adjust the spatial pattern of the krill fishery based on krill availability, predator consumption requirements, and the importance of particular areas to the fishery (agreed during the Working Group on Fish Stock Assessments (WG-FSA) in 2016 and termed *desirability*).

In the case of the krill fishery, the framework combines three components: localised risk to predators, localised risk to krill, and area desirability to the fishery. Localised risk to predators relates to the potential for interference by the fishery on predator foraging performance. Predation pressure (consumption of krill as a proportion of krill biomass) is used as an index of predator risk. Localised risk to krill, above and beyond escape mortality which probably effects all life-history stages (Krafft et al., 2016), relates to areas dominated by juvenile krill, but in future could incorporate information about nursery, breeding and source areas which will impact the krill abundance in other locations. The desirability for the fishery is a measure of the relative importance of each area to the fishery.

The framework assesses the relative risks of the localised impacts of fishing on both predators and krill, apportioning catch levels in space and time to minimise these risks. Areas with lower risk are allocated higher proportions of the catch limit, and areas with higher risk have lower catch proportions. The framework does not generally reduce, or increase, the overall catch limit in a region, but alters the spatial and temporal pattern of catch limits. However, it is possible to include an offset (described below) for higher risk scenarios which may result in a reduced catch limit to maintain the overall risk close to an agreed level. The framework computes relative risks within a region and can evaluate risks associated with different proposals, or scenarios, to subdivide the catch. As catches increase, the fishery distribution is likely to change, thereby altering the risk profile of putative management units.

Kelly et al. (2018) implemented the risk assessment approach of Constable (2016) in East Antarctica. WG-EMM agreed that this provided further support for the approach and that it could provide management advice. In 2020, CCAMLR again endorsed the approach, using Subarea 48.1 as a pilot project for other Subareas within Area 48. WG-EMM has iteratively reviewed the implementation reported here annually since 2018 (Appendix 1).

Currently, the krill catch limit is allocated at the Subarea scale (155,000 tonnes in Subarea 48.1), yet it is clear that the fishery operates at increasingly finer scales within Subareas (Santa Cruz et al., 2018; Trathan et al., 2018), potentially causing the Subarea limit to be taken from small localised areas within the Subarea, thereby causing higher risks to species dependent on those areas (Santa Cruz et al., 2022). In recent years the fishery has concentrated in the west Antarctic Peninsula region, particularly within the Bransfield and Gerlache Straits (Trathan et al., 2018; Krüger, 2019), and increased periods of reduced sea-ice have allowed the fishery to operate further south than previously (Silk et al., 2014). The majority of krill is currently caught in autumn when krill are more concentrated on the continental shelf (Trathan et al., 2022; Warwick-Evans et al., 2022a), though some are caught north of the South Shetland Islands during summer (Appendix 2). The timing of krill catch will have implications for the risk to the ecosystem, due to the variability in requirements and distributions of both krill and predators. Thus, management is probably necessary at finer scales, both spatially and temporally. The risk assessment offers options to do this, using the best data available which can be revised as new data become available. The risk assessment can be applied at any temporal or spatial scale, so long as the necessary data are available. It estimates risk in a number of different ways. The overall regional risk is estimated as either a baseline risk, or a fishing desirability risk. Baseline risk is defined as the risk to predators and krill and is estimated from predation pressure and the proportion of juvenile krill in each management unit. Desirability risk is defined as the risk to predators and krill (as for the baseline risk), but also accounting for the desirability of a given management area to the fishery, i.e., more catch may be attributed to areas where the fishery has previously fished (desirable areas). The regional risk is used as a metric to compare alternative fishing patterns or management approaches. For example, a desirable fishing pattern can generate a regional risk greater than the baseline regional risk because of overlap of the fishery with areas important to predators and krill. In order not to increase risk above the baseline, options for reducing (offsetting) risk to return the regional risk to the baseline level are available (see Constable et al. in Review for further discussion).

Here we apply the risk assessment framework to Subarea 48.1 and evaluate alternative scenarios for delineating management units and apportioning the overall catch limit for this Subarea given the currently available scientific information. Such scenarios have been recommended by previous Working Groups to estimate the distribution of risk and to calculate the proportion of the annual catch limit that could be assigned to each candidate management unit within Subarea 48.1. Our aim was to evaluate alternative spatial scales for management. Our priority was to understand how best to identify management units that capture the fine-scale dynamics of the ecosystem, and operation of the krill fishery.

Materials and methods

This application of the risk assessment framework for Subarea 48.1 follows the method described by Constable (2016) and Constable et al. (in Review). In summary, we evaluate a variety of candidate management units by calculating risk to the ecosystem under different scenarios for management using the risk assessment framework. The data layers that describe spatially-explicit krill requirements by predators, krill density, and fisheries desirability are published elsewhere, but briefly described below. Subsequently, the integration of these layers into the risk assessment framework is described. All analyses were conducted in R version 3.6.1 (R Core Team, 2022).

Our core objective was to use existing available data, rather than develop a new conceptual framework, with management delayed whilst new data collection programmes were implemented. This was a key management requirement as the fishery is becoming increasingly concentrated in a few hotspots, whilst catches were also increasing (e.g. Trathan et al., 2022).

Spatial scale

These analyses focus on Subarea 48.1 (Figure 1) given its increasing importance to the krill fishery (Kawaguchi and Nicol, 2020) and the large abundance and diversity of krill predators. However, the fishery does not operate across the entire Subarea,

operating almost exclusively over shelf waters around the South Shetland Islands and northern Antarctic Peninsula (see Appendix 2), overlapping with most predator monitoring and krill survey effort (Trathan et al., 2022). Additionally, environmental conditions vary considerably across the latitudinal range of Subarea 48.1 (see Figure S4 in Warwick-Evans et al., 2022b). As such, we have not attempted to project species distributions into areas where there are no, or very few, observational data; extrapolating into geographic and environmental space without empirical data that constrain model projections could lead to biased results and unintended management consequences. Consequently, our study area was defined as the area within Subarea 48.1 where the fishery has operated over the period 1979/80 to 2017/18 (Figure 1; see Trathan et al., 2018).

Temporal scale

The risk assessment framework has the ability to operate at any temporal scale if relevant data are available. Data for most species are limited to specific periods during their annual cycle, and data for much of the rest of the year are sparse or non-existent. The temporal scale in our analyses is at the seasonal scale, considering summer (October to March) and winter (April to September) separately. We recognise that this does not fully reflect the intra-annual variation in ecosystem dynamics and the implications of this are discussed below. Further, we highlight that the temporal alignment of the summer breeding season for any given species rarely coincides with the temporal alignment of other species. This means that the full temporal complexity of ecosystem risks is unlikely to be captured in its entirety.

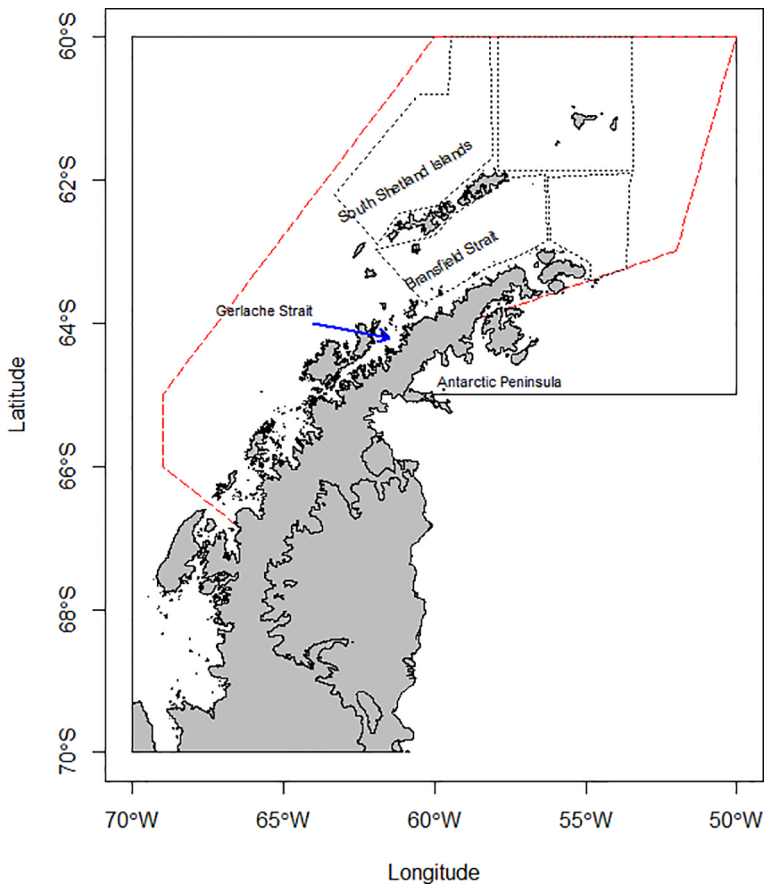

FIGURE 1
CCAMLR Subarea 48.1 (continuous line) with the operational footprint of the krill fishery from 1979/80 to 2017/18 (red dashed line; from Trathan et al., 2018) and the strata surveyed for krill by U.S. Antarctic Marine Living Resources program (black dotted line, Reiss et al., 2008).

Predator krill requirements

Summer

Raster layers describing the at-sea distribution and density of flying seabirds (Figure S1) were created as described in (Warwick-Evans et al., 2021). Briefly, hurdle models were used to model the density and distribution of 11 species of procellariform seabirds using nine years of data obtained from at-sea surveys conducted between January and March by the U.S. Antarctic Marine Living Resources (AMLR) Program (Figure 1). These distribution rasters were used to estimate spatially explicit krill consumption by each species, by combining estimated energy requirements calculated from Field Metabolic Rates (Shaffer, 2011) with estimates of the proportion of krill in the diet of each species (Croxall et al., 1985) and the energy density of krill (Clarke, 1980).

Warwick-Evans et al. (2022b) describe the approach to estimate krill consumption by three species of *Pygoscelis* penguins, fin whales *Balaenoptera physalus*, humpback whales *Megaptera novaeangliae* and Antarctic fur seals *Arctocephalus gazella* (Figure S1). For each cetacean species, sightings data were collected from ship surveys conducted between January and March 2013 - 2020 by the Brazilian Antarctic Program (PROANTAR). For fur seals, sightings data were collected between January and March 2003 – 2011 by the U.S. AMLR. Sightings data were used to create species distribution models to predict the distribution and density of each species (independently) in the study area. These were multiplied by consumption estimates for individual cetacean species by Reilly et al. (2004), and fur seals by (Boyd, 2002) to estimate the spatially explicit consumption of krill by humpback and fin whales and fur seals within the study area.

For penguins, generalised additive models were used to predict the distribution of breeding adult chinstrap *Pygoscelis antarcticus*, gentoo *Pygoscelis papua* and Adélie *Pygoscelis adeliae* penguins within the study area, using tracking data collected during the chick-rearing period on the Antarctic Peninsula and South Shetland Islands. Population estimates from the Mapping Application for Penguin Populations and Projected Dynamics data portal (MAPPPD, Humphries et al., 2017) were used to predict the distribution of all populations within the study area. Energy requirements from Croll and Tershy (1998) were combined with estimates of the proportion of prey in the diet of each species (Hinke et al., 2007) to estimate spatially explicit krill consumption by *Pygoscelis* penguins. See also Trathan et al. (2018; Trathan et al., 2022).

Raster layers for the summer distributions and abundances of pack-ice seals and finfish were created using data from Hill et al. (2007) and Forcada et al. (2012), and converted into estimates of consumption for these species at the Small Scale Management Unit (SSMU, Hewitt et al., 2004) scale by Constable (2016). These data provide the best available estimates for these species (Figure S2).

Winter

Data reflecting the distribution and abundance of krill predators in winter are sparse. Nevertheless, to develop the winter data layers for the risk assessment, we necessarily required estimates of abundance for key species.

The surveys to estimate the abundance and distribution of humpback and fin whales were carried out between January and March. We assume that humpback whales forage in the study area for approximately 120 days per year (Lockyer, 1981); however, this period continues beyond March (when our summer period ends) as aggregations of humpback whales have been observed into June and July (e.g. Nowacek et al., 2011; Weinstein and Friedlaender, 2017). Fin whales have been recorded in the area between February and June, averaging 51 days per year (Širović et al., 2004). However, given that no abundance estimates exist for these species during winter, for the purpose of this risk assessment we have assumed that all krill consumption by whales occurs during summer, when the surveys were undertaken. We recognise the limitation of adopting this approach, which we consider further in the discussion.

Surveys for flying seabirds are also undertaken only in summer and there is little information on the distribution or abundance of flying seabirds in the study area during winter. In summer, flying seabirds account for approximately 2% of the overall krill consumption in the area (Warwick-Evans et al., 2022b), consequently for the purpose of this risk assessment we have assumed that there is no krill consumption by flying seabirds in the study area during winter, something again that we consider in the discussion.

To estimate the winter distribution of adult gentoo penguins the locations and population estimates of gentoo penguins breeding in the study area were obtained from MAPPPD (Humphries et al., 2017). Gentoo penguins remain coastal during the winter months but are not constrained to remain near breeding colonies (Tanton et al., 2004). As such, we have assumed that an even distribution of individuals occurs within 30 km of the coastline of the South Shetland Islands and west Antarctic Peninsula. The distribution was limited to include only areas north of 65.5°S given the most southerly gentoo colony is located at 65.26°S (Figure S3).

Over winter, 62% of adult chinstrap penguins tracked from three colonies on the South Shetland Islands remained local (within 500 km of the colony) (Hinke et al., 2019). The average maximum distance travelled by "local" individuals across these three colonies was 189 km. Therefore, to approximate the winter distribution of chinstrap penguins we have assumed that 62% of all chinstrap penguins that breed in the study area (Humphries et al., 2017) remain within 189 km of the coastline of the South Shetland Islands and western Antarctic Peninsula and are distributed evenly within this area. Although no colonies exist in the south of the study area, Hinke et al. (2019) showed

chinstrap penguins continued to visit these southerly areas during winter, and as such, the distribution of chinstrap penguins was not constrained to the northern section of the study area (Figure S3).

Winter tracking of Adélie penguins breeding at Admiralty Bay on the South Shetland Islands have been carried out using geolocator (GLS) devices that use the timing of dawn and dusk to estimate position (Hinke et al., 2015). These location data were therefore used to estimate the winter distribution of Adélie penguins in the study area. Positions north of 55°S were removed from the data as these are likely to represent locations during the equinox when GLS positions are challenging to interpret (Ekstrom, 2004; Hinke et al., 2015). The remaining positions (including those outside of our study area) were gridded into 30 km by 30 km grid cells to create a continuous grid reflecting the sum of the number of GLS positions recorded in each cell (finer resolution grids showed a very patchy distribution which did not smooth across GLS locations). The relative importance of each grid cell was calculated by dividing the value of each cell by the total of all cells. Estimates of the number of breeding adults from all colonies in the study area were downloaded from MAPPPD. Although penguins from just one colony were tracked, it is likely that Adélie penguins from colonies across the northern Antarctic Peninsula and South Shetland Islands follow a similar distribution. Adélie penguins breeding in colonies towards the south of the study area (9% of all Adélie penguins breeding in the study area) are likely to move westerly from the Peninsula following the expanding sea-ice edge and follow an alternative distribution pattern (see Erdmann et al., 2011). Consequently, individuals breeding at these southerly colonies have been excluded from this analysis. The total krill consumption by all Adélie penguins in the north of the study area were distributed across the raster according to the importance of each cell to create spatially explicit krill consumption estimates for Adélie penguins.

No estimates of the energetic requirements of Adélie or chinstrap penguins outside of the breeding season exist, although Hinke and Trivelpiece (2011) have calculated this for gentoo penguins. Consequently, for all species of *Pygoscelis* penguins the summer estimate of daily krill consumption per individual have been combined with species-specific distribution rasters to estimate the spatially explicit krill consumption by *Pygoscelis* penguins during winter.

Data layers for the winter distribution and abundance of fur seals, pack-ice seals and fish were created using data from Hill et al. (2007) and Forcada et al. (2012), as used by Constable (2016). These data are at the scale of SSMUs and provide the best available estimates for these species.

Krill distribution

The distribution of krill across the study area was estimated using generalised additive mixed models (GAMMs) as described by Warwick-Evans et al. (2022a). Analyses were conducted independently for summer and winter. Briefly, acoustic sampling methods were applied to estimate the density of krill along transects in the Bransfield Strait and north of the South Shetland Islands and Elephant Island annually in January-March (summer) between 1999 and 2011 and in August-September (winter) between 2012 and 2016 by the U.S. AMLR Program (Figure 1). GAMMs with year as a random effect were used to model the relationship between observed krill density and environmental variables, and to predict the distribution and density of krill across the study area. The krill biomass estimates for winter were also adjusted as described in the 'modified risk assessment' section below.

The proportion of juvenile krill was calculated using data from Perry et al. (2019) who used the KRILLBASE database (Atkinson et al., 2017) to determine distribution maps of all krill life stages, using data from 1970-2016. We summed the distribution of adults and juveniles and calculated the proportion of juveniles over two temporal scales, early (October to December) and late (January to May). Krill spawning occurs from December to March (Meyer et al., 2020), and thus we have assumed the early distribution will be similar to the winter distribution, and late season approximately represents the summer distribution.

Fishery desirability

The desirability of an area to the krill fishery was calculated at the scale of 10 km x 10 km following methods by Constable (2016). This analysis focussed on the spatial extent of fishery operations between 2013 and 2018 (Trathan et al., 2018; Trathan et al., 2022). This was prior to the implementation of the Association of Responsible Krill harvesting companies (ARK) voluntary buffer zones (Godø and Trathan, 2022), after which point the distribution of the fishery was restricted as a result of seasonal temporary voluntary restrictions imposed by the krill fishing industry (this strategy was evaluated in a separate scenario). Fisheries catch data during summer and winter were analysed separately. The importance of each 10 km x 10 km cell to the fishery was calculated by dividing the annual seasonal catch from each cell by the annual seasonal total catch within the study area and taking the mean value across all years.

Scenarios

Previously, CCAMLR (WG-EMM-02) identified Small Scale Management Units (SSMUs) as potential units for subdividing the krill catch (SC-CCAMLR-XXI, 2002; Hewitt et al., 2004). However, catch limits at this scale have yet to be implemented. Further, the SSMUs were identified almost two decades ago at a time when the fishery in Subarea 48.1 largely operated to the

north of the South Shetland Islands (CCAMLR, 2018a) and before knowledge was available about cetacean recovery in the region (Branch, 2011; Leaper and Miller, 2011; Jackson et al., 2015). As such, SSMUs may not represent the optimal units of management to spread the risk associated with the krill fishery. Nevertheless, we evaluate the SSMUs within the risk assessment, together with a number of other scenarios.

We evaluated the variation in regional risk and in the spatio-temporal distribution of the catch limit associated with managing the fishery according to a variety of management units. We have evaluated 36 scenarios to divide Subarea 48.1 into smaller management units using:

a. A buffer from land (variations ranging from 20 to 50 km, also including internal subdivisions within the buffers). In this context the term buffer is a way to delineate management units adjacent to the coast and islands and does not mean no-take zones (unless specified);
b. Bathymetric contours (variations at 500 m, 750 m, 1000 m, and simplified variations);
c. The top 25% and 50% of predator consumption areas;
d. Regular grid cells (variations ranging from 50 to 200 km);
e. An approximately north-south division across the study region (termed vertical split), an approximately east-west division (termed horizontal split), an approximately north-south division combined with an approximately east-west division (termed 4-way split);
f. The total area used by the fishery from 1980 to 2018, the total area used by the fishery 2013 to 2018 during summer and during winter;
g. The current SSMUs ((SC-CCAMLR-XXI, 2002) Hewitt et al., 2004);
h. The ARK voluntary buffer zones (Godø and Trathan, 2022; Trathan et al., 2022);
i. The component areas that comprise the proposal for a marine protected area in Domain 1 (D1MPA (see Pew, 2020)); and
j. The strata from the U.S. AMLR acoustic surveys for krill (with variations).

For the scenarios using the ARK voluntary buffer zones and the D1MPA, we set the catch value in each of the no-take zones to zero (summer only for the ARK voluntary buffers). We also note that the D1MPA was proposed for various protection, conservation and management reasons and not solely as a means to manage the krill fishery (Argentina and Chile, 2019). Thus, the risks associated with this scenario should not be considered to reflect upon the intended purpose of this MPA proposal.

The risk assessment assumes that catch is spread evenly within each management unit. However, we know that this is not the case (Trathan et al., 2018; Trathan et al., 2022), and that the fishery is likely to concentrate within preferred areas within management units. This means that the relative risk estimated using the risk assessment framework will not accurately reflect the risk that these management scenarios would represent in practice. As such, for some of these scenarios we have also split the candidate management zones into smaller zones to ensure that the risk assessment measures the risk of the fishery concentrating within candidate management areas (i.e. 50 km buffer from land – see a. above).

Applying the risk assessment framework

We follow the approach of Constable (2016) and Constable et al. (In Review), without variation, in implementing the risk assessment, as this approach has been endorsed by the Commission (CCAMLR, 2019, paragraph 5.17). As CCAMLR becomes more familiar with the approach, fine tuning of the inputs and their equations are plausible.

Risk

Data layers describing krill consumption (tonnes day^{-1} km^{-2}) by flying seabirds, penguins and fur seals were summed to create seasonal layers (summer and winter) of krill consumption by central place foragers (CPF). Data layers describing the krill consumption (tonnes day^{-1} km^{-2}) by whales, fish and pack-ice seals were summed to create seasonal layers describing krill consumption for ideal-free or pelagic (PEL) species. Total seasonal krill demand by CPF and PEL predators was calculated by dividing the daily estimates of krill consumption within each candidate management unit by the area of the candidate management unit (km^2) and scaling this to provide seasonal estimates by multiplying these values by 182 (i.e., to correspond to the nominal durations of summer or winter). Seasonal predation pressure was calculated for each candidate management unit by dividing the krill demand by the krill density. Predation pressure (X) was scaled to range from 0 – 1 using a logistic function to assist with scaling the component factors, f, between 0 and 1 (Equations 1.1 and 1.2, methods described by Constable (2016), (Constable et al. in review)).

$$1(X) = \frac{1}{\left(1 + \quad e^{-h(X-X50)}\right)^{\frac{1}{v}}} \qquad \text{Equation 1.1}$$

$$f = Y0 + Yr\left[\frac{1(X) - 1(X0)}{1(X1) - 1(X0)}\right] \qquad \text{Equation 1.2}$$

where h is the steepness parameter, $X50$ is the value for x for which the function gives a value of 0.5, and v is a shape parameter. $X0$ is the X value for which the function value would be offset to 0. $X1$ is the value for X for which the function is scaled to 1. $Y0$ is the minimum value where $Y0 >= 0$. Yr is the range, where $(Y0 + Yr) <= 1$. Values for the

parameters used to scale the predation pressure were h=3, v=3, $X50$ = 0.5, $X0$ = 0, $X1$ = 4, $Y0$ = 0, $Y1$ = 1. Also see Kelly et al. (2018) and (Constable et al. in review) for more details on the logistic scaling function.

Indices of risk (r) were calculated for summer and winter using Equation 2 where CPF is the scaled predation pressure of central place foragers, PEL is the scaled predation pressure of pelagic predators, and JUV is the proportion of juvenile krill.

$$r = 1 - ((1 - JUV) * (1 - CPF) * (1 - PEL)) \quad \text{Equation 2}$$

Desirability

Seasonal desirability by the fishery was scaled to range from 0 to 1 using Equations 1.1 and 1.2. Values for the parameters used to scale the fishery desirability were h=60, v=1, $X50$ = 0.08, $X0$ = 0, $X1$ = 1, $Y0$ = 0, $Y1$ = 1 following Constable (2016).

Assessment of alpha

Alpha (α, the proportion of catch to be taken from each area) was calculated using Equation 3, where r is risk, c is fisheries desirability, Z is the proportion of annual catch, K = krill density (tonnes km^{-2}), A is area (km^2), $_a$ is local area (i.e. management unit), $_p$ is a specific period (i.e. summer or winter), $_{a'}$is across all areas and $_{p'}$ is during all periods. We set the proportion of the annual catch taken during summer = 0.38 and winter = 0.62, which reflects the fisheries operations prior to establishment of ARK voluntary buffer zones (2013-2018). These values could be changed in future implementations to reflect any changes in fisheries operations. However, one of the output results from the assessment of risk, is altered proportion of catch limits assigned to summer and winter.

$$a_{a,p} = \frac{\left((1 - r_{a,p}) * c_{a,p} * z_{a,p} * K_{a,p} * A_{a,p}\right)}{\sum_{a',p'} \left((1 - r_{a',p'}) * c_{a',p'} * z_{a',p'} * K_{a',p'} * A_{a',p'}\right)} \quad \text{Equation 3}$$

Baseline risk

The baseline risk provides a means of identifying which management units may result in the overall lowest regional risk to predators and krill when the desirability of the fishery is not taken into account. This can be used to identify the proportion of the catch to be taken from each management unit in each season to spread the risk and not disproportionately affect some areas more than others. The baseline risk is calculated by setting the fisheries desirability to 1 for all locations and all periods. The baseline regional risk $\widehat{R}$ is calculated using Equation 4 where $\hat{a}_{a,p}$ is the baseline alpha for the scenario where c = 1 (i.e., identity multiplier as no information on desirability is conveyed in this risk estimator).

$$\hat{R} = \sum_{a,p} r_{a,p} \hat{a}_{a,p} \quad \text{Equation 4}$$

Desirability risk

The desirability by the fishery can be incorporated into Equation 3 by setting the value of c to the scaled value for the seasonal desirability by the fishery. From this we can calculate new values for alpha for each management unit and a new regional risk R_d. This provides a means of identifying which management units may result in the lowest regional risk to predators and krill when the desirability of the fishery is taken into account. If $R_d > \widehat{R}$, the regional risk of localised effects of the fishing has increased above the baseline. The ideal scenario would be to identify management units with a low baseline risk, which does not increase when fisheries desirability is taken into account. If the desirability scenario increases the risk, then it is possible to introduce offsets to close high risk areas or reduce the catch limit in order to not exceed the baseline regional risk (Constable et al. In review).

Modified risk assessment framework

Adjusting winter krill biomass estimates

The density and distribution of krill vary seasonally at the west Antarctic Peninsula (Lascara et al., 1999, Reiss et al., 2017), with important consequences for both predators and the commercial fishery. Similar intra-annual patterns of density have been established elsewhere (Saunders et al., 2007, Reid et al., 2010), suggesting intra-annual variation in krill probably reflects some key ecological property of krill life-history. Plausibly, biomass is likely to increase during spring and summer, as a result of spawning and somatic growth, whilst continued mortality and transport in ocean currents away from a region may result in decreased biomass during winter.

Our estimates of krill biomass during winter were considerably lower than those for summer which were based on long-term averages. Model validation suggests that the winter models are robust in their predictions of krill distribution within the study area. This is consistent with previous studies; for example, at the west Antarctic Peninsula, Lascara et al. (1999) reported that spatially averaged estimates of krill biomass were an order of magnitude higher during spring (32 gm^{-2}) and summer (95 gm^{-2}), than during autumn (12 gm^{-2}) and winter (8 gm^{-2}). Nevertheless, the winter krill surveys were conducted during 4 years where krill biomass was lower than average (WG-EMM-2021/05 R1), so the winter estimates of krill biomass may be lower than the long-term average.

During WG-EMM in 2021, some scientists were concerned that these low estimates of biomass in winter may not properly reflect the long-term ecological situation in the west Antarctic Peninsula and suggested that the winter estimates of biomass need to be adjusted. As such we have evaluated each management scenario after updating the winter krill distribution model to have the same total biomass as for summer, whilst maintaining the spatial variation in the

distribution between summer and winter. This was achieved by dividing the value of each cell in the winter raster by the sum of all cells in the winter raster to obtain the importance of each cell (summing to 1), then multiplying this by the total biomass estimated from the summer model (which is a long-term average).

We have compared the outcomes using both the original and adjusted estimates for winter krill biomass, to better understand how the uncertainty in this layer could lead to different outcomes of the risk assessments. Determining a more realistic biomass estimate for krill during the winter is now urgent, if CCAMLR is to properly assess risks to the ecosystem.

Accounting for uneven spatial spread of catch

One of the key assumptions of the risk assessment is that the catch within each management unit is harvested evenly from across that management unit. In Subarea 48.1, historical fishing patterns (Trathan et al., 2018; Trathan et al., 2022) show that the fishery actually concentrates at a finer scale (Appendix 2).

Thus, to account for the concentration of the fishery within candidate management units and better characterise the relationship of the fishery with the risks in the management units, we have implemented the risk assessment at a scale more closely aligned with the scale at which we believe the fishery operates. We have used a selection of the lowest risk scenarios and scenarios where management would be plausible (i.e. without very large numbers of management units). As such, within those management units in which the fishery operated (2013 - 2018, summer and winter), the risk assessment was run assuming that all catch would be taken within the footprint of where the fishery actually operated, rather than spread evenly across each management unit. For management units where the fishery did not operate, we have assumed that there would be an even spread of catch within each management unit. Though this assumption is unlikely, we have no prior information about where the fishery would operate in these areas. Figure 2 provides an example to illustrate how we have implemented this. This implementation used the adjusted winter krill layer as described above.

Results

Estimated daily consumption of krill across the study area during summer was highly variable between groups. Fish were estimated to have consumed 76% of the summer daily krill consumption in the area, followed by fin whales (11%), humpback whales (6%), chinstrap penguins (4%), Adélie penguins (3%), flying seabirds (2%), pack-ice seals (2%), gentoo penguins (0.2%) and fur seals (0.1%). Fish also consumed 76% of all krill consumed during winter, followed by pack-ice seals (8%), chinstrap penguins (7%), Adélie penguins (5%), gentoo penguins (2%) and fur seals (1%).

Detailed results of the regional risk and the total proportion of the catch that could be taken from each management unit during summer and winter, for both baseline and desirability scenarios are presented in Appendix 4. For all scenarios, a higher proportion of the catch was assigned by the risk assessment method to the summer period than to winter. In most cases, including the desirability for the krill fishery caused desirability

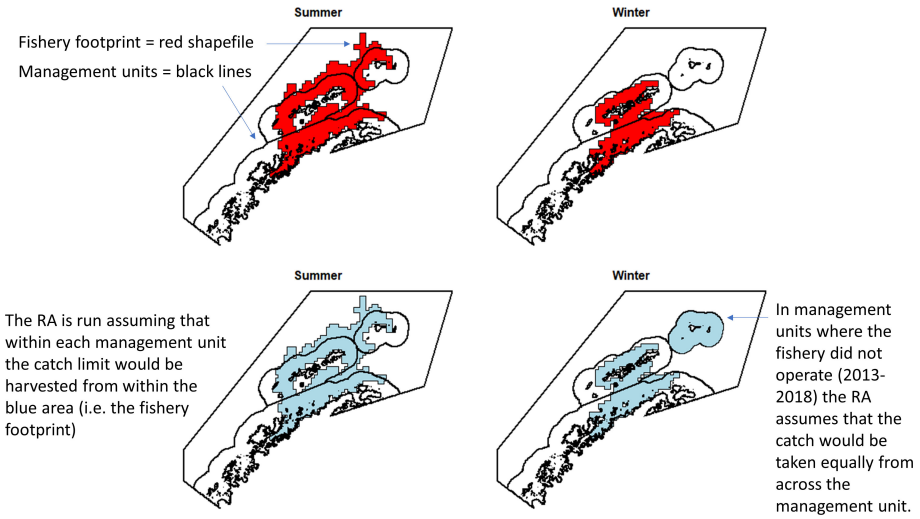

FIGURE 2
Example, using the 50 km buffer scenario, of how the risk assessment (RA) was run at a scale similar to that at which the fishery operates. This assumes the catch limit would not be taken equally across a management unit but would be concentrated according to previous behaviour of the fishery. This means that the risk is actually calculated from the blue areas, not the management unit areas.

regional risk to exceed baseline regional risk. For the majority of scenarios the baseline scenario assigned the majority of the catch limit to the outer management units (away from the coast), and the desirability scenario assigned the majority of catch to the Bransfield and Gerlache Straits.

The baseline regional risk varied from 0.62 to 0.84 (Table 1; Appendix 3) and was lowest when the 50 km grid cells were used as candidate management units (Figure 3). As the grid cells incrementally increased in size, the risk increased. In general, smaller scale management units had lower risk, as it is more feasible to capture the risk and assign catch to lower risk areas in these scenarios. The desirability regional risk varied from 0.68 to 0.81 (Table 1; Appendix 3) and was lowest when the 500 m bathymetry contour was used as candidate management units (Figure 4). Using a slightly simplified version (where just the three main shelf areas were included rather than all of the small areas where bathymetry < 500 m, see Appendix 4) showed the same level of risk as when the detailed isobaths were used to delineate candidate management units (Appendix 4). The scenarios using existing SSMUs as candidate management units also had relatively low risk. The scenarios using different buffer distances from the coast showed higher risks. As the distance from shore increased, the baseline risk decreased whereas the desirability risk increased. The scenarios using isopleths of predator krill consumption as candidate management units also showed higher risks, though the management units defined by these isopleths were small and patchily distributed. The scenarios using the existing fisheries distribution to delineate candidate management units resulted in some of the highest risk levels, with the highest risk level when the area used by the fishery from 2013-2018 during winter was used to define the management units.

Modified risk assessment framework

Adjusting winter krill biomass estimates

For all scenarios where the krill biomass was adjusted to be equal to the summer krill biomass (based on the recommendation of WG-EMM-2021, see above), a higher proportion of the catch was assigned to the winter period than to summer. In most cases, including the desirability to the krill fishery caused very little catch to be assigned to summer, and desirability regional risk to exceed baseline regional risk. For the majority of scenarios the baseline scenario assigned the majority of the catch limit to the outer management units, and the desirability scenario assigned the majority of catch to the Bransfield and Gerlache Straits.

The baseline regional risk varied from 0.40 to 0.49 (these values are not comparable with those mentioned above as different krill data layers were used in the analyses, Table 1; Appendix 5) and was lowest when the 100 km grid cells were used as candidate management units. When the desirability of the fishery was also taken into account the regional risk ranged from 0.41 to 0.62 and the 50 km buffer from land had the lowest risk (Figure 5). The scenarios based on the U.S. AMLR krill survey strata also had relatively low risk. The U.S. AMLR scenario with 2 additional management units had a lower baseline risk, and the desirability risk was lowest in the scenario with one extra management unit.

The scenarios using bathymetry to delineate candidate management units also had relatively low baseline regional risk, lowest when using a 500 m isobath. However, in the desirability scenarios, using bathymetry resulted in some of the highest levels of risk (Table 1). The scenarios using existing SSMUs as candidate management units also had relatively low risk.

Accounting for uneven spatial spread of catch

For selected scenarios, using the adjusted krill biomass (winter biomass equal to the summer biomass; based on the recommendation of WG-EMM-2021, see above), the baseline regional risk varied from 0.37 to 0.58 (Table 1; Appendix 6). The lowest risk baseline scenarios were those where candidate management units were delineated using the 50km buffer split into smaller management units (Figure 6), followed by the original SSMUs and the U.S. AMLR survey strata, split further into additional management units (Figure 7). We did not evaluate some of the lower risk scenarios from previous implementations (i.e regular grid cells), given the complex requirements to manage at these small scales, with numerous or patchy management units. The desirability regional risk varied from 0.43 to 0.58 (Table 1; Appendix 6). The lowest risk desirability scenarios were those where candidate management units were delineated using the U.S. AMLR survey strata, split further into additional management units (Figure 7). The next lowest risk scenarios were using the U.S. AMLR strata with additional management units added (Figure 8).

Discussion

We have applied the risk assessment framework developed by Constable (2016) and Constable et al. (in Review) to Subarea 48.1 in order to evaluate alternative management units which can be used to spatially and temporally distribute the catch limit of the krill fishery, given our access to the best available science. We have evaluated 36 scenarios and found that using a regular grid with small grid cells leads to the least risk. However, these scenarios, with large numbers of management units would probably be highly complex to manage, particularly given the complexities of advance notification to the fishery of dates when management areas will be closed. Also, fine-scale delineation of management units may not be appropriate due to uncertainty in the data layers. In contrast, the scenarios using the scale and location at which the fishery currently operates resulted in some of the highest risks of all scenarios evaluated.

TABLE 1 A selection of scenarios detailing the relative risk from each candidate management scenario assuming the proportion of catch is taken from each management unit as detailed in Appendices 2–4.

Candidate scenario information			Original analysis			Adjusted winter krill			Accounting for uneven distribution of catch		
Name	**Description**	**Number of management units**	**Baseline risk**	**Desirability risk**	**Ratio**	**Baseline risk**	**Desirability risk**	**Ratio**	**Baseline risk**	**Desirability risk**	**Ratio**
50kmgrid	Grid of 50 km^2 cells	331	**0.62**	0.72	1.16	0.41	0.49	1.20	Not run	Not run	NA
100kmgrid	Grid of 100 km^2 cells	49	0.65	0.80	1.23	**0.40**	0.50	1.25	Not run	Not run	NA
150kmgrid	Grid of 150 km^2 cells	25	0.67	0.78	1.16	0.42	0.49	1.17	Not run	Not run	NA
200kmgrid	Grid of 200 km^2 cells	15	0.70	0.81	1.16	0.44	0.49	1.11	Not run	Not run	NA
SSMUs	Small scale management units (Hewitt et al., 2004)	8	0.71	0.77	1.08	0.46	0.49	1.07	0.41	0.50	1.22
depth500	Units separated by the 500m contour	14	0.72	**0.68**	0.94	0.45	0.58	1.29	Not run	Not run	NA
50km	50km buffer from land	4	0.73	0.78	1.07	0.46	**0.41**	0.89	0.48	0.55	1.15
20km	20km buffer from land	5	0.75	0.76	1.01	0.47	0.45	0.96	Not run	Not run	NA
fishery2013-2018winter	Area where the fishery operated during winter between 2013-2018	2	0.84	0.83	0.99	0.49	0.47	0.96	Not run	Not run	NA
50kmsplit	50km buffer from land with buffers split into smaller units	9	Not run	Not run	NA	0.43	0.50	1.16	**0.37**	0.52	1.41
AMLRstrata added	AMLR krill survey strata adjusted to be continuous and 2 extra units added	7	Not run	Not run	NA	0.45	0.49	1.09	0.43	0.45	1.05
AMLRstratanew5	AMLR krill survey strata adjusted to be continuous with an extra stratum added	6	Not run	Not run	NA	0.46	0.48	1.04	0.45	0.45	1.00
AMLRstratasplit	AMLR krill survey strata adjusted to be continuous and split further	8	Not run	Not run	NA	0.47	0.50	1.06	0.41	**0.43**	1.05

For a full list please see Appendix 3. These values are relative but can be used to compare the risk between different candidate management units, though not between implementations (i.e. between those with and without an adjusted krill layer, or between those that account for, or do not account for unevenly distributed catch). The baseline scenario does not incorporate the desirability of an area to the fishery, and just accounts for the risk to predators and krill. The fisheries desirability scenario incorporates the baseline risks and how desirable each management area is to the fishery (i.e., it allows more of the catch limit to be taken from areas in which the fishery has operated historically). Note, not all scenarios were run for adjusted krill or for uneven distribution of catch based on discussions during WG-EMM-2021 and WG-FSA-2021. The lowest risk scenario in each column is highlighted in bold. Where the ratio exceeds 1 the desirability risk exceeds the baseline risk, and methods to offset the additional risk must be considered if the desirability scenario is used.

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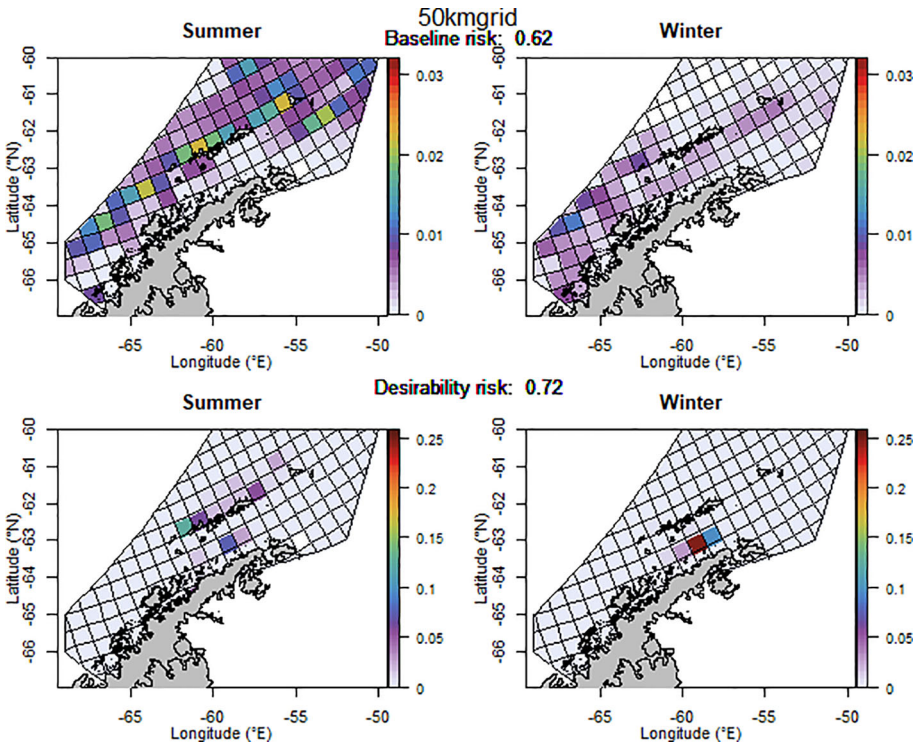

FIGURE 3
The proportion of the annual krill catch limit that could be taken from each management unit (50 km x 50 km grid cell) during summer and winter if the grid cell management units are used, when the initial analysis for the risk assessment was implemented (i.e. unadjusted layer for winter krill and assuming even catch distribution within management units). Values sum to 1 across all management units and for both seasons for each of the baseline (upper panel) and desirability (lower panel) scenarios.

Our results suggest that in order to minimise risk, spatial management needs to occur at scales smaller than the Subarea scale, and that managing at small scales at least in those areas where the fishery operates is important for maintaining CCAMLR's precautionary approach to management. We discuss our findings in two parts. First, how the fishery might be structured spatially and temporally in Subarea 48.1. Second, what the next steps will be to refine this process as CCAMLR moves forward with developing a sustainable fishery.

Choosing the appropriate framework for krill fishery management

Baseline or desirability risk

During the early development of the risk assessment approach the concept of desirability was introduced because baseline scenarios tended to assign the majority of the catch limit to the outer management units (remote from the coast), to locations where the fishing industry had previously rarely operated. As such, and given the diversity of views about protection, conservation and fishing held by different CCAMLR Members (see Godø and Trathan, 2022), use of management units that forced the fishery into the outer units would probably remain challenging. However, desirability helps with this, particularly if and when catch limits increase. If evidence shows catches can increase, at some point desirable management units may need to receive capped catch allocations in order to ensure overall risk does not increase beyond the baseline risk. Thus, the inclusion of desirability remains a key issue, and as such we focus our discussion on those scenarios that take into account desirability.

Original or adjusted winter krill biomass

It is likely that our models underestimate krill biomass during winter as they were based on four years of data when biomass was lower than average. However, krill biomass during winter should plausibly be lower than during summer (e.g. Lascara et al., 1999). By using the upscaled estimates of winter krill biomass, more of the catch limit is assigned to winter than summer, the opposite of the original implementation. By increasing krill biomass, predation pressure is reduced, resulting in lower estimates of risk during the winter period, and thus allowing increased catch limits during this time. As

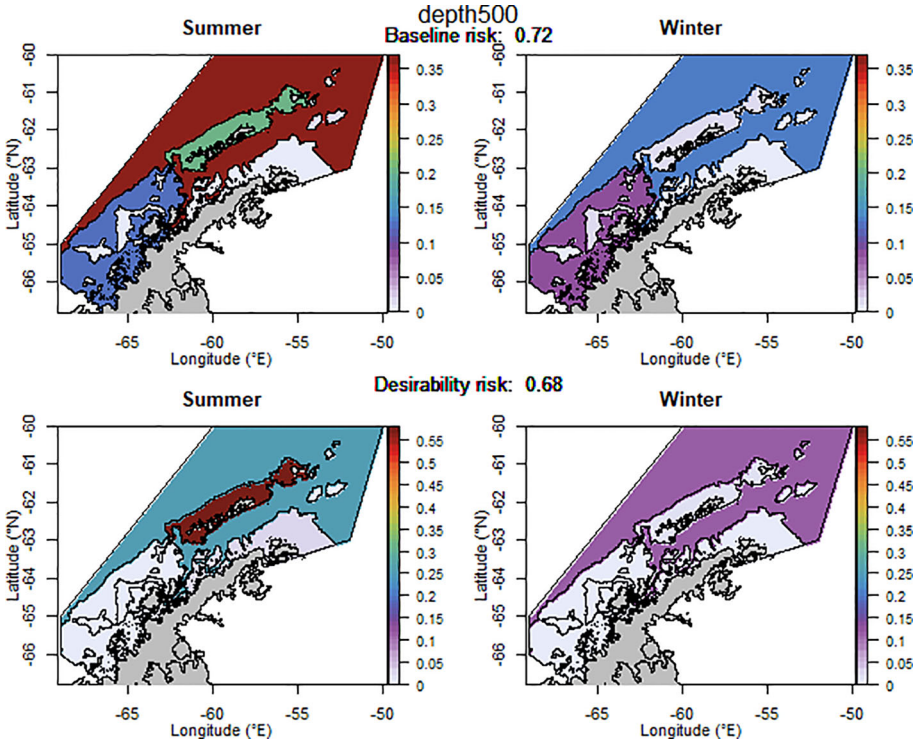

FIGURE 4
The proportion of the annual krill catch limit that could be taken from each management unit (delineated using a simplified version of the 500 m isobath) during summer and winter when the initial analysis for the risk assessment was implemented (i.e. unadjusted layer for winter krill and assuming even catch distribution within management units). Values sum to 1 across all management units and both seasons for each of the baseline (upper panel) and desirability (lower panel) scenarios.

such, the seasonal estimates of krill biomass are highly influential to the temporal assignment of krill catch limits. Nevertheless, because upscaling of winter biomass estimates was requested by WG-EMM, we focus our discussion using results from these adjusted analyses.

Even or uneven spatial spread of catch

In implementing the risk assessment at scales that reflect the current operation of the krill fishery (e.g. Figure 2), we account for the assumption that all catches within a given management unit are evenly distributed. We do this by restricting catch within each management zone to reflect the current operation of the fishery providing a more realistic estimate of risk, even though we could not fully implement this for management units where the krill fishery has not operated previously, given the absence of knowledge about preferred fishery distributions. Accounting for the concentration of the fishery within candidate management units does offer a better representation of risk. As such, we focus the rest of the discussion on the scenarios where we attempt to account for risk in this way.

Determining an appropriate spatial and temporal management structure for the krill fishery

Temporal distribution of catch

A higher proportion of catch was assigned to winter than to summer in all scenarios (using the adjusted winter krill biomass estimates), with <30% assigned to summer in most cases. This is not surprising given the presence of large numbers of breeding penguins and cetaceans that depend on krill during the summer. Additionally, consumption by finfish, which make up a large proportion of overall krill consumption is very much reduced in winter (see Appendix 2). In addition to consumption estimates being lower for winter than for summer, the consumption is more widely distributed as central place foragers are no longer constrained to remain near breeding sites. However, adjusting the winter krill layer so that it matches the biomass of the summer layer effectively reduces risks in winter, which in turn assigns more catch to winter. The degree to which this inadvertently increases risks is unknown.

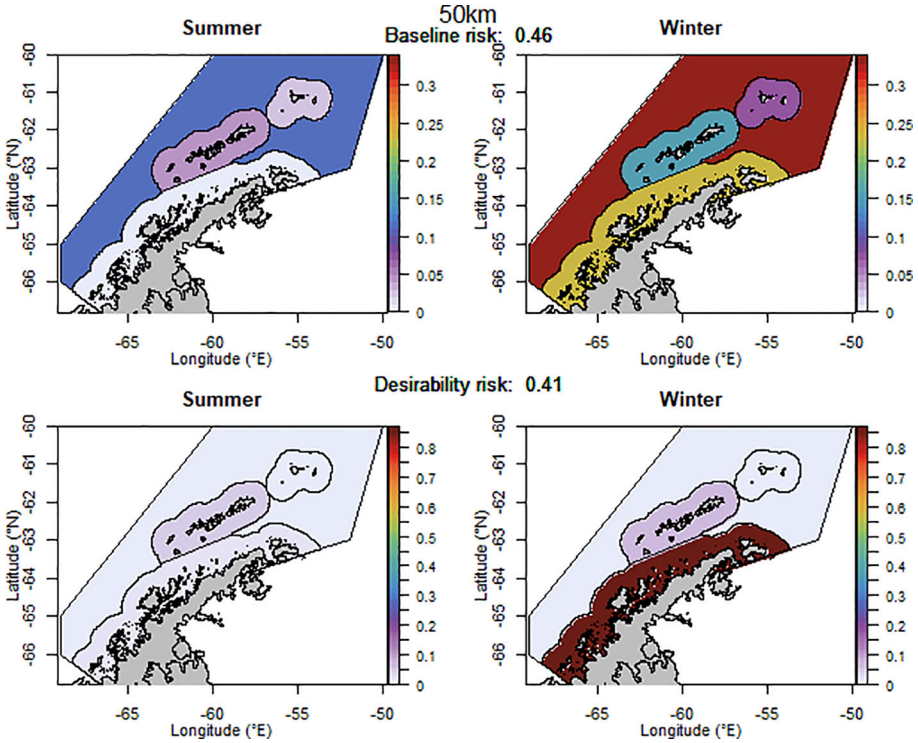

FIGURE 5
The proportion of the annual krill catch limit that could be taken from each management unit (delineated using the 50 km buffer from land) during summer and winter when the risk assessment was implemented after the winter krill layer was adjusted. Values sum to 1 across all management units and both seasons for each of the baseline (upper panel) and desirability (lower panel) scenarios.

Spatial distribution of catch

Our original implementation of the risk assessment showed that the management units which had the lowest desirability risk to the ecosystem were those delineated using the 500 m depth contour. However, after adjusting the winter krill layer, the lowest risk scenario occurred when management units were delineated using a 50 km buffer from land. A scenario where the 50 km buffer from land was split further into smaller management units resulted in an increase in risk (in the desirability scenario), emphasising our concerns that the fishery focuses effort within candidate management units and led to our decision to account for an uneven spread of catch.

Of the scenarios tested that assume uneven distribution of catch, the lowest risk management units were those based on the U.S. AMLR survey strata, in particular the scenario where these strata were split into smaller management units (*AMLR strata split*). In these scenarios, the majority of catch was assigned to the Bransfield and Gerlache Straits during winter, whilst summer catches were assigned north of the South Shetland Islands. Similar scenarios (*AMLR strata added and AMLR strata new5*) resulted in a similar proportion of catch assigned to the Bransfield and Gerlache Straits. However, in all of these cases, catch concentration occurs in areas preferred by the fishery, meaning these scenarios may not be as suitable for management as they appear. If the purpose of the new management approach is to reduce catch concentration, then limiting the catch to desired areas may be counterproductive.

Scale of management zones and the fishery

We show that risks associated with unconstrained operation within the current areas used by the fishery result in some of the highest risks of all scenarios evaluated. Though risks are relative, and not absolute, this is a major concern, and one already recognised by CCAMLR. Indeed, Kelly et al. (2018) show that the regional risk of the current conservation measures in Subareas 58.4.1 and 58.4.2 exceed baseline risk. This suggests that if catch limits are reached, then predators in these areas could be exposed to disproportionate effects from the fishery.

Extrapolating from analyses based on regular grid cells (50 km, 100 km, 200 km), suggests that larger management areas facilitate concentration of catch, which may deplete local krill populations and increase risk to predators and krill alike (Klein and Watters, 2020). This highlights the need to manage the krill fishery at smaller scales and is consistent with findings by Watters et al. (2020). This has been recognised at the Subarea scale through Conservation Measure 51-07 (CCAMLR, 2016),

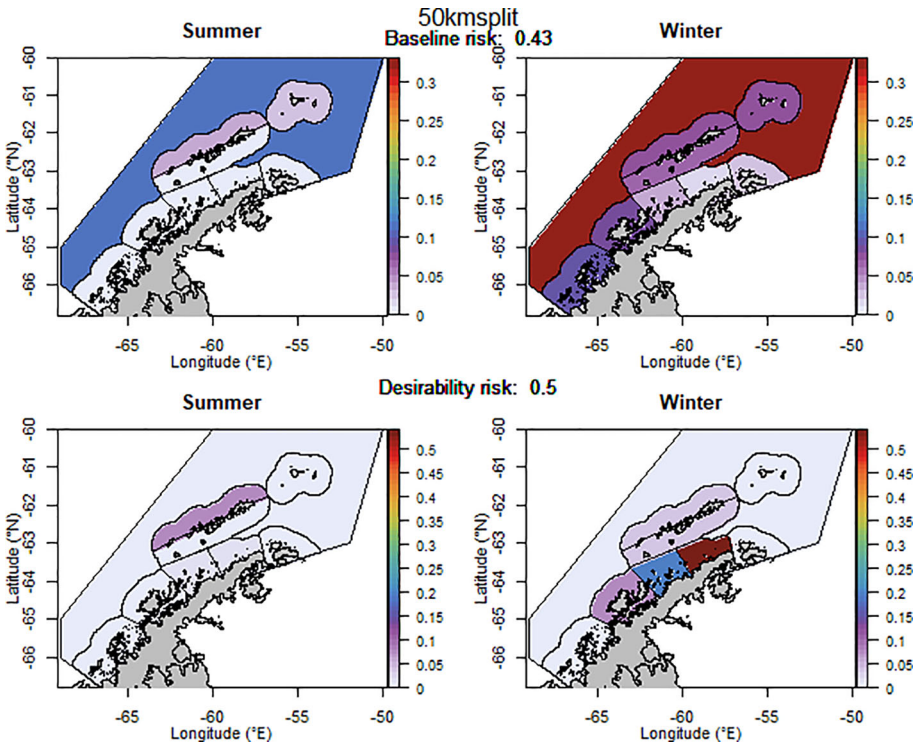

FIGURE 6
The proportion of the annual krill catch limit that could be taken from each management unit (delineated using the 50 km buffer from land divided into smaller management units) during summer and winter when the risk assessment was implemented after the winter krill layer was adjusted. Values sum to 1 across all management units and for both seasons for each of the baseline (upper panel) and desirability (lower panel) scenarios.

and now needs to be developed within Subareas (see also Watters et al., 2009). By implementing a small-scale approach to management, CCAMLR would be able to set specific catch limits according to fine scale ecosystem processes, such as consumption by predators, or important areas for krill.

Although it is apparent that managing the fishery at a smaller scale is likely to reduce the risk to the ecosystem, we recognise that this is more challenging from a management perspective than working at larger scales. It is likely that a compromise between risk and simplicity of management will be needed, as has been recognized for nearly three decades (e.g. Watters and Hewitt, 1992). A realistic compromise may be to use finer scale management units in areas of higher risk, and larger scale managements in areas of reduced risk. We are also mindful that managing at very small spatial scales relies on modelled data layers that include spatial (and temporal) error.

In addition to spatial concentration of catch we must consider temporal concentration of catch. If catch limits are reached during winter and remain concentrated in inshore areas such as the Bransfield Strait, there is an increased likelihood that recruiting or spawning females may be disproportionally caught by the fishery (Perry et al., 2019; Meyer et al., 2020). This has the potential to negatively impact both the krill stock and the wider ecosystem. Thus, depletion of winter concentrations of krill by the fishery may lead to impacts on predators in the following spring, when abundant krill supplies may be important to predators in preparation for breeding (Trathan et al., 2021).

A key issue is whether the low-risk scenarios developed from the U.S. AMLR survey strata continue to facilitate concentration of fishing effort at scales that will have ecosystem consequences.

Ecological weighting

There are three main ecological components factored into the assessment of risk; these are the risk to central place foragers, the risk to pelagic species and the risk to juvenile krill. Each are weighted equally in the current implementation (Constable, 2016; Constable et al. in review).

During summer, central place foragers are constrained to remain near breeding colonies in order to return to land to provision their developing young (Orians and Pearson, 1979). As such, if krill are depleted in areas adjacent to the colony, then the adults must forage further from the colony, potentially resulting in reduced breeding success or reduced adult survival (Ashmole, 1963). For pelagic species this is not the case as they have more flexibility in where they are able to forage and can travel to nearby areas with increased krill density. However,

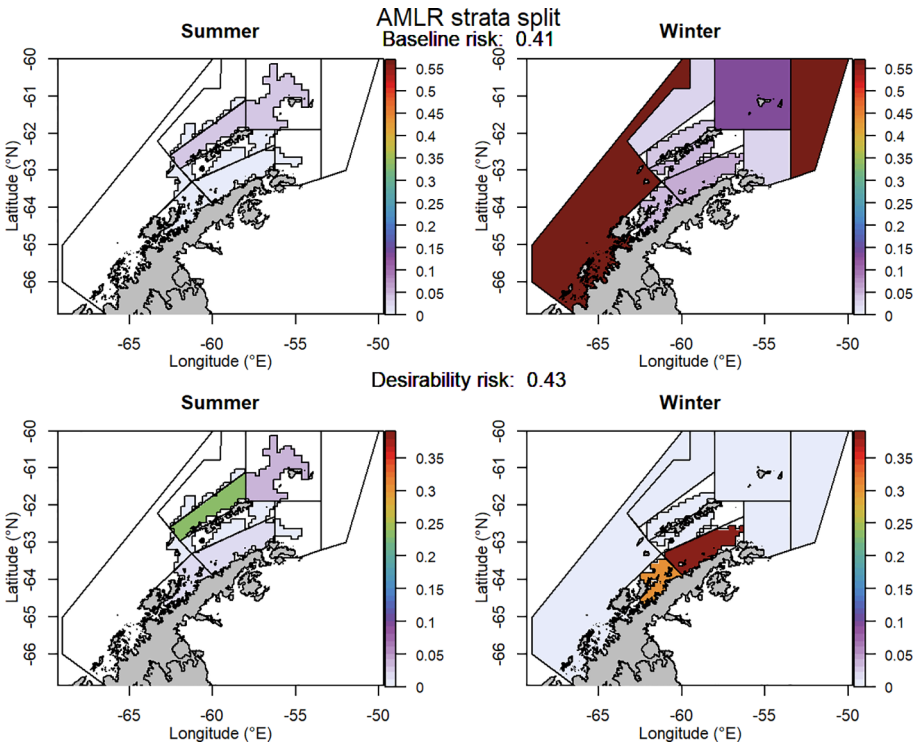

FIGURE 7
The proportion of the annual krill catch limit that could be taken from each management unit (delineated using the US-AMLR survey strata divided into smaller management units) during summer and winter when the risk assessment was implemented after the winter krill layer was adjusted and assuming catch is not evenly distributed within management units. Values sum to 1 across all management units and for both seasons for each of the baseline (upper panel) and desirability (lower panel) scenarios.

evidence now suggests that individuals of some pelagic species such as humpback whales and pack-ice seals also have preferred feeding grounds (e.g. Burns et al., 2004; Dalla Rosa et al., 2008; Nowacek et al., 2011; Weinstein and Friedlaender, 2017). Some fish species build nests (e.g. Daniels, 1978), but their spatial and temporal dynamics remain largely unknown at scales relevant to the risk assessment.

Information about different life history stages of krill is important, particularly as only certain stages are targeted by the commercial fishery. Risks to the krill stock as a whole could occur if particular stages were to be reduced below any given ecological threshold. As such, risks are likely to reflect different scales of ecosystem operation (Perry et al., 2019; Veytia et al., 2020). Having implemented the risk assessment for Subarea 48.1, coupled with information about commercial net selectivity and the circumpolar distribution of krill, we suggest that CCAMLR might reconsider ecological risks to juvenile krill. For example, it would be useful to determine if krill should be weighted equally to central place foragers and pelagic species. Although it is important to protect krill in early life stages, these early-life stages are widespread, and are not targeted by the fishery. Additionally, it may be important to protect other krill life-history stages such as spawning adults, which may also be impacted by the fishery due to their restricted distribution (Meyer et al., 2020). Weighting the risk to juvenile krill as equal to the risk to central place foragers and pelagic species may therefore be disproportionate.

Model limitations and future work

The approach we have taken to apply the risk assessment, whereby data layers are created for each species and for the fishery, allows us to identify areas of increased risk at fine spatial scales. However, we recognise that some of the predator and krill data layers could be improved, particularly for winter, but also for summer. The estimated proportion of krill consumed by each predator group and the spatial distributions of consumption will influence the outcome of the risk assessment. However, the data we used are the best currently available. Therefore, should CCAMLR continue to use the risk assessment approach in the future, a revision of predator monitoring data will be necessary and this should, at least partially, be designed to parameterise the needs of the risk assessment.

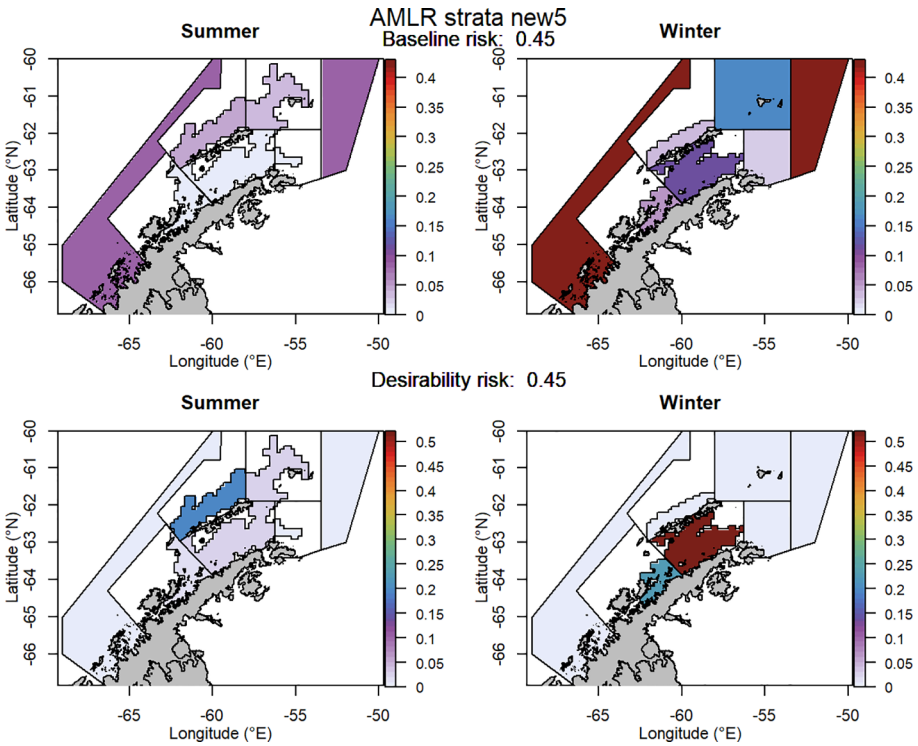

FIGURE 8
The proportion of the annual krill catch limit that could be taken from each management unit (delineated using the US-AMLR survey strata with an added management unit) during summer and winter when the risk assessment was implemented after the winter krill layer was adjusted and assuming catch is not evenly distributed within management units. Values sum to 1 across all management units and for both seasons for each of the baseline (upper panel) and desirability (lower panel) scenarios.

Data gaps

Spatial scale

The available data and modelling approaches we have used for penguins, flying seabirds, Antarctic fur seals, humpback and fin whales and krill allow us to identify important areas at fine spatial scales. However, the best available estimates of the abundance of pack-ice seals, and finfish are at the SSMU scale, which is far broader than the scale of some of the scenarios tested. It is likely that the distribution of species will vary within such broader spatial scales, and plausible that risk to these species may not be adequately captured, especially for winter, when observations are sparse.

In some cases it was necessary to predict habitat-use distributions outside of surveyed areas, and it was not always possible to validate the predictions in these areas. The modelling approaches we used associate observed species distributions with particular environmental characteristics and our predictions assume that these relationships remain consistent across the study area. Although it is probable that the environmental characteristics identified by these models are important drivers of species distributions, there are also likely to be additional factors that influence the distributions of these species (e.g. competition, density dependence, and prior knowledge). Consequently, although our models combine the best available data with robust modelling approaches, it is plausible that they do not fully identify all important areas for some species.

We also note that the U.S. AMLR krill survey area no longer overlaps with much of the area used by the krill fishery, as the fishery has become more concentrated in nearshore shallow waters at depths of <1000 m (Warwick-Evans et al., 2022a). We emphasise that it is important to collect new krill acoustic density data, including in areas representative of those areas where the fishery currently operates, to validate our models. This is also true for all predator species, and without such data, it will remain challenging to parameterise new models and/or to validate the models we have already developed.

Temporal scale

This risk assessment operates at a seasonal scale, with summer and winter considered separately. The distribution of both krill and predators is variable throughout the year (see Appendix 2) and by working at this scale we can begin to capture some of this variation. However, species distributions are likely to be variable within and across these broad temporal scales (e.g.

Lascara et al., 1999; Curtice et al., 2015). For example, penguins are most constrained during the chick-rearing period, when these data were collected, with a wider range during the rest of summer (Orians and Pearson, 1979; Warwick-Evans et al., 2018; Warwick-Evans et al., 2019). As such, it is likely that penguins will have a wider distribution than shown in these data layers during some of the summer period. Additionally, the energy requirements of penguins vary considerably throughout the year at finer temporal scales than the seasonal scale at which we are working (Croll and Tershy, 1998). As far as we are aware, the energetic requirements or field metabolic rates of penguins have not been estimated for the winter period, and it was necessary for us to use summer estimates. Energy requirements will be elevated during periods when they are preparing for and recovering from breeding and moult and when provisioning chicks (Croll and Tershy, 1998). As a result, krill consumption will be highly variable throughout the year (e.g. Boyd, 2002; Southwell et al., 2015). Although some of these periods of increased krill consumption will fall during winter it is likely that krill consumption will be considerable during the summer chick provisioning period. As such, it is plausible that we overestimate individual krill consumption by penguins during winter. However, these data layers for penguins consider only breeding adults (and nestlings), and do not account for juvenile or non-breeding individuals. As a result, it is likely that the overall estimates of krill consumption by penguins are conservative (see Boyd, 2002; Emmerson and Southwell, 2017).

We also assumed humpback and fin whales congregate to feed in the study area for approximately 120 days during summer (as per Lockyer, 1981), although more recent estimates suggest that they may inhabit the area into June and July (e.g. Širović et al., 2004; Nowacek et al., 2011; Weinstein and Friedlaender, 2017). As such, this period does not directly align with the October – March definition of summer used in this risk assessment. It was not possible to subdivide these krill-consumption estimates across the seasons defined here as a result of the ongoing uncertainty about the abundance and distribution of whales later in the season. Consequently, by assigning all krill consumption by cetaceans to the summer period we might be underestimating these estimates of predation pressure on krill during the winter months, and potentially overestimating it during summer. If such biases are substantial, more catch would need to be assigned to summer and less to winter.

Ecological data used to assess krill consumption and therefore risk, cannot be neatly partitioned into simple time periods if they are to adequately capture the ecosystem dynamics within the study area. Thus, although it would be meaningful to align the temporal scale of management with the dynamics of the ecosystem, this remains a challenge. In the future, the risk assessment framework may require working at finer temporal scales which highlight periods when risks to predators are greatest, but also recognising restrictions of available data and implementation.

A consequence of this temporal mismatch is the spatial mismatch. Currently, the same management units are used for each season. However, it is plausible that different management unit boundaries may be appropriate in summer and winter.

Additionally, most predator surveys or tracking studies are conducted between January and March, and very little data exists for the winter months. This is important as the autumn and winter period is the time during which the fishery is most active in Subarea 48.1 (Trathan et al., 2022) and thus the ecosystem is potentially most at risk from the fishery. The consequences of these limited data may be variable amongst predator groups. For example, we were not able to estimate the consumption of krill by flying seabirds over winter. However, our estimates of summer krill consumption suggest that they consume approximately 2% of all krill consumed in the study area (Warwick-Evans et al., 2021). It is likely that most flying seabirds will be less abundant during winter as advancing sea-ice may prohibit foraging in the area. Consequently, we believe that excluding flying seabirds from the winter analysis is unlikely to greatly affect the outcome of the risk assessment. However, excluding cetaceans from our winter estimates may have far more impact, due to the quantity of krill they consume.

Similarly, the U.S. AMLR Program has only conducted a limited number of krill surveys during winter, but these allowed us to develop separate layers for krill in summer and winter. However, the estimated krill biomass during winter was considerably lower than estimated summer biomass, and it is plausible that the winter estimate is an underestimate of the long-term winter krill biomass. As a short-term solution on advice from WG-EMM, we have adjusted the winter biomass to match the summer biomass, whilst maintaining the variation in distribution. However, as krill biomass during winter is expected to be lower than during summer (Lascara et al., 1999), we emphasise that this is a short-term solution and that additional krill survey data covering a broader temporal and spatial scale are now urgently needed. This is made more urgent as the krill fishery preferentially operates into winter (Trathan et al., 2022).

Outdated data and missing species

Although we were able to use recent tracking or survey data to estimate the abundance and distribution of some predators, for others these estimates are outdated and may not reflect current population sizes. For example, surveys for pack-ice seals were carried out in 1999, whilst demographic models parameterised with data from the 1990s were used to estimate the abundance of finfish (Hill et al., 2007; Hückstädt et al., 2020). The layer for finfish will have a large impact on the outcome of the risk assessment (~76% of all krill consumed) and thus it is key that these estimates are updated as part of a long-term

management strategy. In this study, this will have resulted in lower levels of catch being assigned to areas with higher abundance of finfish. Given that the fish layer currently has a large influence on the model outcome, and we do not include models of their fine-scale distribution we suggest that developing a habitat model using recent trawl data would be useful.

Additionally, population estimates for some penguin colonies are from the 1980s. It is likely that at least some of these species have experienced long-term population trends and these outdated estimates have the potential to bias the risk assessment (Trathan et al., 2019). Indeed, several populations of penguins in the area are experiencing declines (Lynch et al., 2012; Strycker et al., 2020). Furthermore, some important krill predators may have been omitted from the analyses entirely. For example, it is likely that the local abundance of blue whales has increased as they begin to recover from historical harvesting (Calderan et al., 2020) and the recovery status of minke whales is unknown, yet these species have not been considered in these analyses. We highlight that without up-to-date abundance estimates for all krill predators the outcome of the risk assessment may be biased in unknown ways.

Energetic requirements

Reilly et al. (2004) evaluated four approaches to calculate the consumption of krill by individual humpback and fin whales, and we have used the approach they considered to be the most robust. However, these estimates were the most conservative of those evaluated; consequently, estimates of krill consumption by whales in the study area would have almost doubled if other approaches evaluated by Reilly et al. (2004) were used. Humpback whale populations are recovering after historical whaling, with the population considered to feed in Subarea 48.1 potentially increasing at a rate of 4.6% per annum (Branch, 2011). As such it is important that we use robust estimates of individual consumption to calculate the predation pressure and thus the risk to predators. If these higher estimates had been used to calculate krill consumption by whales it is likely that this would have impacted the outcome of the risk assessment. Further, recent estimates of baleen whale feeding rates (Savoca et al., 2021), suggest estimates of krill consumption may be much greater than those estimated by Reilly et al. (2004) and those used here, whilst Baines et al. (2022) suggest that these higher feeding rates may predominantly occur at the start of the feeding period.

We emphasize that as CCAMLR develops a long-term management strategy, addressing these data gaps will be vital.

Uncertainty

As with all ecological models, there is inherent uncertainty in all model parameters, and this is an important underlying consideration with any management approach. Uncertainty exists for each step of the modelling framework used here, and ideally all such associated sources of uncertainty should be propagated through to provide a measure of uncertainty for each scenario of the final risk assessment. However, for many of the elements used in our analyses, it is not straightforward to calculate the uncertainty around our estimates, although it may be possible with enough time and resources. In Table 2 we identify some of the main sources of uncertainty in our analyses and how they may be addressed in the future.

An initial approach to incorporating uncertainty into the risk assessment, would be to combine estimates of the high and low confidence intervals for each of the layers, and to implement the risk assessment using various combinations of these layers. To take a precautionary approach, we could combine upper confidence intervals for predator consumption with lower confidence intervals for krill density. Additionally, having an alternative idea on the distribution of krill and its impact might be a useful exercise for examining sensitivity. We suggest that further work focused on propagating uncertainty, or around reducing uncertainty would be useful.

Ecosystem dynamics

One aspect of the risk assessment framework is that the ecosystem is treated as a static snapshot, with no consideration of temporal ecosystem dynamics, other than a summer/winter assessment of risk. This is an important consideration as average ecosystem states rarely exist (Trathan et al., 2022). Nevertheless, to implement the risk assessment, it was necessary to develop data layers that reflect a spatio-temporal average for species distributions. By adopting this approach, we were unable to account for inter-annual variation in the abundance or distribution of species (stochasticity), or process error in the way these values might have been measured (uncertainty). For some predators, such as penguins and flying seabirds, it is highly likely that population numbers are generally stable across years (Humphries et al., 2017), although long-term trends in abundance do exist (Lynch et al., 2012). However, for other ecosystem components, considerable inter-annual variation exists; for example, the maximum acoustic density of krill sampled along the U.S. AMLR survey transects ranged from 827 to 6944 g m^{-2} but with no long-term trend observed. Indeed, estimates of summer krill biomass were lower than the 13 year average in seven of the sampled years (Warwick-Evans et al., 2022a), potentially resulting in an underestimate of risk in those years. Fortunately, and as noted previously, our results are largely consistent with those from dynamic ecosystem models (e.g., Plagányi and Butterworth, 2012; Watters et al., 2013) that do attempt to quantify risks while the underlying abundances of species change.

One of the key processes for identifying risk involves estimating krill predation pressure. With such high inter-annual variation in krill abundance, a multi-year smooth means that there is a real possibility that in years of extreme

TABLE 2 A list of uncertainties present in each aspect of the risk assessment framework and how each may be included in future iterations. .

Uncertainty	How to include in future
Which habitat variables are used in ecological models	Not possible
Relationship between habitat variables and species distributions	Standard errors from model outputs can be used to create confidence bounds and could be included
Density of krill	Standard errors from model outputs can be used to create confidence bounds and could be included
Abundance of cetaceans	Density surface models output uncertainty in abundance estimates, which can also include uncertainty from detection functions
Penguin population sizes	Estimates do not include uncertainty at present, but could be included in the future
Abundance of flying seabirds	Warwick-Evans et al. (2021) calculate confidence intervals and these could be included
Abundance of finfish and seals	Estimates published in Constable (2016) do not include uncertainty, but it may be possible to develop these from the original papers
Consumption by cetaceans	Estimates by Reilly et al. (2004) do not include uncertainty. They do include different approaches to estimate consumption which could be included; other methods might also be feasible
Energy requirements by penguins	Estimates do not include uncertainty at present and estimates have not been developed for some species, or outside the breeding season
Consumption by finfish and seals	Estimates published in Constable (2016) do not include uncertainty, but it may be possible from original papers
Proportion of juvenile krill	The distribution estimates by Perry et al. (2019) do not include uncertainty. It may be possible to estimates uncertainty by looking directly at the KRILLBASE data
Winter krill biomass estimates	Additional winter krill surveys

high or low krill abundance, the index of risk is inaccurate (e.g. being too risk averse when krill abundance is high or too risk prone when krill abundance is low). It would be useful, therefore, to identify an approach by which CCAMLR could incorporate inter-annual variation in the abundance of krill in a risk-based framework, or in a yield model. Though a key concern for krill, this issue is also relevant to all data layers – reducing each species to a single layer brings with it inevitable analytical problems with increased ecological uncertainty.

Krill flux, which is the movement and retention of krill by ocean currents (Hofmann and Murphy, 2004; Thorpe et al., 2007), is also not incorporated in this static snapshot approach. Krill transportation, redistribution or replenishment after local aggregations are depleted is a key feature of the Antarctic ecosystem. It has been well established that krill are transported in ocean currents, so incorporating flux into management is an important next step. In future iterations of the risk assessment it will be important to investigate the effects of differentially weighting areas upstream and downstream of the fishery, or adding a buffer around areas important for krill reproduction, or influx into an area. For example, considering a dynamic framework that protects the major oceanographic gateways into each area preferred by the fishery might be plausible (Trathan et al., 2022). In such a scenario, estimating krill input through each gateway would allow a yield to be determined for each source, which might then be taken in the fished area. Such considerations are however for the future, as CCAMLR has agreed that initial management deliberations should not include krill flux (CCAMLR, 2018b; CCAMLR, 2021).

Measuring success

As the new krill management strategy is implemented, it is vital that monitoring occurs in all management units in which the fishery operates. We have highlighted that there are many caveats associated with this implementation of the risk assessment, and it is imperative that any unforeseen implications of these are detected at an early stage. Thus, in addition to acoustic surveys for krill at appropriate spatial and temporal scales, similar such surveys for predators should be initiated. Because the fishery will aggregate within any management zone it is likely that the risk estimated by the risk assessment will be less than experienced by the ecosystem, and catches should only be increased in line with monitoring. Initially, identifying a means of detecting any impacts of fishing on the ecosystem is essential. Subsequently, a staged approach to increasing catch limits (if the evidence indicates this is feasible) whilst monitoring impacts and reviewing management would be precautionary, and is discussed in detail in Constable (2011).

Our work suggests that a large proportion of the catch limit will be assigned to winter. As such, understanding the carryover effects into the following summer will be vital (Trathan et al., 2021).

Key questions for CCAMLR

We have identified a number of aspects that may bias the outcome of the risk assessment, and it is vital that CCAMLR address some of these issues as it proceeds with the new management strategy. Constable (2016), (Constable et al. in review) emphasised that this approach does not require perfect

data but instead relies on approximating the relative risks between areas. Whilst we agree with this in principle, if the data does not adequately reflect the distribution of risk within the management area, then the outcome of the risk assessment will be biased. In particular, CCAMLR must consider how to align management with the spatial and temporal resolution at which the ecosystem operates (Watters et al., 2020). Key questions include:

- Is it ecologically meaningful to work at the seasonal (summer/winter) scale, or should alternative seasonal timescales be considered? If so, how should each season be parameterised given existing data availability?
- Do management units need to be the same for each season or can different management units be used in the winter and summer?
- How do we capture the considerable inter-annual variation in the krill-based ecosystem?
- How does CCAMLR deal with uncertainty and stochasticity?
- How does CCAMLR weight krill early-life history stages, compared with central placed foragers and pelagic predators?

Conclusions

The risk assessment framework provides a useful tool to understand the spatial and temporal scales at which to apportion krill catch limits to minimise the risks to predators and krill. The risk assessment can be updated as and when new data become available, either by survey area, season or taxon. We draw six main conclusions from the current implementation of the risk assessment for Subarea 48.1:

i. The footprint in which the fishery has operated over recent years (2013-2018) results in the highest risk to predators and krill of all of the scenarios evaluated. This means that spatial management at scales smaller than Subarea scale are now appropriate;
ii. Managing the fishery at a fine spatial scale reduces risks to krill and predators, although this may be more challenging for management procedures;
iii. In general, baseline scenarios showed lower risk estimates than when fisheries desirability was included. Given that consensus on which management units to use is most likely to be achieved using scenarios that include fisheries desirability, it is likely that CCAMLR will progress its management framework using the desirability scenarios. Options exist to offset the increase in risk if desirability scenarios are used (Constable (2016), (Constable et al. in review), but these have not yet been considered by CCAMLR;
iv. More catch is currently taken in winter, than in summer, which is consistent with proportions assigned by the risk assessment using the adjusted krill layer. As such, CCAMLR may wish to define strict seasonal allocations for catch limits, as well as spatial allocations;
v. Management units delimited using one of the variations of the U.S. AMLR krill survey strata are likely to provide a means to manage the krill fishery at a scale more closely aligned with ecosystem dynamics, with a relatively low risk to the ecosystem, whilst remaining relatively straightforward to manage. However, these still allow the fishery to aggregate and may not be appropriate if catches increase; and
vi. Inappropriate parameterisation of the risk assessment leads to erroneous estimates of risk from fishing.

The study supports earlier findings that management at scales smaller than the Subarea scale are appropriate (Watters et al., 2013; Watters et al., 2020). New data have become available and are likely to continue to do so. As such, it will be useful to update the risk assessment at regular intervals (e.g. every 5 years) to ensure that risks do not increase following any changes in the operation of the krill fishery, or changes to the ecosystem.

The overall management strategy essentially considers the ecosystem as a photographic snapshot, whereas, in reality, the ecosystem should be considered as a photographic video (Trathan et al., 2022). As CCAMLR moves forward and continues to develop the strategy into a long-term management framework, it will be important to account for certain fundamental dynamic processes within the ecosystem.

In addition to exploring the appropriate spatial scale for management units, CCAMLR will also need to remain cognizant of the tractability of implementation. The value of regional risk provides one tool that could help managers decide upon how best to choose between different scenarios with different management scales. The risk assessment provides a pragmatic approach that is tractable and transparent, providing community ownership of the management process within CCAMLR.

In this paper, we have raised a number of implementation issues that we believe CCAMLR now needs to address. However, we believe that they could all be addressed but their resolution will take further community effort. As such, we consider these risk analyses for Subarea 48.1 could be used to provide management advice in the short term, with the intention of addressing some of these issues as CCAMLR moves forward in developing a long-term management strategy.

As CCAMLR develops the risk assessment framework, it is imperative that management remains precautionary. We highlight

that the existing spatial subdivision of catch offers more risk to the ecosystem than do other scenarios tested. The implications of this are that it would not be precautionary to allow catches to increase at this time, and that spatial subdivision of catches within each Subarea is now urgent. A key message for CCAMLR is that management should best occur at the same spatial and temporal scales as ecosystem function. Finally, we highlight that the endeavours reported here are the result of a community effort, demonstrating the value of common enterprise.

Data availability statement

Publicly available datasets were analyzed in this study. Data are available from the dryad data repository (doi: 10.5061/dryad.4qrfj6qc5).

Author contributions

VW-E: formal analyses (lead), methods (supporting), conception (joint lead), writing (lead) and funding (supporting). PT: conception (joint lead), methods (supporting), writing (supporting), editing and funding (lead). AC: methods (supporting), editing. LD: data provision and editing. ERS: data provision and editing. ES: data provision and editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.1015851/full#supplementary-material

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Biological responses to change in Antarctic sea ice habitats

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Sea ice is a key habitat in the high latitude Southern Ocean and is predicted to change in its extent, thickness and duration in coming decades. The sea-ice cover is instrumental in mediating ocean–atmosphere exchanges and provides an important substrate for organisms from microbes and algae to predators. Antarctic krill, *Euphausia superba,* is reliant on sea ice during key phases of its life cycle, particularly during the larval stages, for food and refuge from their predators, while other small grazers, including copepods and amphipods, either live in the brine channel system or find food and shelter at the ice-water interface and in gaps between rafted ice blocks. Fish, such as the Antarctic silverfish *Pleuragramma antarcticum*, use platelet ice (loosely-formed frazil crystals) as an essential hatching and nursery ground. In this paper, we apply the framework of the Marine Ecosystem Assessment for the Southern Ocean (MEASO) to review current knowledge about relationships between sea ice and associated primary production and secondary consumers, their status and the drivers of sea-ice change in this ocean. We then use qualitative network

modelling to explore possible responses of lower trophic level sea-ice biota to different perturbations, including warming air and ocean temperatures, increased storminess and reduced annual sea-ice duration. This modelling shows that pelagic algae, copepods, krill and fish are likely to decrease in response to warming temperatures and reduced sea-ice duration, while salp populations will likely increase under conditions of reduced sea-ice duration and increased number of days of >0°C. Differences in responses to these pressures between the five MEASO sectors were also explored. Greater impacts of environmental pressures on ice-related biota occurring presently were found for the West and East Pacific sectors (notably the Ross Sea and western Antarctic Peninsula), with likely flow-on effects to the wider ecosystem. All sectors are expected to be impacted over coming decades. Finally, we highlight priorities for future sea ice biological research to address knowledge gaps in this field.

KEYWORDS

Southern Ocean, storms, warming, copepods, fish, primary production, krill, MEASO

1. Introduction

Sea ice is a major structuring component in Antarctic marine ecosystems and a key driver of Southern Ocean biogeochemical cycles (Thomas, 2017; Henley et al., 2020). It forms a physical and chemically-active barrier on the surface of the ocean, and strongly affects fluxes of gas (e.g., climate-active gases such as carbon dioxide and various sulphur compounds, e.g., dimethyl sulphide) and energy across the atmosphere–ocean interface (Tison et al., 2017). Sea ice also forms a key habitat for ice algae (Arrigo, 2017); it is highly reflective (particularly when snow covered) and reduces light levels under the ice to 0.1%–1% of incoming surface radiation (Arndt et al., 2017), resulting in strong control on Southern Ocean phytoplankton production and phenology (Henley et al., 2020; Pinkerton et al., 2021). Sea-ice cover also decreases wind-driven mixing of the surface ocean, and its seasonal melt can induce stratification in the upper layers of the water column that is conducive for pelagic phytoplankton blooms during ice retreat in spring (Saba et al., 2014; Sabu et al., 2014; Kauko et al., 2021). Antarctic sea ice extent is sensitive to both atmospheric and oceanic forcing; however, regional-scale atmospheric circulation changes are thought to be the dominant driver of recent trends, i.e., a slight increasing overall trend in sea-ice extent since 1979 comprising different regional and seasonal contributions (Hobbs et al., 2016; Turner et al., 2022).

The life cycles of many Antarctic species are attuned to the seasonal cycle of sea-ice advance and retreat. For example, penguins and seals use sea ice as a resting and breeding platform; their sea-ice requirements are complex and include icescape variables such as landfast ice extent and duration, pack-ice concentration and seasonality and local snow cover thickness and surface roughness (e.g., Massom and Stammerjohn, 2010; Bestley et al., 2020). Sea ice also provides a substrate and habitat for ice-associated (sympagic) communities consisting of bacteria, micro-algae, heterotrophic protists and small metazoans including copepods, flatworms, gastropods and ctenophores (Bluhm et al., 2017). Larger organisms living in the water column below can also use sea ice as a refuge from predators and/or as feeding grounds (Figure 1).

Ecosystem services provided by sea ice and their associated communities include biogeochemical cycling, food web maintenance, primary productivity and climate regulation, along with benefits for science, tourism and recreation, food security and fisheries (Grant et al., 2013, 2021; Cavanagh et al., 2021; Murphy et al., 2021; Steiner et al., 2021). At present, our understanding of how global environmental change will affect the biota associated with Antarctic sea ice is limited (IPCC, 2019, 2021). Here we apply the Marine Ecosystem Assessment of the Southern Ocean (MEASO) framework to synthesise the present state of knowledge of key lower trophic level biota that have strong connections with sea ice, either by occupying the sympagic habitat or by living in seasonally ice-covered waters. We then build a qualitative network model to show the interactions between these physical, chemical and biological components of the Southern Ocean ecosystem and explore how cascading feedback effects might affect the system under the influence of future global environmental change.

2. Sea ice

The annual cycle of Antarctic sea ice coverage represents the largest seasonal physical change on the surface of the Earth, varying between ~3.1 million km^2 in February and 18.5 million km^2 in September (Eayrs et al., 2019; Parkinson, 2019). For ecosystems, a crucial distinction is between extensive mobile pack ice and stationary coastal landfast ice, because they provide different habitats for different species (e.g., Massom et al., 2009;

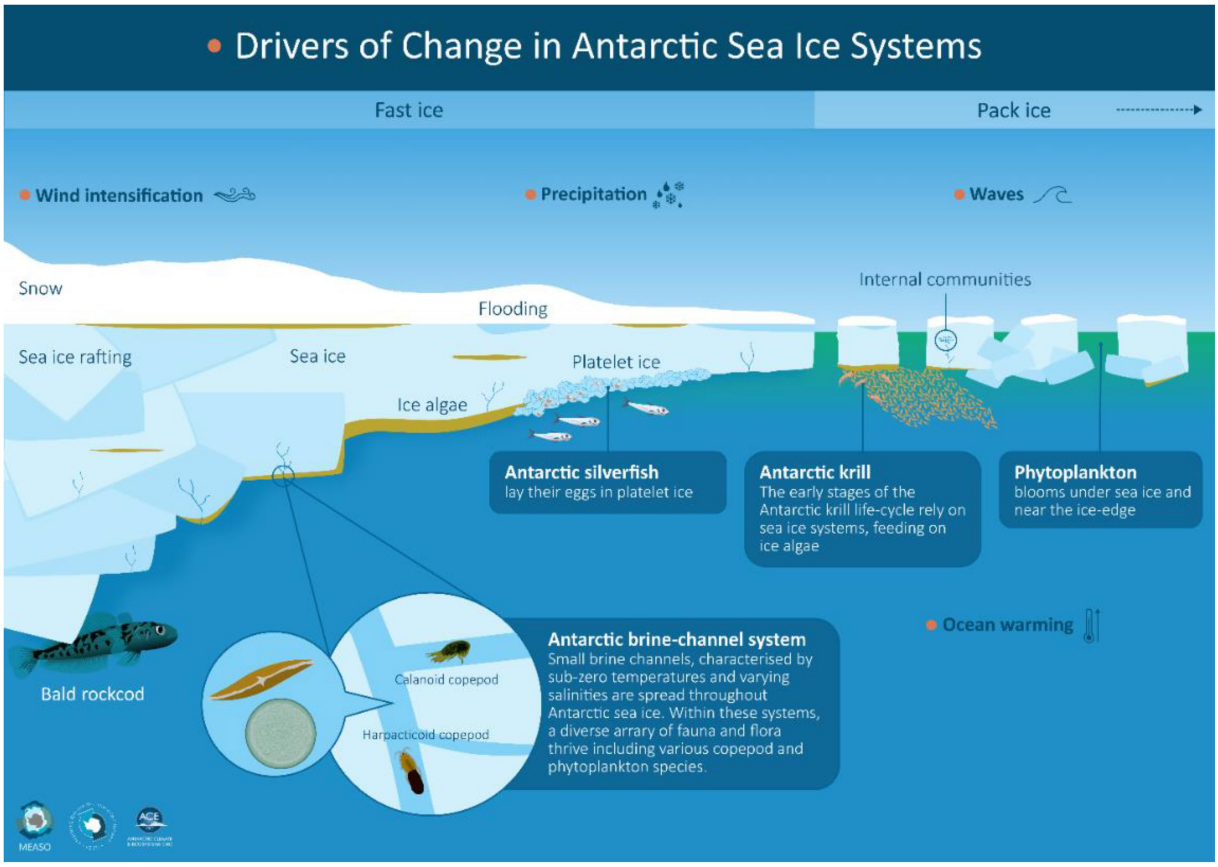

FIGURE 1
Sea ice habitat showing transition from inshore (stationary) landfast ice to offshore (mobile) pack ice. The diagram features key ice-associated biota and the drivers of change that are used as perturbations in the qualitative network analysis (see Table 1B).

Massom and Stammerjohn, 2010; Meiners et al., 2018; Labrousse et al., 2019). Around the Antarctic coast, landfast ice distribution is largely governed by coastal configuration and bathymetric depth (Fraser et al., 2012, 2020). Landfast ice can be either seasonally-recurring or perennial (persist through one or more summers), and the limit of its offshore coverage is generally determined by the location of icebergs grounded on seafloor shoals at a depth of ~400 m below sea level (Giles et al., 2008). The ice spanning from the coast to these pinning points can reach widths up to 300 km in certain areas, but is generally less extensive (Fraser et al., 2020). Although the spatial distribution and variability of Antarctic landfast ice are well-characterised (Fraser et al., 2021), detailed understanding of the drivers of its annual variation is currently lacking, though it is clear that it is affected by both oceanic and atmospheric forcing (Massom et al., 2009; Fraser, 2011; Aoki, 2017; Arndt et al., 2020). At some locations offshore from ice shelves, the shoaling of supercooled water originating from ice shelf basal melting, with its temperature below the freezing point, results in the formation of free-floating ice crystals that may form along the ice shelf gradient; these are known as platelet crystals, which accumulate and grow locally beneath fast ice (Foldvik and Kvinge, 1974; Langhorne et al., 2015). As shown in Figure 1, platelet ice represents an important sub-habitat for some species. A comprehensive review of platelet ice and its role in the Antarctic ecosystem is provided by Hoppmann et al. (2020).

By comparison, pack-ice comprises a matrix of floes of varying size, age, concentration and thickness that are in constant motion in response to ocean currents and winds, which may cause complex rafting or dispersal of ice floes. In winter, the maximum width of Antarctica's pack-ice zone varies from a few hundred kilometres (e.g., off East Antarctica from 120°E to 135°E) to >2,000 km in the deep poleward embayment of the Weddell Sea. Antarctica's pack-ice zone is the dominant part of the sea-ice system that undergoes annual advance and retreat. Although Antarctic pack-ice thickness is a major unknown (IPCC, 2019), largely due to difficulties in making *in situ* measurements, it is thought to be typically 0.3–2.0 m thick (Worby et al., 2008), although larger thicknesses (of ~10 m) can occur through ice deformation where floes collide (Massom et al., 2006). Perennial ice is largely confined to the southwestern Weddell, Amundsen and eastern Ross seas (Parkinson, 2019).

The key attributes of Antarctic sea ice include areal coverage/extent, the thickness distributions of the ice and its snow cover,

rates and patterns of advance and retreat and resultant duration, and the associated variability (Massom and Stammerjohn, 2010). These attributes result from the complex interplay of both thermodynamic processes (freeze/formation and melt) and dynamic processes (movement and deformation of the ice by winds, ocean currents, swell and waves; Weeks, 2010). Although this combination of processes and the frequent passage of storms creates a highly heterogeneous mixture of different ice types, thickness, age and degree of deformation at small scales, overall the Antarctic sea-ice zone is characterised by distinctive large-scale zones (Massom and Stammerjohn, 2010). Moving from north to south, these are: (1) the marginal ice zone or MIZ (outer pack strongly influenced by the high-energy Southern Ocean and ocean waves); (2) the mid pack-ice zone, which is buffered by the MIZ and generally characterised by larger floes and thicker snow cover, but still influenced by storms; and (3) the coastal zone, where sea-ice conditions are strongly influenced by the Antarctic Coastal Current, coastal configuration and the distribution of icebergs; this is also the realm of landfast ice. Recurrent coastal polynyas (i.e., persistent areas of open water bounded by sea ice) are of particular importance as areas of both high sea-ice formation rates (during freezing months) and enhanced primary production in spring–summer (Barber and Massom, 2007). Around coastal Antarctica, polynyas generally form in the lee of blocking features such as coastal promontories and areas of landfast ice, where they are also maintained by strong katabatic winds blowing seawards from the ice-sheet interior (Nihashi and Ohshima, 2015).

At the microscale (millimetres), sea ice is made up of a matrix of ice crystals separated by small inclusions (pockets) of high-salinity brine (Petrich and Eicken, 2017), the characteristics of which are constantly modified by the interaction of physical, biological and chemical processes that vary in space and time. Regarding the ice crystals themselves, Antarctic sea ice comprises a mix of both granular (or "frazil" ice), which forms under turbulent conditions, and elongated columnar ice, which grows downwards under calmer conditions (Weeks and Ackley, 1986). Near peripheral ice shelves, platelet crystals form a porous layer beneath the sea ice called the sub-ice platelet layer which has a high liquid fraction (~75%, e.g., Wongpan et al., 2015). The columnar ice acts as an advancing interface, filling in the "interplateletary" space of the layer, and is where incorporated platelet ice is formed (e.g., Hoppmann et al., 2020).

Snow is a crucially-important part of the Antarctic sea-ice system, for both landfast and pack ice (Massom et al., 2001). It accumulates as an insulative and high-albedo blanket on the ice surface, to substantially modify the optical, thermodynamic and physico-chemical properties and evolution of the underlying ice (Sturm and Massom, 2017). Notably, and depending on its thickness and properties, which themselves change over space and time (Massom et al., 2001), snow exerts strong influence on the intensity and spectral properties of light available for algal growth both within and under the ice (Wongpan et al., 2018). It can also depress the ice surface below sea level (Massom et al., 2001), leading to surface flooding and creation of an "infiltration community" (Fritsen et al., 1994; Kattner et al., 2004; Arrigo, 2017).

2.1. Variability in sea ice in Marine Ecosystem Assessment for the Southern Ocean sectors

Satellite passive microwave time series data obtained since 1978, when the records began, show a slight increasing trend in overall circumpolar Antarctic sea-ice extent (Parkinson, 2019). This overall extent masks contrasting sectoral contributions [i.e., loss in the Amundsen-Bellingshausen seas sector and gain elsewhere (Parkinson, 2019)], as well as widely-varying patterns of change and variability in sea-ice seasonality (i.e., the timings of annual advance and retreat and resultant duration of coverage Massom et al., 2013; Stammerjohn and Maksym, 2017). Moreover, the last decade has been characterised by extreme variability in overall Antarctic sea-ice extents, with record maxima in 2012–2014 (Reid and Massom, 2015) being followed by a strong negative anomaly beginning in 2015/2016 (e.g., Turner et al., 2017; Meehl et al., 2019), and, most recently, the lowest extent on record in 2021/2022 (Reid et al., 2022; Turner et al., 2022).

The MEASO framework divides Antarctica into five sectors, namely the Atlantic, Central Indian, East Indian, West Pacific and East Pacific sectors (Figure 2; Table 1). The Antarctic Peninsula, bordering the East Pacific and Atlantic sectors, is the best studied region biologically, with the western Antarctic Peninsula (wAP) currently the region of greatest environmental change, even when accounting for the cooling trend in the 1990s (Bozkurt et al.,

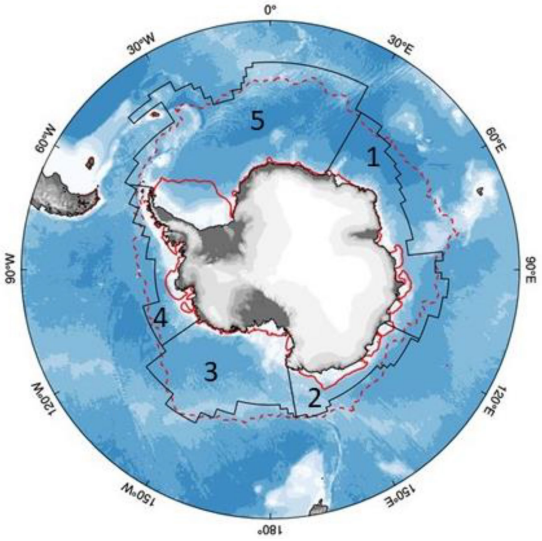

FIGURE 2
Map showing the five MEASO sectors, with average minimum (solid red line) and maximum (dotted red line) sea-ice extent highlighted. Sectors are numbered 1 (Central Indian), 2 (East Indian), 3 (West Pacific), 4 (East Pacific) and 5 (Atlantic).

TABLE 1 Summary of the variation in physical factors of Antarctic sea ice between MEASO sectors (see Figure 2).

(a) Traits and trends of sea ice						
Features	Central Indian	East Indian	West Pacific	East Pacific	Atlantic	Ref
Minimum extent of sea ice reached (month/s)	February	February	February	February, March	February	[1]
Maximum extent reached (month/s)	October	September and October	Variable, July–November	August, September	Variable, August to October	[1]
Trend in sea ice extent over 40 years	Positive trends in all months	Positive trends for 10 months, negative trends for 2 months (September, November)	Positive trends for 10 months, negative trends for 2 months (February, March)	Summer and autumn trends are negative, winter are positive and autumn are mixed	Negative trends in winter and spring but positive trends in summer and autumn.	[1]
Trends in snow cover	Steady increase that reversed in late 20th century	Steady increase that reversed in late 20th century	Decreased accumulation over western WAIS*	Increased accumulation over Antarctic Peninsula and eastern WAIS	There was an overall increase in snow depth between 1986 and 2013	[2,3]
Platelet ice		Common offshore from Mirny, possible accretion adjacent to Mertz Glacier Tongue	In west McMurdo Sound occurs earlier in the season and makes up a high % of sea ice thickness; sometimes absent in east McMurdo Sound.	No platelets observed in Amundsen Seas or Bellingshausen, except for Pine Island	Platelets close to ice-shelf edge or coastal polynyas can be 4–10 m thick; 11–50% of total sea ice thickness	[4]
Fast ice, climatological minimum extent (km^2)†	66,534	68,960	25,092	20,982	33,504	[5]
Fast ice, climatological mean extent (km^2)†	157,452	145,996	35,561	49,726	63,663	[5]
Fast ice, climatological maximum extent (km^2)†	14,229	198,165	43,506	78,762	85,744	[5]
Pack ice, climatological minimum extent (10^6 km^2)	0.187	0.378	0.575	0.457	1.228	[6]
Pack ice, climatological mean extent (10^6 km^2)	1.896	1.232	2.846	1.413	4.244	[6]
Pack ice, climatological maximum extent (10^6 km^2)	3.778	2.000	4.142	2.258	6.643	[6]

(b) Summary of qualitative differences between drivers in MEASO sectors relative to the Atlantic Sector (based on Morley et al., 2020. Central and East Indian Sectors are combined)				
	West Pacific	**East Pacific**	**Indian**	**Future**
Drivers				
Temperature (T)	–	–	+	+
Storminess (S)	0	0	+	+
Time of freeze (F)	0	+	0	+
Time of melt (M)	+	0	+	–
Circumpolar Deep Water (C)	0	+	+	+
Latitude (L)	0	+	+	0

+ denotes change greater than the Atlantic, – change less than the Atlantic and 0 is no change.
[1]Parkinson (2019).
[2]Medley and Thomas (2019).
[3]Tison et al. (2017).
[4]Hoppmann et al. (2020).
[5]Fraser et al. (2020).
[6]Reid et al. (2022), values calculated based on satellite passive-microwave ice concentration data (Cavalieri et al., 1996).
*West Antarctic Ice Sheet.
†Calculated for the years 2000–2018.

2021). Landfast ice represents between 4.0% (during winter) and 12.8% (during late summer) of total sea ice area, with the largest area found in the central and east Indian sectors, and only small areas in the remaining three sectors (Fraser et al., 2021). While circum-Antarctic sea-ice extent showed no significant changes based on satellite data from 1979 to 2018 (IPCC, 2019, 2021), the regional response is divergent, with the East Pacific sector (wAP, including Bellingshausen and Amundsen Seas) showing ice loss, while West Pacific (Ross Sea) and Atlantic (Weddell Sea) sectors gained sea ice and the Indian sectors show no clear trend. There is also significant seasonal variability in the trends (Table 1), such that some seasons are associated with decreases in the ice while others remain static; only the western Ross Sea shows a trend that is statistically significant during all seasons (Holland, 2014). The IPCC (2021) ranks meridional winds as an important driver of sea-ice extent with *high confidence*. Antarctic sea ice is changing at a rate that is much lower than observed for Arctic sea ice, which is likely due to Southern Ocean circulation driving surface heat from anthropogenic warming deeper into the water column. While the decrease in overall Antarctic sea-ice coverage is believed to be too modest to be separated from natural variability (*high confidence*; IPCC, 2021), it is probable that if anthropogenic greenhouse gas emissions continue at the current rate, the loss of seasonal sea ice within the next 50 years could be as high as 40% (Rintoul et al., 2018).

3. State of knowledge of the sea ice associated biota

Biogeographical patterns for Antarctic sea-ice biota are largely based on patchy sampling efforts in both time and space. However, there are considerable data available on the distribution, population structure and ecology of Antarctic krill (*Euphausia superba*), as a result of its importance as key species in the food web (Johnston et al., 2022), and in supporting an international fishery managed by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The SCAR (Scientific Committee on Antarctic Research) Biogeographic Atlas of the Southern Ocean (De Broyer et al., 2014) summarised knowledge of distributions of many key species, including those that associate with sea ice (Duhamel et al., 2014; Swadling, 2014). Much of these data are geographically patchy and insufficient in duration for evaluating the current status of ice-associated species. In many cases chlorophyll *a* concentration is the only biological parameter recorded from ice cores and there are limited winter biological data available for most ice-covered regions (Meiners et al., 2012). Sampling of landfast ice habitats is biased in favour of locations close to Antarctic research stations (Meiners et al., 2018), while for the pack ice there is a strong seasonal emphasis on sampling during spring–summer marine research cruises, particularly around the Antarctic Peninsula and the Weddell Sea (Meiners et al., 2012). This paper focusses on the lower trophic levels that are associated with sea ice, including algae, zooplankton and fish. Further analyses in relation to the MEASO can be found in Pinkerton et al. (2021) for phytoplankton and Johnston et al. (2022) for zooplankton. Pelagic marine predators are discussed in Bestley et al. (2020).

3.1. Ice algae

The biomass of ice-associated communities is generally dominated by autotrophs, in particular pennate diatoms, but also flagellated algal species (e.g., van Leeuwe et al., 2018). Ice-algal communities form distinct communities in bottom, interior and surface layers of sea ice floes (Meiners et al., 2012, 2018). Spatial and temporal distributions of ice-algal communities, and their productivity, are strongly controlled by environmental processes, e.g., light availability and nutrients. Surface communities are promoted by snow loading resulting in surface flooding by seawater and brine, which creates surface-slush and gap layers that form habitat (Fritsen et al., 1994; Kattner et al., 2004; Ackley et al., 2008). In thicker pack ice, interior communities are likely to emerge following the rafting and ridging of ice floes, which are two processes that significantly contribute to the dynamical thickening of Antarctic sea ice (Worby et al., 2008). Furthermore, scavenging of phytoplankton during ice formation (and particularly frazil-ice formation Garrison et al., 1989; DeJong et al., 2018) and subsequent growth of incorporated algae may explain the occurrence of interior communities in undeformed sea ice (Arrigo et al., 2010). Bottom ice-algal communities thrive in the lowermost porous parts of sea ice floes characterised by favorable brine salinities and high nutrient availability. Surface and interior sea-ice algal communities are a characteristic feature of Antarctic pack ice (Meiners et al., 2012), while bottom algal communities generally dominate integrated ice algal biomass in Antarctic pack ice (Meiners et al., 2012). Extremely high ice algal biomass concentrations (with values >1,000 mg chlorophyll *a* m^{-3} of melted ice) have been reported for Antarctic fast ice containing platelet ice (Arrigo et al., 1995; Günther and Dieckmann, 1999), which forms from super-cooled Ice Shelf Water at the base of sea ice adjacent to ice shelves (see Section 2; Langhorne et al., 2015; Hoppmann et al., 2020). This sub-ice platelet layer under landfast ice provides a large surface area that serves as an important algal micro-habitat and a critical hatching and nursery ground for Antarctic silverfish, *Pleuragramma antarcticum* (e.g., Vacchi et al., 2004, 2012; Ghigliotti et al., 2017).

Ice algae contribute substantially to the regional annual primary production of Southern Ocean ice-covered areas (Legendre et al., 1992; McMinn et al., 2010; Pinkerton et al., 2021). The ice algal communities are strongly affected by light availability and by the thermodynamic sea ice regime and its phase-equilibrium that regulates percolation and convection of sea ice brines, thereby controlling vertical material transport within the sea ice and across the ice-water interface (Saenz and Arrigo, 2014).

In general, there is an increase in the relative contribution of ice-algal production to overall production with increasing sea-ice cover duration. Model outputs suggest that ice algae contribute about 10%–20% to the overall sea-ice zone production of the Southern Ocean (Saenz and Arrigo, 2014). The ice algal production generally continues through the autumn and becomes re-invigorated in spring when light conditions for water column production is low, extending the productive season and reducing seasonal oscillations in food supply for pelagic and benthic food webs (Swadling et al., 2000, 2004; Kohlbach et al., 2018; Wing et al., 2018). Dominant taxa in pack ice include the diatoms *Fragilariopsis curta, Fragilariopsis cylindrus, Nitzschia stellata* and *Pseudonitzschia tugiduloides* while *F. curta, Entomeneis kjellmanii* and *N. stellata* (Scott et al., 1994; Takahashi et al., 2022) and *Berkeleya adeliensis* (Ryan et al., 2006) are more characteristic of fast ice. Surface communities tend to be dominated by flagellated taxa such as the dinoflagellate *Polarella glacialis* (Thompson et al., 2006).

3.2. Copepods (Arthropoda)

There are four common species of copepods that inhabit the brine channel system of sea ice, namely the calanoids *Stephos longipes* and *Paralabidocera antarctica* and the harpacticoids *Drescheriella glacialis* and *Harpacticus furcatus*. These copepods are small in size, measuring no more than 600 µm in width, and can number in the thousands of individuals per square metre of ice (Swadling et al., 1997, 2000; Kramer et al., 2011; Bluhm et al., 2017). All of these species have circum-Antarctic distributions, although *P. antarctica* is abundant along the East Antarctic coast (Tanimura et al., 1984; Swadling et al., 2000; Loots et al., 2009), while *S. longipes* is prevalent in the Weddell, Amundsen, Bellingshausen and Ross seas (Schnack Schiel et al., 1995, 1998; Guglielmo et al., 2007). Copepods are important in coastal sea-ice ecosystems as prey items for fish (e.g., *Trematomus borchgrevinki*, Hoshiai et al., 1989), which in turn are food for other marine predators (Johnston et al., 2022). Both *P. antarctica* and *S. longipes* have also been found in summer platelet ice (Günther et al., 1999) in the Drescher Inlet (72°50′S, 19°02′W) in the Weddell Sea. Kiko et al. (2008a) also found high abundances of *S. longipes* in the infiltration layer and Kiko (2010) argues that the acquisition of antifreeze properties *via* horizontal gene transfer might be an adaptation specifically to the occurrence of extremely low temperatures in this habitat. The four common ice-associated copepods use sea ice as a nursery ground, although the extent of their reliance on ice varies seasonally. *Paralabidocera antarctica* show synchronised development, with an unusually long overwintering phase as the naupliar stages that live within the brine channel system; when they reach late copepodid and adult stages in spring, they leave the sea ice to feed and reproduce at the under-ice surface (Tanimura et al., 1996; Swadling et al., 2004). *Stephos longipes* occupies the sea ice predominantly as nauplii (Schnack Schiel et al., 1995; Costanzo et al., 2002) then relocates to the water column, with some individuals remaining in contact with the ice (Guglielmo et al., 2007) and others moving into deeper waters (Kurbjeweit et al., 1993). *Drescheriella glacialis* carry their eggs in paired sacs and show overlapping generations throughout the year. This species inhabits the interstices of the ice, feeding on ice algae and other particulate organic matter (Schmidt et al., 2003). These ice-associated species are also known to appear in the water column as sea ice is melting, highlighting the inter-relationships between sea ice and the pelagic systems (Makabe et al., 2022).

At the ice-water interface, a greater diversity of copepod species uses the ice as feeding grounds and/or for refuge. Frequently-recorded species include the calanoids *Ctenocalanus citer*, *Calanus propinquus* and *Microcalanus pygmaeus*, while cyclopoid copepods include *Oithona similis*, *Oncaea curvata* and *Pseudocyclopina belgicae*. *Calanus propinquus* is a biomass dominant species in the Southern Ocean; a proportion of the population remains in surface waters during winter where the individuals stay trophically active (Burghart et al., 1999), with stable isotope analysis suggesting this species could change its feeding mode to include sea-ice algae (Jia et al., 2016). *Calanus propinquus* also showed nocturnal feeding activity during winter and a modest vertical migration by descending into deeper layers during daytime (Hunt et al., 2014). *Pseudocyclopina belgicae* is the only cyclopoid copepod that might have a strong association with sea ice during its reproductive cycle, possibly overwintering in the ice as late-stage copepodites (Waghorn and Knox, 1988; Menshenina and Melnikov, 1995). Note that while copepods represent considerable diversity and biomass in ice-associated habitats, other groups including pteropods (Thibodeau et al., 2019) and amphipods (Rakusa Suszczewski, 1972; Richardson and Whitaker, 1979; Krapp et al., 2008) can be important in the under-ice environment. Moreover, ciliata, foraminifera, platyhelminthes, and rarer species such as the nudibranch *Tergipes antarcticus* and the anemone *Edwardsiella andrillae* (Daly et al., 2013) and even ctenophores are found inhabiting the brine channel system and/or the infiltration layer (e.g., Kiko et al., 2008a,b; Kramer et al., 2011 and references therein). These taxa are not addressed in this review.

3.3. Euphausiids (Arthropoda)

Antarctic krill, *Euphausia superba*, are a major link between primary producers and higher trophic levels, and use seasonal sea ice as habitat and as a potential source of their winter food supply (Quetin and Ross, 2009). Survival through the first winter is a critical time in the life cycle of krill (Kohlbach et al., 2018; Murphy et al., 2018; Johnston et al., 2022). Larval krill rely on habitat complexity (e.g., rafting, ridging) in sea ice for refuge from predators (Daly, 2004; Meyer, 2012; Meyer et al., 2017, 2020) and as a site of reduced competition for resources (David

et al., 2021). Recruitment is driven largely by winter survival of krill larval stages, which is the period of growth, when they are very susceptible to climate change (Flores et al., 2012; Meyer et al., 2020). Under poor feeding conditions, larval krill cannot grow and moult to their next stage of development (Ross and Quetin, 1991). Larval krill enter their first winter with no lipid reserve and, unlike adult krill, they need to feed continually to meet their energetic needs (Kohlbach et al., 2018; Thorpe et al., 2019). Without food they die within days (O'Brien et al., 2011). Furcilia larvae are capable of scraping ice algal films from the ice surface, especially from greenish sea ice (Hamner et al., 1989). However, as the larvae are not well-equipped to actively harvest sea ice-entrained algal cells in the winter when algal films on the ice surface are not well developed, they rely on the cells being released into the water column by physical processes including ice melting (Meyer et al., 2017). In the autumn, algae are entrained into sea ice as it grows, and these algae serve as potential food for larval krill (Kohlbach et al., 2018). Krill can exploit additional food sources in addition to sea ice algae, such as microzooplankton or detrital material within sea ice (Schmidt et al., 2014; Virtue et al., 2016). There is a strong correlation between sea ice extent and krill populations, which varies regionally (Massom et al., 2006; Atkinson et al., 2019), while the timings of annual sea-ice advance and retreat are another important factor (Quetin et al., 2007). In the Antarctic Peninsula region, krill recruitment is directly correlated with winter sea ice extent (Loeb and Siegel 1995; Johnston et al., 2022). Warming and ice loss has led krill populations in the Southwest Atlantic sector to contract southward. Numerical densities have declined sharply and the population has become more concentrated towards the Antarctic shelves (Atkinson et al., 2019). However, how representative these findings are for the entire Southern Ocean remains unknown and needs to be investigated.

Crystal krill, *Euphausia crystallorophias*, has a circumpolar distribution and is a smaller counterpart of Antarctic krill, replacing it in neritic environments (Harrington and Thomas, 1987; Thomas and Green, 1988; Ainley et al., 2004; Johnston et al., 2022). Highest crystal krill densities are generally associated with ice shelves and coastal polynyas (Boysen Ennen et al., 1991; Pakhomov and Perissinotto, 1996; La et al., 2015; Davis et al., 2017). The crystal krill synchronise the its reproduction with coastal sea ice conditions including the appearance and persistence of polynyas. Spawning is initiated under fast ice but peaks during coastal polynya breakout (Pakhomov and Perissinotto, 1996). Eggs of crystal krill are neutrally buoyant, which allows them to concentrate in the upper layers, while hatched larvae are often associated with sea ice (Pakhomov and Perissinotto, 1996; Daly and Zimmerman, 2004; Wiebe et al., 2011). Crystal krill has a narrow thermal habitat restricted to coldest, coastal waters and thus can be vulnerable to climate change (Guglielmo et al., 2009; Papot et al., 2016). Changes in sea ice "dynamics", potential pelagic ecosystem modifications and shift of the Antarctic krill into the coastal environments under climate change may rebalance interactions and increase competition between two species, although with unknown outcomes at this point (Smith et al., 2014; Papot et al., 2016). Nevertheless, coastal seas with large continental shelves may provide crystal krill with refugia pockets, limiting its range.

3.4. Salps (Chordata)

Salps are gelatinous organisms that are found over a wide area of the Southern Ocean and are most numerous north and south of the Antarctic Polar Front (Foxton, 1966; Pakhomov et al., 2002; Johnston et al., 2022). Salps exhibit a complex life cycle and reproduction consisting of alternating generations of sexual (colonial forms or blastozoids) and asexual (single forms or oozoids) forms that differ morphologically (Foxton, 1966; Bone and Trueman, 1983). Salps can pump water through their internal cavity using their muscles, to create water currents that they use for propulsion, breathing, and feeding (Bone et al., 2000). Salps are indiscriminate filter feeders and ingest a wide range of particles, from 1 μm (bacteria) to several mm (small crustaceans; Sutherland et al., 2010) in size and, based on lipids and molecular observations, flagellates are a large component of their diet (von Harbou et al., 2011; Metfies et al., 2014). It has been documented that at high chlorophyll *a* concentrations (>>1 mg m^{-3}) salps can suffer clogging of the feeding mesh and are rarely found in regions of dense phytoplankton blooms (Perissinotto and Pakhomov, 1998). Observations of the faecal pellets of salps suggest that some of these larger particles are passed through the digestive tract relatively intact and are therefore lost to epipelagic food webs as the heavy pellets sink rapidly out of the euphotic zone (Cabanes et al., 2017; Iversen et al., 2017; Pauli et al., 2021a). They appear to flourish in warmer waters in the Southern Ocean and in regions of low to moderate chlorophyll *a* concentration (Loeb et al., 1997; Pakhomov et al., 2002; Pillai et al., 2018). In the sea ice zones of the Southern Ocean, information about salps is limited but it is noted that in the Antarctic Peninsula region, where temperatures are warming much faster than the global average, they replace krill on a regular basis and this appears to be contingent on sea ice conditions (Pakhomov et al., 2002; Atkinson et al., 2004). Over the last century, salps expanded southward, which increased their spatial overlap with the Antarctic krill distribution range (Atkinson et al., 2004). However, salp populations in the high Antarctic are not permanently established (Pakhomov et al., 2011). Although salps have been observed under the seasonal sea ice (Perissinotto and Pakhomov, 1998; Pakhomov et al., 2018), krill are not yet replaced by salps because the species occupy different water masses and salps do not respond directly to sea ice conditions.

3.5. Fish (Chordata)

Sea ice in the Southern Ocean is an important habitat for a variety of notothenioid fish species, traditionally defined as "cryopelagic" species (Andriashev, 1987). *Trematomus borchgrevinki* is the best known ice-associated fish, with adaptations for cryopelagic life including camouflage against the background colour of the ice owing to silvery reflective layers beneath the skin and in the eyes, and protection from freezing provided by the high quantity of antifreeze glycoproteins in their body fluids (Eastman and DeVries, 1985). Other notothenioid species, which also contain antifreeze glycoproteins and associate with sea ice, include *Trematomus amphitreta, Trematomus (=Pagothenia) brachysoma* and *Trematomus (=Cryothenia) peninsulae* (Duhamel et al., 2014). Cryopelagic fishes often stay inactive, in an upside-down position, with their ventral side against the ice, and move erratically over short distances, possibly using the underside of the sea ice as a resting structure to reduce energetic requirements (Gon and Heemstra, 1990; Kock, 1992; Gutt, 2002). Large adult specimens of *T. borchgrevinki* swim slowly, in the normal position, in close vicinity to the sea ice, and hide between crevices (Eastman, 1993; Gutt, 2002), using the sea ice as a protective structure to avoid predation.

Although not included in the list of cryopelagic species, there are species whose distribution is influenced by the presence/absence of sea-ice cover; e.g. *Trematomus newnesi* occupy a cryopelagic niche as juveniles (Duhamel et al., 2014). Although living in swarms and being largely planktivorous, *T. newnesi* feeds on sea ice-associated fauna (Casaux et al., 1990; La Mesa et al., 2000). *Trematomus eulepidotus* occurs in the shallow coastal waters of Terra Nova Bay early in the summer, when the area is covered by sea ice, while moving into deep waters later in the season and after the sea-ice melting, thus suggesting an advantageous use of the sea-ice cover as shelter by this species (Vacchi, personal observation).

Some other fish species are linked to the sea ice during a crucial phase of their life, notably their embryonic development. Dragonfish *Gymnodraco acuticeps* eggs have been found in nests in shallow waters amongst anchor ice (submerged fast ice that is attached to the bottom), and ready-to-hatch eggs of *T. borchgrevinki* have been collected within a crevice on the side of an iceberg (Cziko et al., 2006). The most striking example is provided by the Antarctic silverfish *Pleuragramma antarcticum* (a commonly cited synonym is *P. antarctica*), whose developing eggs have been found dispersed in the platelet ice layer under the solid fast ice at Terra Nova Bay (Ross Sea), where they form the only known to-date silverfish hatching area (Ghigliotti et al., 2017). Survival of embryos and early larvae in that icy environment is possibly due to a suite of morphological adaptations (Cziko et al., 2006; Bottaro et al., 2009). Furthermore, the platelet-ice layer with its tridimensional crystal lattice structure provides protection from large predators (Guidetti et al., 2015).

4. Qualitative network modelling

In the following sections, we use qualitative network modelling (based on Melbourne-Thomas et al., 2012) to investigate potential synergistic, antagonistic and cascading effects on the ecosystem, given long-term change in the physical and chemical nature of the sea ice system. Details of the rationale behind qualitative network modelling are presented in Appendix. In short, we applied the network diagraph approach of Melbourne-Thomas et al. (2012) to construct a qualitative network model where plausible interactions (edges) between the components (nodes) are either positive, neutral or negative, but with no quantitative magnitude of change. Such a network can be used to synthesise information on individual relationships between nodes to better capture the chains of interactions (cascades), compounding effects (synergisms, antagonisms) and positive and negative feedback loops. Many simulations (up to 10,000) can then determine probabilities of nodes increasing, decreasing or not changing when one or more of the physical attributes of the system are permanently changed (positively or negatively), in a process known as a press perturbation (Melbourne-Thomas et al., 2012). We undertook several press perturbations using the R package *QPress* (Melbourne-Thomas et al., 2012). In describing the outcomes, we focus on those impacted nodes where the directional change has a probability greater than or equal to 0.6, but report all probabilities.

The interactions between the different physical and biological components investigated are shown in Figure 3. The habitat variables that were considered in the model are precipitation (falling as rain or snow, depending on temperature), snow cover thickness, habitat in the sea ice (complexity, e.g., ridging and rafting, total ice volume, a function of area, duration, and thickness, and brine volume), platelet ice, nutrients in the ice and pelagic and light (in the autumn, winter and spring seasons; Table 2). Biotic variables that were included are ice algae and seasonal phytoplankton, copepods and Antarctic krill (with larvae of both groups as a separate node), salps, fish (myctophids, *Pleuragramma antarcticum*) and ecosystem metabolism in the ice and pelagial (Table 2). The nodes and edges are simplified from a more complex system structure. Nodes may represent many attributes that interact with other nodes in the same way. Most edges are self-explanatory and represent the links between nodes. Some edges represent the outcome of complex interactions rather than a full chain of events in order to avoid unwanted feedbacks in the qualitative model. For example, an increase in the proportion of ice that is brine will give rise to a decrease in nutrients released from the ice in spring. This is because the increase in brine increases the availability of particulate nutrients in the ice to algal production, which therefore reduces the particulate nutrients in the ice released in the spring melt. A different combination of edges would make this difficult to represent. Similarly, we have not represented the full complexity of the brine system food web, which in some regions contains many small meiofaunal species with numerous trophic interactions.

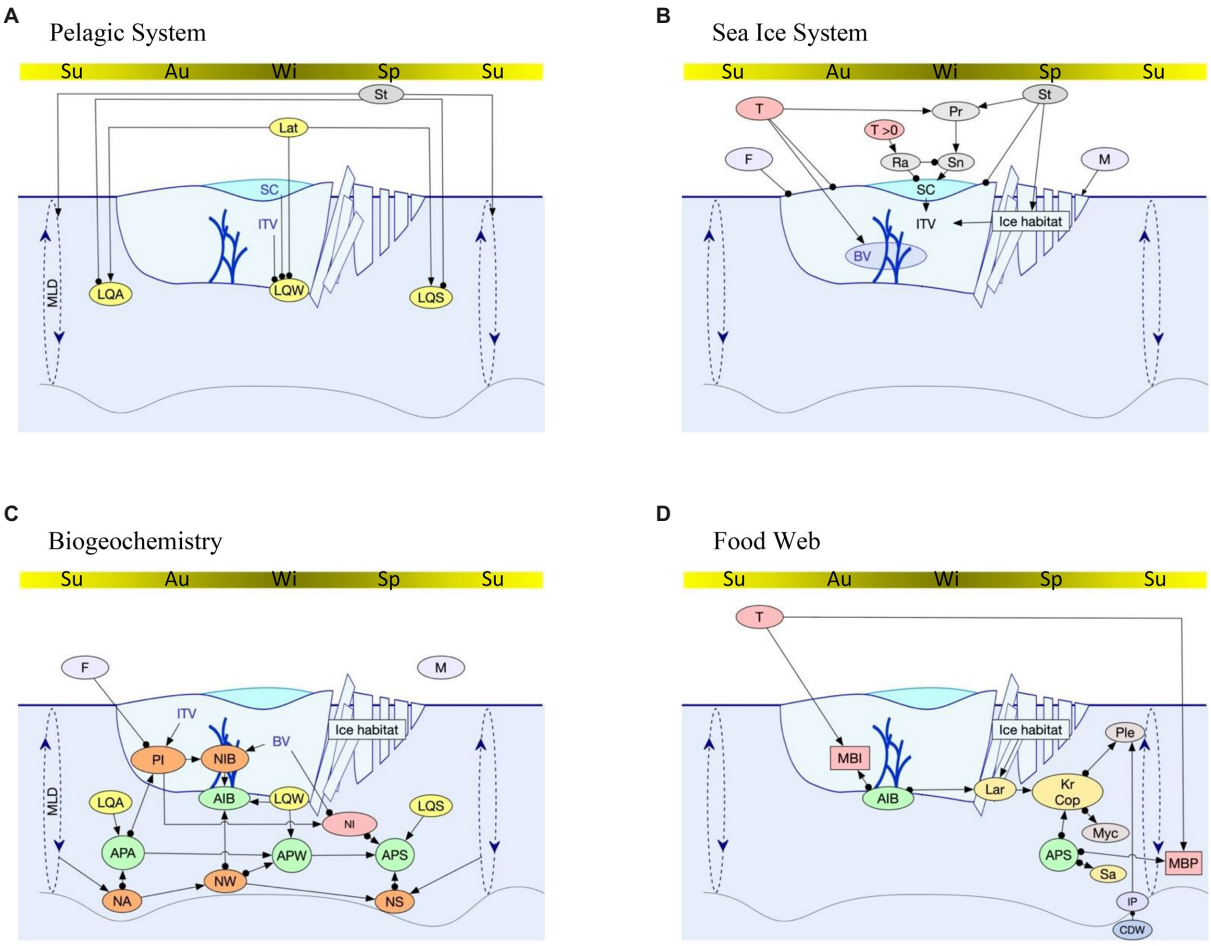

FIGURE 3
Nodes and linkages (edges) used in the qualitative network model. Each panel represents a part of the overall sea ice system. Top bar on a panel represents annual seasonal sea ice cycle from summer, autumn, winter, spring, summer. The remainder of a panel from top to bottom represents atmosphere, sea ice and pelagic realm with the bottom line indicating the bottom of the mixed layer. Cumulative symbols are as follows (Explanations in Table 2): **(A)** Pelagic system: Lat=Latitude; SC=Snow cover; ITV=Ice total volume; MLD=Mixed layer depth; LQA/LQW/LQS=Photosynthetically active radiation in autumn, winter, spring. **(B)** Sea ice system: T=Temperature; T>0 is air temperatures >0°C. St=Storms; Pr=Precipitation; Ra=Rain; Sn=snow; F=Freezing; M=Melting; BV=Brine volume. **(C)** Biogeochemistry: PI=Particulates taken up into ice; NIB=Nutrients in sea ice brine; AIB=Algae at lower sea ice boundary; APA/APW/APS=algae in pelagic waters in autumn, winter, spring; NI=Nutrients from melting sea ice; NA/NW/NS=Nutrients in pelagic water in autumn, winter, spring. **(D)** Food web: MBI/MBP=Biological metabolism in sea ice, pelagic; CDW=Circumpolar Deep Water; IP=Platelet Ice; Lar=Larvae; Kr=Antarctic Krill; Cop=Copepods; Ple=Pleuragramma; Myc=Myctophids; Sa=Salps.

5. Response of sea ice and biota to spatial and temporal shifts in sea ice habitats

The primary drivers of sea ice habitats that are considered in this paper are ocean temperature, air temperatures changing the type of precipitation, storminess, change in the length of sea ice season, the potential effects of Circumpolar Deep Water, and the latitude in which the system is located. We use the qualitative network model to understand how changes in all of these drivers may impact the sea ice physical and biological systems. First, to assist our understanding of the roles of different drivers, we examined the effects of changes in individual drivers according to common hypotheses. Second, we applied known differences in the drivers around Antarctica to investigate the likely differences in sea ice systems between MEASO sectors. Last, we examined the consequences of future change in the drivers for Antarctic sea ice systems.

5.1. Responses of sea ice systems to change in individual drivers

The following hypotheses were tested with the qualitative network model, with the results presented in Table 3:

1. Increasing temperature leads to an increase in the relative cost of sympagic and pelagic metabolism and a decrease in biomass;

TABLE 2 Description of the nodes used in the qualitative network model, as displayed in Figure 3.

Name	Code	Explanation
Drivers		
Latitude	L	Governs light available per day – higher latitude means more daylight hours in early autumn and late spring but less light in winter; 0–90°S
Time of freeze	F	Sea ice season – Timing of advance of sea ice formation in autumn likely to be later (Julian days)
Time of melt	M	Sea ice season – Timing of retreat of sea ice in spring likely to be earlier (Julian days)
Storms	S	Storms break up ice and give rise to rafting etc., thereby increasing habitat for krill. Storms also give rise to increased mixed layer depth, and increases in cloud cover, precipitation, wind strength and wave action
Temperature > 0°C	Tg0	If temperature is >0°C, then precipitation falls as rain rather than snow; there is a likelihood of increased days at these temperatures
Temperature	T	Warming air temperature leads to increases in brine volume and brine channel connectivity (permeability) in ice, increases the metabolic rate for animals, and causes ice loss through melt (°C)
CDW with ice shelf cavity	C	Interaction of Circumpolar Deep Water with ice shelves causes formation of platelet ice
Physical: Light		
Light Autumn	LQA	Light available to pelagic algae in autumn, affected by latitude, cloud cover, sea ice cover, snow cover and mixed layer depth
Light Winter	LQW	Light available to pelagic algae in winter, affected by latitude, cloud cover, sea ice cover, snow cover and mixed layer depth
Light Spring	LQS	Light available to pelagic algae in spring, affected by latitude, cloud cover, sea ice cover, snow cover and mixed layer depth
Physical: Precipitation		
Precipitation	P	Total precipitation that could fall as snow or rain
Precipitation wet (rain)	PW	Precipitation will fall as rain if temperature is >0°C
Precipitation dry (snow)	PD	Precipitation will fall as snow if temperature is <0°C
Surface snow	IS	Snow cover that accumulates on the ice; thickness will vary in response to surface conditions (storms, temperature)
Physical: Ice Processes		
Ice total volume	ITV	Total volume of ice, proxy for available habitat, is a function of ice thickness, ice extent and age of ice. This node governs the relative importance of sea ice processes compared to pelagic processes, i.e., more sea ice results in more particulates taken up into the sea ice which means less remaining in the water column
Brine volume	IB	Proportion of the total ice volume that is brine, thereby influencing the proportion of particulates in the ice available as nutrients. The factors influencing this at present are temperature (modulated by snow cover), salinity, rate and mode of ice formation (frazil v columnar ice), and thickness
Habitat complexity	IH	Habitat complexity is a product of ice deformation (ridging, rafting) and reformation. It is influenced by storms as ice motion is a response to winds and currents
Platelet Ice	PI	Platelet ice is needed for reproduction of *Pleuragramma antarcticum*. Platelet ice results from the interaction of CDW and ice shelves
Nutrient pools		
Nutrients Winter	NW	Nutrients in the water in winter
Nutrients Autumn	NA	Nutrients in the water in autumn
Nutrients Spring/Summer	NS	Nutrients in the water in spring and summer
Ice Particulate Pool	IPP	Phytoplankton frozen into ice as a particulate pool during autumn freeze-up
Ice Available Nutrients	NI	Nutrients made available to the ice-dependent community through brine channels
Nutrient Pool Released from Ice	NIR	Nutrients released from ice upon melting in spring
Biology: Algae		
Algae Pelagic Autumn	APA	Phytoplankton in the water column in autumn

(Continued)

TABLE 2 (Continued)

Name	Code	Explanation
Algae Pelagic Winter	APW	Phytoplankton in the water column in winter
Algae Pelagic Spring	APS	Phytoplankton in the water column in spring, including that released from ice upon melting in spring
Ice Algae Bottom	AIB	Growing in the bottom of the ice and at the ice/water interface
Copepods and krill larvae	ZCKL	Copepods and krill larvae, in the sea ice and pelagos, grazing on algae
Copepods and krill	ZCK	Copepods and krill, in the sea ice and pelagos, grazing on algae
Salps	ZS	Salps feeding on pelagic algae
Myctophids	FM	Small pelagic fish – using the sea ice habitat as a feeding ground and/or refuge from predators
Pleuragramma	FP	Antarctic silverfish, *P. antarcticum,* require platelet ice as a nursery ground
Metabolism in sea ice food web	MI	Relative food web metabolism in sea ice, affected by temperature
Metabolism in pelagic food web	MP	Relative food web metabolism in pelagos, affected by temperature

2. Increasing air temperatures (number of days when $T > 0°C$) will result in decreased habitat and increasing light, and therefore pelagic primary productivity will increase;
3. Storminess will increase habitat complexity, which will lead to increases in sympagic biota;
4. Later freezing will lead to less habitat space available for primary producers and ice algae biomass will decrease;
5. Earlier melting of sea ice will lead to decreased abundance of ice-associated species;
6. Increasing Circumpolar Deep Water (CDW) will result in less platelet ice and therefore the fish *Pleuragramma antarcticum* will decrease in abundance and biomass;
7. Higher latitude ecosystems are subjected to less light from late autumn. Increased latitude means shorter days in winter and longer days in summer, shifting primary production away from winter to the advantage of the pelagic system.

5.1.1. Change in physical habitat

Increasing temperature would contribute to a decrease in total ice volume over a season, although the decrease would be most likely if atmospheric temperature was >0°C due to an increase in precipitation as rain. The proportion of the ice as brine would also increase. Temperature of sea ice directly affects porosity and permeability, chemical composition of the pore microstructure and salinity. At −5°C, the ice fraction of brine represents 35%, and the salinity of the brine is around 87 (Golden et al., 1998). At −30°C, the brine fraction falls to below 8%, reducing the habitat available for microorganisms, while the salinity of brine increases (Ewert and Deming, 2013), consequently restricting the habitat space to only species that are tolerant to high salinities. Based on the relationships between temperature and brine volume, and given warming air temperatures (Tg0 increasing), brine volume, and therefore available habitat, will increase on scales <10 mm. However, warming will also increase melting, leading to reduced duration and thickness of the ice cover on the larger scale.

Increased storminess can be described as increased wind speed, higher rates of precipitation (under blizzard conditions) and increased strength and duration of waves. These changes will have complex and possibly contradictory implications for the Southern Ocean sea ice system. Increased windiness will increase wave energy, possibly resulting in deeper ocean mixing while also bringing warmer waters to the surface; this could then increase the loss of ice through basal melt. Increased storminess could also enhance deformation of the ice, leading to greater habitat complexity (IH) and ice total volume (ITV, depending on coincident change in ice areal coverage – also affected by changes in wind direction). Notably, habitat complexity was directly related to storminess in our model. Yet the influences on sea ice-dependent species may be more complex than just the relationship with habitat complexity. Many of the responses relate to changes in extent and duration of sea ice, the timing of the sea ice season relative to the spring and autumn blooms, and the relative importance of pelagic algae and ice algae in the productivity of species.

5.1.2. Responses of the biological system

i. *Increasing temperature*. Warming produced positive responses in relative metabolism for both sympagic and pelagic communities, while negative or neutral responses in the algae, copepods, krill, salps and fish suggest that their overall numbers would either decrease (negative) or remain the same (neutral). An increase in temperature is likely to result in more resources going towards metabolism rather than growth of individuals and reproduction. Thus an increase in temperature means an increase in the cost of metabolism relative to the production of biomass, resulting in a reduction in biomass.

ii. *Increase in the number of days >0°C*. Increases in the number of days that are above 0°C produced opposing responses in the two habitats, whereby sea ice metabolism

TABLE 3 Assessment of the impacts of key physical drivers of change on the magnitude of food web components associated with sea ice, based on the Qualitative Network Modelling.

Node	Temperature (+)	Storms (+)	Temperature greater than zero (+)	Freezing (later)	Melt (earlier)	Circumpolar Deep Water (+)	Latitude (+)
Ice particulate pool frozen into ice (IPP)	0.50	0.72	−1.00	−1.00	−1.00	0.00	1.00
Nutrient pool released from ice (NIR)	−0.59	0.73	−0.96	−0.99	−0.98	0.99	0.64
Nutrients available in ice (NI)	0.81	0.72	−1.00	−1.00	−1.00	0.00	1.00
Nutrient supply autumn (NA)	0.50	0.97	−1.00	−1.00	−1.00	0.00	−1.00
Nutrient supply winter (NW)	0.61	0.81	−0.93	−0.82	−0.88	0.00	0.72
Nutrient supply spring (NS)	0.79	0.84	−0.59	0.51	−0.54	1.00	−0.79
Bottom ice algae (AIB)	−0.55	−0.63	−0.52	−0.76	−0.64	0.00	−0.57
Pelagic algae spring (APS)	−0.79	−0.57	0.59	−0.51	0.54	−1.00	0.79
Pelagic algae autumn (APA)	−0.50	−0.71	1.00	1.00	1.00	0.00	1.00
Pelagic algae winter (APW)	−0.60	−0.72	0.93	0.97	0.95	0.00	−0.69
Copepods & Antarctic krill (ZCK)	−0.68	0.61	0.54	−0.70	−0.59	1.00	0.64
Copepod nauplii and Antarctic krill (larvae) (ZCKL)	−0.55	0.71	−0.52	−0.76	−0.64	0.00	−0.57
Salps (ZS)	−0.79	−0.57	0.59	−0.51	0.54	−0.99	0.79
Metabolism in sea ice (MI)	0.77	−0.63	−0.52	−0.76	−0.64	0.00	−0.57
Metabolism in pelagic (MP)	0.66	−0.57	0.59	−0.51	0.54	−0.99	0.79
Myctophids (FM)	−0.68	0.61	0.54	−0.70	−0.59	1.00	0.64
Pleuragramma antarctica (FP)	−0.68	0.61	0.54	−0.70	−0.59	−1.00	0.64
Precipitation (P)	1.00	1.00	0.00	0.00	0.00	0.00	0.00
Precipitation – snow (PD)	1.00	1.00	−1.00	0.00	0.00	0.00	0.00
Precipitation – rain (PW)	0.00	0.00	1.00	0.00	0.00	0.00	0.00
Surface snow (IS)	1.00	1.00	−1.00	0.00	0.00	0.00	0.00
Habitat complexity (IH)	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Total ice volume (ITV)	0.50	0.77	−1.00	−1.00	−1.00	0.00	0.00
Brine volume (IB)	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Platelet ice (PI)	0.00	0.00	0.00	0.00	0.00	−1.00	0.00
Light autumn (LQA)	0.00	−1.00	0.00	0.00	0.00	0.00	1.00
Light winter (LQW)	−0.65	−0.84	1.00	1.00	1.00	0.00	−1.00
Light spring (LQS)	0.00	−1.00	0.00	0.00	0.00	0.00	1.00

Probability of a response from 10,000 simulations: the sign represents whether the probability is for a positive or negative response. Colours show responses with probability >0.6. Blue – negative response; Yellow – positive response; White – probability <0.6.

decreased and pelagic metabolism increased. As expected, pelagic algae increased due to the reduced ice cover and an increase in light. Ice algae decreased, most likely due to a reduction of the available habitat. There were increases in krill, copepods, salps and fish, though the larvae of krill and copepods decreased, indicating the contrasting influences of the pelagic and ice habitats, respectively. Larval and juvenile krill are highly ice-dependent, and consequently any perturbations in sea ice deformation, thickness and extent (species-specific sea ice "quality") will directly affect population dynamics (Melbourne-Thomas et al., 2016). Nevertheless, decreased survival of larvae may be offset by increased biomass accumulation by adults. The qualitative model is unable to differentiate between the relative importance of adult productivity and larval/juvenile survival to the overall dynamics of the populations. How increases in adult survival may balance out concurrent decreases in juvenile recruitment depends on the strength of the responses, and cannot

be determined from a qualitative network model. Thus the effects on the total population size are unknown.

iii. *Storminess*. Increased storminess led to decreased light, increased ice habitat and ice volume and concomitant decreases in ice algae and phytoplankton. Algae require a minimum day length to initiate growth so increased cloud cover, particularly in early spring, could decrease the growing season. In contrast, storminess could enhance deep mixing, bringing warmer, nutrient-rich, iron-rich water to the surface, resulting in favourable conditions for algal growth; overall, the model results suggests that light is the primary factor influencing algae in the sea ice and water column. Krill and copepods benefit from the increased habitat that can result from greater storminess, e.g., greater habitat area provides a refuge for krill (Meyer et al., 2017, 2020). The increases in prey could be beneficial for ice-associated fish that are feeding on crustaceans.

iv. Later freezing and v. earlier melting. The model simulations show negative responses from krill, copepods and fish and a decrease in larvae of krill and copepods, largely from the reduced volume of sea ice. Lower numbers of crustacean larvae could be a phenological response to reduced annual duration of the ice cover, preventing the ice-associated species from completing their life cycles; e.g. early retreat of sea ice leads to poor recruitment of krill in warm years (Loeb and Santora, 2015). Salps on the other hand responded positively to reduced sea ice coverage, which is to be expected based on observations that salps thrive under conditions of reduced ice cover (Quetin et al., 2007; Loeb and Santora, 2015). At the same time, lower duration of sea ice coverage could lead to increases in phytoplankton in spring as the amount of light reaching the surface layers is increased and sets off the open-ocean bloom earlier in the year.

vi. Increasing Circumpolar Deep Water (CDW). Increased CDW resulted in a negative response in platelet ice and the fish *P. antarcticum*. Upwelled CDW near ice shelves leads to basal melting, and, consequently, platelet ice production is reduced (as per Hoppmann et al., 2020). As *P. antarcticum* requires platelet ice for early life stages (eggs and larvae; Guglielmo et al., 1998; Vacchi et al., 2004, 2012; Ghigliotti et al., 2017), reduction in this ice type leads to poor recruitment of the fish. Evidence from the Antarctic Peninsula (La Mesa et al., 2015; Corso et al., 2022) has shown that numbers of *P. antarcticum* have decreased substantially in line with reductions in sea ice. Consequent effects include increases in copepods and krill and their predators, myctophid fish, while salps decrease.

vii. Increased Latitude (L). Increased latitude means shorter days in winter and longer days in summer, shifting primary production away from winter to the advantage of the pelagic system.

5.2. Expectations for differences between Marine Ecosystem Assessment for the Southern Ocean sectors

Using an assessment of drivers in each sector, following Morley et al. (2020), we examined how the response of biota associated with the sea ice system might vary between the five MEASO sectors (Table 4). We compare how the different sectors might vary relative to the Atlantic Sector because of that sector having a mid-range sea-surface temperature regime in the Antarctic Zone compared to the other sectors.

Table 1 outlines differences in sectors based on available literature. If the global temperature warms by the expected 1.5°C by 2030, it is likely that the Antarctic Peninsula, particularly the northern region, will experience up to 130 days above 0°C (Siegert et al., 2019). Ocean-air interactions will lead to increased ocean turbulence resulting in shoaling of CDW. Increased heating in shallow waters is contributing to the basal melting of ice shelves and, consequently, a reduction in the formation of platelet ice (Hoppmann et al., 2020). Positive CDW incursions yield decreased platelet ice in the East Pacific and Indian sectors compared to the Atlantic, giving an expectation that *Pleuragramma antarticum* would be less in number in those sectors than the Atlantic. In contrast, while CDW incursions are not expected to be different in the Atlantic sector and the West Pacific (Ross Sea), changes to *P. antarcticum* are expected to be larger in the Ross Sea due to other factors such as difference in productivity, through less metabolic demand in the Ross Sea and greater spring algal growth (Table 4). Silverfish comprise up to 90% of the mid-water fish biomass in the Ross Sea (Smith et al., 2007) and are prey for Weddell Seals, whales, Adélie penguins, emperor penguins and other seabirds (Smith et al., 2007). Sampling for *P. antarcticum* along the western Antarctic Peninusula (wAP) has shown that they are severely reduced in number around the central wAP, a region where they were historically abundant (La Mesa et al., 2015). This was linked by the authors to catastrophic loss of spawning habitat as a result of sea ice loss. The loss of silverfish as a prey item in the central wAP is likely leading to marine predators in the region exhibiting dietary switching, e.g., to myctophids (Moline et al., 2008), for which there is an expectation in our results that myctophids will be more abundant in the East Pacific.

The perturbation responses for the sea ice system in the Pacific sectors are consistent with observations. Sea ice extent and duration are currently increasing in the Ross Sea and decreasing in the Amundsen Sea (Comiso et al., 2011; Stammerjohn et al., 2012; Parkinson, 2019). In the Ross Sea, colder sea surface temperatue (SST) and/or more southerly winds lead to a northward extensions of the productive marginal ice zone (MIZ), highlighted in Table 4 by an increase in pelagic algae in the East Pacfic sector in spring, though no change occurred in the bottom ice algae. Algae contained in the ice are released by earlier melting, then mixed in the upper layers of the water column to be consumed by meso- and microzooplankton grazing (Hecq et al., 2000). Copepods and krill also increased, while their larvae decreased, perhaps indicating that earlier melting meant less habitat space available for the young stages, reinforcing the importance of adult productivity compared to recruitment driving this population. A reduction in light penetration through the ice may limit sea ice algal biomass, with consequences for krill and other zooplankton. Krill collected under less deformed, thinner ice with less snow cover had higher lipid levels as a result of a

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TABLE 4 Responses of attributes of the sea ice system from qualitative press perturbations of (i) differences in key drivers between MEASO sectors (see Figure 2) relative to the Atlantic Sector, and (ii) changes in the key drivers in all sectors into the future.

	(i) Differences of sectors compared to Atlantic	(ii) Change of all sectors in future		
	West Pacific	East Pacific	Indian	Future
Drivers				
Temperature (T)	–	–	+	+
Storminess (S)	0	0	+	+
Freezing (F)	0	+	0	+
Melting (M)	+	0	+	–
Circumpolar Deep Water (C)	0	+	+	+
Latitude (L)	0	+	+	0
Responses				
Ice particulate pool frozen into ice (IPP)	0.65	−0.72	0.84	−0.59
Nutrient pool released from ice (NIR)	0.69	−0.60	0.69	−0.58
Nutrients available in ice (NI)	−0.66	−0.85	0.92	0.59
Nutrient supply autumn (NA)	0.65	−0.92	0.84	0.68
Nutrient supply winter (NW)	0.50	−0.68	0.81	0.62
Nutrient supply spring (NS)	−0.74	−0.73	0.78	0.82
Bottom ice algae (AIB)	0.57	−0.58	−0.55	−0.66
Pelagic algae spring (APS)	0.74	0.73	−0.64	−0.70
Pelagic algae autumn (APA)	−0.65	0.92	−0.61	0.55
Pelagic algae winter (APW)	−0.53	0.75	−0.78	−0.52
Copepods & Antarctic krill (ZCK)	0.68	0.71	0.66	0.57
Copepod nauplii and Antarctic krill (larvae) (ZCKL)	0.57	−0.58	0.64	0.55
Salps (ZS)	0.74	0.73	−0.64	−0.70
Metabolism in sea ice (MI)	−0.71	−0.79	0.62	0.53
Metabolism in pelagic (MP)	−0.66	−0.57	0.58	0.53
Myctophids (FM)	0.68	0.71	0.66	0.57
Pleuragramma antarctica (FP)	0.68	−0.68	−0.64	−0.72
Precipitation (P)	−1.00	−1.00	1.00	1.00
Precipitation – snow (PD)	−1.00	−1.00	1.00	1.00
Precipitation – rain (PW)	0.00	0.00	0.00	0.00
Surface snow (IS)	−1.00	−1.00	1.00	1.00
Habitat complexity (IH)	0.00	0.00	1.00	1.00
Total ice volume (ITV)	0.65	−0.77	0.81	−0.52
Brine volume (IB)	−1.00	−1.00	1.00	1.00
Platelet ice (PI)	0.00	−1.00	−1.00	−1.00
Light autumn (LQA)	0.00	1.00	0.51	−1.00
Light winter (LQW)	0.50	0.65	−0.92	−0.61
Light spring (LQS)	0.00	1.00	0.50	−1.00

Key drivers are pressed according to the sign for set of perturbations. Responses show the largest proportion of outcomes of 10,000 simulations, with the sign and colour indicating whether the largest proportion was positive (increase, +, yellow) or negative (decrease, −, blue). Colours are only shown for responses that were >0.6 of outcomes.

higher biomass of sea ice biota (Virtue et al., 2016). Models also indicate that Antarctic marginal ice zones are important areas of carbon export driven by krill grazing and faecal pellet production (Belcher et al., 2019). Phytoplankton blooms form at retreating ice-edges due to a combination of melt-water stratification, and release of micronutrients (e.g., iron) and algae from the melting

sea ice (Lancelot et al., 1993; Lannuzel et al., 2016). Ice-edges serve as hotspots for pelagic food-web interactions by providing critical food for pelagic herbivores (Schmidt et al., 2018), which, in turn, are preyed on by higher trophic levels.

Antarctic krill, copepods and their larvae showed mixed responses to the environmental perturbations (Table 4). The Southwest Atlantic (20°W–80°W), which holds >50% of the circumpolar krill stock (Atkinson et al., 2019) has warmed rapidly over the last decades. Their distribution has contracted southward by ~440 km over the past 90 years and become centred more strongly over Antarctic continental shelves (Atkinson et al., 2019). Krill further showed an increase of ~75% in body mass, indicating the presence of more adults and less juveniles in the population and, consequently, a reduction in recruitment. No directional trends in krill population and sea ice have been established outside of the Atlantic sector (Flores et al., 2012).

Our perturbation experiments give an expectation that Antarctic krill would have better conditions in the other sectors in relation to the sea ice zone. These perturbations do not account for total productivity and the size of the area in which that occurs. Nevertheless Antarctic krill populations in other sectors may be relatively stable at present (Yang et al., 2020). With more stable sea ice coverage, no significant evidence for decline in krill stocks in the Indian sector was found (Nicol et al., 2000; Atkinson et al., 2017). The Ross Sea represents a mosaic of functionally different marine subsystems. The environmental changes in the Ross Sea could benefit diatoms and change krill distributions in future, although krill were not considered able to invade much of the continental shelf owing to the requirement for larval development at great depth (Smith et al., 2014). In Terra Nova Bay, large amounts of biopolymeric carbon accumulated in the bottom layer of the ice column concomitantly with the early spring increase in sympagic algal biomass. Such organic material, mostly accounted for by autotrophic biomass, was characterised by high food quality and was rapidly exported to the sea bottom during sea ice melting (Pusceddu et al., 2000). The Amundsen Sea was considered to be a potential new habitat supporting successful krill spawning in future due to delayed sea ice formation and smaller ice concentration which could benefit phytoplankton blooms and facilitate krill recruitment (Piñones and Fedorov, 2016). These models suggest that other regions besides the Atlantic sector could be potential krill biomass hotspots in future.

5.3. Expectations for future change

The fate of Antarctic sea ice under a range of greenhouse gas emissions scenarios to 2,100 has been investigated under the auspices of the IPCC's various assessment reports, underpinned by the Coupled Model Intercomparison Project (CMIPs). However, confidence in long-term projection of Antarctic sea ice extent is currently low due to the inability of many global climate models (GCMs) to accurately reproduce large-scale patterns observed by satellite, i.e., either the seasonal cycle or multi-decadal trends (Turner et al., 2013). Moreover, model estimates of changes in Antarctic sea ice thickness (and hence volume) are of even lower confidence (IPCC, 2021). This is due to a lack (until recently) of reliable large-scale snow and ice freeboard estimates required for accurate computation of the thickness of both sea ice (Paul et al., 2018; Fons and Kurtz, 2019; Kacimi and Kwok, 2020) and its snow cover (Webster et al., 2018). Nevertheless, the former CMIP5 models project a range of decreases in Antarctic sea ice extent of between 8% and 67% for the 21st Century, depending on month of trend and emissions scenario (Collins et al., 2013). Most models predict nearly ice-free summertime (minimum extent) conditions by 2,100 under the highest emissions scenario, known as RCP 8.5 (Collins et al., 2013). There are currently no projections for coastal fast ice, since this ice type is currently not represented in any GCM.

Application of the environmental perturbations to future conditions produced only negative and neutral responses for krill and copepods, including their larvae (Table 4). Changes in the extent and area of the sea ice habitat have not been uniform or unidirectional, so the implications for sea ice-associated organisms are not clear. The magnitude and timing of the spring ice-associated algal bloom has changed over the last three decades and this change is directly related to sea-ice extent and duration of the previous winter (Stammerjohn et al., 2008, 2015). Changes in the timing of annual sea ice advance and retreat will impact the capacity for ice-associated microbes to initiate bloom events in spring. For example, ice algae are a food source for larval Antarctic krill during late winter and early spring. Other studies have highlighted the role of complex under- and intra-ice habitats in providing shelter for larval krill (Frazer et al., 2002; Massom et al., 2006; Meyer et al., 2017) and the importance of sea-ice drift patterns in transporting krill larvae to areas in which they can thrive in spring (Meyer et al., 2017). Strong relationships have also been established between sea-ice conditions (e.g., duration/persistence), their influence on ice algal carbon productivity and export, and subsequently, on coastal benthic community characteristics (e.g., Clark et al., 2017; Cummings et al., 2018). Few copepod species appear to be obligate ice dwellers. The harpacticoid copepod *Drescheriella glacialis* seems to be very ice-dependent due to its poor swimming capabilities, and *Stephos longipes* has acquired antifreeze protection (Kiko, 2010), which also indicates a high level of adaptation to the ice environment. It is possible that copepods can continue to thrive under scenarios of thinner or less frequent ice cover, as plasticity in their diets and life cycles might be the key to their continual success (e.g., Swadling et al., 2004). Understanding the relative importance of factors that drive organisms to colonise sea ice (e.g., response to predation versus reproductive needs) would enhance our ability to predict their responses to environmental change.

Salps responded positively to increased storminess and the number of days >0°C and negatively to a positive press perturbation of CDW (Table 4). There appears to be considerable spatial segregation between krill and salp populations (Nicol et al., 2000; Atkinson et al., 2004), although a comparative study of their

feeding behaviour showed similar diets, which might enhance the competition between both species (Pauli et al., 2021b). Currently it is assumed that temperature, sea ice and chlorophyll *a* drive large-scale population segregation between the two species, at least in the Indian sector (Nicol et al., 2000). Observations from the wAP also indicate that *E. superba* and *S. thompsoni* rarely, if ever, co-exist in high abundances in that region (Pakhomov et al., 2002; Steinberg et al., 2015) and instead oscillate between years of salp dominance and years of krill dominance (Ross et al., 2014). However, the rapid reproduction capacity of salps under favorable conditions could change current ecosystem structure and thus alter the behaviour and distribution of *E. superba*. The direct effect of increased *S. thompsoni* presence on *E. superba* populations, however, is unknown.

6. Discussion

The sea ice environment is pivotal for the Southern Ocean ecosystem and is likely to change (Meredith et al., 2019) over the 21st Century. There is *high confidence* that changes in meridional wind stress will have a strong effect on sea ice variability (IPCC, 2021), and Southern Ocean westerlies are expected to intensify. Understanding how sea ice will respond to environmental change is key to predicting the effects on the biota that rely on sea ice for all or part of their life cycles. Some species are already adapted to the ephemeral nature of sea ice, so it is the magnitude and rate of change to this habitat that might be key determinants of how well species fare in the future. For these species, developing a means of weighting CMIP models for their ability to represent the Southern Ocean sea ice system is an important step to making informative predictions about the future of sympagic and pelagic biota. Climate variations may influence the duration of sea ice by disrupting the timing of formation and retreat and thus primary productivity, with consequences for entire food webs (Seibel and Dierssen, 2003; McCormack et al., 2021; Murphy et al., 2021). One example is differences between phytoplankton assemblages, with blooms of *Phaeocystis antarctica* often dominating in the Ross Sea vs. diatoms occurring in the WAP (Ducklow et al., 2007; Smith et al., 2007; Mangoni et al., 2017; Schofield et al., 2017; Pinkerton et al., 2021).

Our qualitative network model showed realistic expectations for differences between sectors. For that reason, it is a useful tool for exploring different future scenarios for the ecosystems in different sectors, given that changes in the physical system are likely to vary in more nuanced ways than the future scenario we present here. A key lesson from our results is that different taxa did not respond in a consistent direction (positive or negative) across all environmental perturbations, highlighting the complexities of networks of interactions between the physical and biological variables. Increasing storminess produced positive responses in the pelagic nutrient pools, possibly due to deeper ocean mixing bringing nutrient-rich waters to the surface. At the same time, warming temperatures might lead to increased stratification trapping nutrients at depth. If temperature is the more important driver, then we might expect to observe decreases in biomass of phytoplankton and grazers.

Species that require the presence of sea ice are more-or-less certain to fare badly under reduced ice scenarios, e.g., the dependency of the silverfish *P. antarcticum* on platelet ice during its early development. Kramer et al. (2011) also argued that the perennial sea ice of the Weddell Sea is colonised by highly adapted species that probably rely on year-round sea ice (e.g., *D. glacialis* and *T. antarcticus*), and therefore a change to a seasonal ice cover might be detrimental for these species. Also *S. longipes* might be adversely impacted by sea ice loss, as it seems to rely on sea ice as a nursery ground. In this case, the seasonal timing of sea ice formation and melting might also be important. Other species, such as *Paralabidocera antarctica*, appear to be facultative rather obligate inhabitants of sea ice (Arndt and Swadling, 2006) and might be able to adjust their life history strategies to meet their needs in a reduced sea-ice world.

Of course, it is most likely that species will have variable responses to changing sea-ice conditions and will depend upon how much their populations as a whole depend on a sea-ice phase in their overall dynamics, coupled with the potential for non-linear responses by various taxa (Constable et al., 2014). However, for benthic organisms it is already predicted that there will be "more losers than winners" (Griffiths et al., 2017). It is these complex adjustments in biology and ecology that will pose the biggest challenges to attempts to manage the Southern Ocean ecosystem (Atkinson et al., 2019).

Temperature affects sea ice structure, freeze/melt and extent and its carrying capacity for biota, expressed as biomass, at the same time as impacting metabolism in a system. The qualitative network model showed metabolism increased while primary producers and grazers decreased with increasing temperatures. However, as the model is purely qualitative, it is not possible to scale metabolism according to the biomass of each component and to obtain a measurable response from a change in temperature. Carrying capacity is determined by complex interactions between habitat complexity (e.g., deformation processes), the volume of brine available for colonisation and the total volume of the ice. Earlier we discussed how increased ice complexity can improve outcomes for larval krill (Frazer et al., 2002; Meyer et al., 2017) by providing them with refuge from predators and competitors. This underlines the importance of better defining the relationships between Antarctic sea ice physical properties and processes and biological and ecological processes, as they relate to optimal "habitat quality" for key species, including at different life stages (e.g., Quetin et al., 2007). As stated by Janssen et al. (2021), this is critical for robust projections of future states of the Southern Ocean ecosystem. A critical step will be to evolve the qualitative model into a quantitative model where the effects of quantitative change in the drivers can be better explored.

Understanding the ways that biota will respond between and within sectors is also a high priority. This research should be undertaken at a multi-national level, with sampling strategies designed to facilitate our understanding of poorly-studied regions along with those where we have better information (e.g., the Southern Ocean Observing System 2021–2025 Science and

Implementation Plan, Newman et al., 2022). There is patchy data coverage between sectors and the key taxonomic groups have been sampled on varying timescales. We know that sea ice is not changing uni-directionally, with some regions (primarily the southwestern Atlantic and eastern Pacific) showing rapid change while other regions (Ross, Indian) are showing some increases or not changing substantially – although there was an unexpected switch to high variability in 2012 (Parkinson, 2019). Additionally, as fast ice contains high biomass of true ice inhabitants (e.g., the algae and small grazers), being able to predict whether it will increase, decrease or stay the same is important and is an area needing attention.

Understanding and quantifying these changes will require rigorous scientific data collection drawn from species and ecosystems that are sensitive to multiple stressors of climate change, using novel field and laboratory technologies and methodologies to fill knowledge gaps in our understanding of the fundamental biology and ecology of many Southern Ocean species. This should ideally involve long-term cross-disciplinary monitoring of the coupled interactive sea ice-ocean–atmosphere-biology-biogeochemistry system in key regions, i.e., along the lines of the long-running Palmer Long-Term Ecological Research program (Ducklow et al., 2013) – noting that Antarctica's sea ice habitat is also affected by ice sheet and ice shelf melt and icebergs (Massom and Stammerjohn, 2010).

7. Key messages for policy makers

Key message 1 Sea ice in the Southern Ocean is fundamentally important to the lower trophic levels of this ecosystem, including for primary productivity, krill and fish. This has major implicatons for marine predators, including marine mammals, penguins and other bird species, that collectively support different parts of the Antarctic marine food webs (very high confidence).

Key message 2 The sea-ice-system, including fast ice and the marginal ice zone, is threatened by both atmospheric and ocean warming as well as strengthening oceanic winds as a result of climate change, but the timing and magnitude of these impacts is uncertain (high confidence).

Key message 3 Reduction in global greenshouse gas emissions is the only mitigation approach as sea ice is too expansive to be manipulated by direct human intervention (statement of fact).

Key message 4 While reduced sea-ice extent may impact the range of sea-ice dependent species examined here, such as Antarctic krill, the increased complexity of habitat may be a positive local benefit to these species (medium confidence).

Key message 5 Whole-of-system research on the role of sea ice in Antarctic ecosystems needs to be extended beyond the Antarctic Peninsula and Weddell Sea to establish a circum-Antarctic understanding of the coupled physical-chemical-biological sea ice system.

Key message 6 Predicting how perturbations in sea-ice extent and duration will impact Antarctic krill populations and in turn the Southern Ocean ecosystem requires both regionally-focussed and multidisciplinary experimental approaches, together with coupled physical and biological models of the sea-ice system embedded within Earth System models.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

KS and AC conceived the study. AF, RAM, MB, LGh, AG, LGu, NJ, SK, FK, RK, PK, RM, AMa, AMc, MM, EP, IP, JR, PR, KR, MV, PV, CW, PW, and SW wrote sections and/or provided comprehensive comments. All authors contributed to the article and approved the submitted version.

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Conflict of interest

AC is a Topic Editor of this MEASO Special Issue.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Appendix: Qualitative network modelling

There is often considerable uncertainty surrounding the strength, functional forms, and even occasionally the direction of interactions within an ecological community. If we are confident in the type of interaction (e.g., predator–prey), but not the strength, we face parametric uncertainty. If we lack confidence in the nature of an interaction (e.g., whether a relationship is parasitic or mutualistic), then we face structural uncertainty. Qualitative network models were first developed to provide insights into community dynamics in the presence of parametric uncertainty. Early efforts to take a qualitative approach to existing community network theory harnessed the tools of graph theory and matrix analysis (Levins, 1974; Puccia and Levins, 1985). By shifting the focus away from precisely specified interaction terms and towards capturing the general community structure qualitatively, qualitative models can provide insights into the cumulative effects of simultaneous direct and indirect community interactions.

Qualitative network models may be understood most intuitively through the construction of a directed graph representing a community assumed to be at equilibrium. Graph nodes represent community members (either species or functional groups) and edges represent interactions between community members. An arrow at the terminus of an edge represents a positive interaction effect for that node, while a dot is typically used to indicate a negative interaction effect. The directed graph has a corresponding signed community matrix, A, where entry a_{ij} is either +, −, or 0, denoting a positive, negative, or neutral effect of the density of node j on the density of node i. Insights are gained by analysing this signed community matrix (see Puccia and Levins, 1985; Dambacher et al., 2002, 2003 for a more thorough treatment of these topics). If all eigenvalues of A are negative, then the community structure is stable (May, 1973). The effects of sustained changes to a model parameter (a so-called press perturbation) can be seen in the signed entries of $-A^{-1}$ (Bender et al., 1984), or, alternatively, by considering the signs of the adjoint matrix, adj(−A) (Dambacher et al., 2002). This analysis suggests whether the density of each node will increase, decrease, or experience no change in response to a press perturbation in each of the other nodes.

Qualitative network models have been used to address a wide range of topics, such as identifying indicators of the effects of fishing (Metcalf et al., 2011), interpreting marine ecosystem changes in response to climate warming (Melbourne-Thomas et al., 2013), and exploring alternative strategies for invasive species eradication (Raymond et al., 2011). Analyses based on qualitative network models have been extended to incorporate modified interactions, in which the strength of an interaction between two species is modified by the density of a third species (Dambacher and Ramos-Jiliberto, 2007), as well as structural uncertainty (Raymond et al., 2011; Melbourne-Thomas et al., 2012).

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A dynamic framework for assessing and managing risks to ecosystems from fisheries: demonstration for conserving the krill-based food web in Antarctica

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The ecosystem approach to fisheries has been discussed since the 1980s. It aims to reduce risks from fisheries to whole, or components of, ecosystems, not just to target species. Precautionary approaches further aim to keep the risk of damage to a low level. Here, we provide a dynamic framework for spreading the ecosystems risk of fisheries in space and time, a method that can be used from the outset of developing fisheries and continually updated as new knowledge becomes available. Importantly, this method integrates qualitative and quantitative approaches to assess risk and provides mechanisms to both spread the risk, including enabling closed areas to help offset risk, and adjust catch limits to keep regional risk to a baseline level. Also, the framework does not require uniform data standards across a region but can incorporate spatially and temporally heterogeneous data and knowledge. The approach can be coupled with the conservation of biodiversity in marine protected areas, addressing potential overlap of fisheries with areas of high conservation value. It accounts for spatial and temporal heterogeneity in ecosystems, including the different spatial and temporal scales at which organisms function. We develop the framework in the first section of the paper, including a simple illustration of its application. In the framework we include methods for using closed areas to offset risk or for conserving biodiversity of high conservation value. We also present methods that could be used to account for uncertainties in input data and knowledge. In the second section, we present a real-world illustration of the application of the framework to managing risks of food web effects of fishing for Antarctic krill in the Southern Ocean. Last, we comment on the wider application and development of the framework as information improves.

KEYWORDS

CCAMLR, Southern Ocean, ecosystem-based management, EBFM, MPA, risk management

1. Introduction

Fisheries can impact ecosystems in many ways, including disruption of the dynamics of species targeted by the fishery or those killed incidentally in fishing operations, such as seabirds, destruction of habitat and the concomitant disruption of associated species, such as bottom fisheries impacts on reef systems, and alteration of food webs through the removal of species. The ecosystem approach to fisheries has been considered since "Our Common Future" (World Commission on Environment and Development, 1987) and the rise of sustainable development. The policy on what constitutes ecosystem-based fisheries management (EBFM) is articulated by the UN Food and Agriculture Organisation (FAO, 2003), following their publication of the precautionary approach to fisheries (FAO, 1996).

Emphases on EBFM have varied between a number of approaches. First, methods to implement ecosystem-oriented policies in decision rules and actions have been developed (Constable et al., 2000; Constable, 2006). Second, ecosystem risks of fishery management strategies are being evaluated using dynamic modelling, such as for understanding the food web effects of fishing (Constable, 2002, 2004, 2005; Fulton et al., 2019). Last, vulnerable species and habitats that may be directly affected are being identified and action taken to minimise impacts on them, such as for eliminating by-catch or avoiding sensitive areas (Smith et al., 2007; Constable, 2011).

All approaches aim to reduce risk of fisheries to whole, or components of, ecosystems. Unless of course, the management strategy is reactive, waiting for damage to be detected before action is taken; a strategy that obviously fails to meet ecosystem objectives because the damage has been done. Approaches aiming to keep risk of damage to a low level, risk assessments, sometimes called a precautionary approach, may seem to be costly, particularly when some argue that everything needs to be measured to properly assess risk. However, qualitative ranking of conditions to be avoided or reduced may be a first step in management before quantitative assessments of risk can be done (Smith et al., 2007). Consider the difference in approaches to minimising incidental seabird mortality in longline fisheries compared to reducing risk through stock assessments in the krill fishery by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Constable et al., 2000).

Stock assessments aim to provide sustainable catch limits for a region and for a designated time period, say one or 2 years. A particular challenge for managers is when fishing may become concentrated in space or time within the assessed region, causing ecosystem effects. Ecosystem risks may be related to areas fixed in space, such as reefs, or at particular times of the year, such as breeding periods, or some combination of the two, such as nursery areas. These risks may arise from fishing effort, such as the length of longline set or swept area of trawls, or simply from the total catch. The question then arises as to how to use ecosystem-oriented risk assessments to set finer-scale spatial and temporal measures to control a fishery in order to reduce the potential for ecosystem effects. Here, we present a dynamic framework of risk assessment and management that can help distribute a fishery in space and time to avoid ecosystem effects. It enables use of available data and knowledge to set ecosystem-based catch controls on a fishery to maintain ecosystem risk at a low level, and then be easily updated as new information and assessments arise.

While the framework could be applied to determining how fishery controls may be varied over years, we focus on developing the framework for its use to distribute a fishery in space and between the seasons within a year to maintain low risk of ecosystem impacts despite spatial variability in data and knowledge. The approach may be coupled with considerations of the conservation of biodiversity in marine protected areas (Grorud-Colvert et al., 2021) and can serve to address the potential overlap of fisheries with areas of high conservation value. It is designed to account for heterogeneity in ecosystems, including the different spatial and temporal scales at which organisms function. We develop the framework in the first section of the paper, including a simple illustration of its application. In the framework we include methods for using closed areas to offset risk or for conserving biodiversity of high conservation value. We also present methods that could be used to account for uncertainties in input data and knowledge. In the second section, we present a real-world illustration of the application of the framework to managing risks of food web effects of fishing for Antarctic krill in the Southern Ocean.

2. Framework for managing heterogeneity in risk

With perfect knowledge, catches can be distributed to avoid high risk of ecosystem impacts, equivalent to using an accurate dynamic ecosystem model for determining a spatially and temporally resolved fishing strategy. However, with imperfect knowledge, how might we avoid ecosystem impacts in a heterogeneous world?

2.1. Composite risk index

Risk, r, is the product of the probability, p, of the catch or effort from the fishery (F) and the probability of significant ecosystem impact, E, given the fishery (see Fenton and Neil, 2013 for a broad discussion on mathematical formulation of risk):

$$r = p(F)\,p(E|F) \tag{1}$$

Here, we are seeking specific fishery controls in space and time to reduce risk to acceptable levels, thereby setting $p(F)$ to equal 1. If the relationship between F and probability of significant ecosystem impacts is known then we can easily solve for the limits to the fishery that satisfactorily reduces risk. This logic underpins the framework. Moreover, it can be usefully applied even when the relationship between the magnitude of fishing and impacts is only approximated in the early stages of a fishery.

2.1.1. Index of risk

The concept of significant ecosystem impact arising from F has three parts: (i) a combination of specific effects on the ecosystem, (ii) a judgement on the degree to which levels of effects are regarded as significant impacts, and (iii) the method for combining the effects into a single risk. In reality, Equation 1 becomes an index of risk, R, ranging from 0 to 1. The probabilities of the effects are standardised to a scale of significance of impact in order for them to be combined. This may be achieved by rescaling the effects to significance of impact and

retaining the probabilities, or by rescaling the probabilities to range from 0 to 1 and retaining the levels of effects. The latter may be done in order to keep the discussion around observed effects/biological quantities rather than more abstract quantities. For this reason and because probabilities may be expert judgements in early stages of applying the framework, we use the term "pseudo-probabilities" for individual ecosystem effects in presenting the framework.

The index of risk for a given area will be derived from pseudo-probabilities, $r(F)_n'$, relating to n different risks. The combining of pseudo-probabilities cannot be additive. Nor can it result in the apparent risk indicated by the index to be less than any individual risk. We choose a formulation that increases the index as more risks arising from fishing activities are included:

$$R(F) = 1 - \prod_n (1 - r(F)_n') \quad (2)$$

where $0 \le r(F)_n' \le 1$

2.1.2. Scaling pseudo-probabilities to reflect relative importance of risk

Here, pseudo-probabilities are a means of scaling risks as to their importance for minimising or avoiding. They are also a means of standardising different risks for use in Equation 2. Later, this scaling process is also used for standardising ecosystem vulnerabilities in the early stages of a fishery. A "naïve" approach to pseudo-probabilities is to anchor them solely in their respective probabilities of significant effects given the fishing level. When different risks are aligned for a given fishing level then avoidance or reduction is straightforward. However, when the relative levels of risk are not aligned in their relative importance, the combined risk in one area may not be comparable to another area.

Figure 1 provides examples of scaling risks to better reflect relative importance. We found that a logistic function provides a useful method for scaling risks:

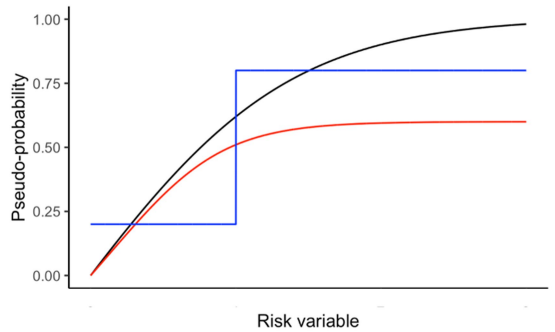

FIGURE 1
Examples of scaling pseudo-probabilities from a risk variable. Black line is used in the Antarctic krill example below to represent scaling of predation pressure using (h=3; v=3; X_{50}=0.5; X_0=0; X_1=4; Y_0=0; Y_r=1). Red line shows similar curvature to the black line but with a maximum value less than one. The blue line shows a threshold scaling, where the importance is at a minimum below the threshold risk and at a maximum above it.

$$Y = Y_0 + Y_r \left[\frac{l(X) - l(X_0)}{l(X_1) - l(X_0)} \right]$$

$$\text{where } l(X) = \frac{1}{\left(1 + e^{-h(X - X50)}\right)^{1/v}}$$

$$Y_0 + Y_r \le 1 \quad 3$$

and the symbols are: Y_0 (Y intercept), Y_r (range of Y), X (value of risk to be scaled), X_0 (minimum risk), X_1 (maximum risk), h (steepness), X_{50} (risk at which half of Y_r is reached), v (shape).

2.1.3. Critical value of the risk index

Once the pseudo-probabilities of the risks relative to fishing level have been determined for a given area, the fishing level in that area could be that at which the resultant risk index is at a satisfactory low level, i.e., a target level, $\dot{R}$. In the first instance, the target level may be determined from the combination of critical levels for each risk, $\dot{r}$, such that, using Equation 2:

$$\dot{R} = 1 - \prod_n (1 - \dot{r}_n) \quad 4$$

Meeting the target level in Equation 4 by reducing some risks may result in other risks being left at too high a level. Care will be needed in how target composite risks are applied.

2.1.4. Region-wide mean risk

The region-wide mean risk is the sum across all areas, a, of the area-specific risk, weighted by the size of areas, A_a, in which the area-specific risk index is assessed. It can be used as a guide to the consequences of different spatially-distributed fishing strategies in the region, including the use of closed areas for moderating risk:

$$\hat{R} = \frac{\Sigma_a A_a R_a(F_a)}{\Sigma_a A_a} \quad 5$$

We have focussed on heterogeneity of risks in space within the region of a stock for developing the framework. The framework could be further extended for a suite of fisheries with different spatial structures and for when fishing in one area impacts on the ecosystem in other areas (Constable, 2014).

2.2. Using the risk index for spreading risk during developing fisheries

Knowledge on the relationship of many ecosystem risks and the magnitude of fishing is often only coarse (Smith et al., 2007). Nevertheless, a first step for identifying spatial variation in ecosystem properties can be to assess spatial structure in the system from satellite-obtained environmental data (Constable, 2011). This spatial structure can then be refined and potential risks from fishing identified with the addition of field observations, species distribution modelling, dynamic modelling and other tools (Melbourne-Thomas

et al., 2017; Brasier et al., 2019; McCormack et al., 2021). We extend the framework above to spread the fishery to reduce risks while the fishery develops and data on risks to the ecosystem from different levels of fishing and its distribution are obtained. The aim is to guide the fishery to have a higher fishing pressure, such as catch density, in lower risk areas than higher risk areas.

2.2.1. Baseline regional risk

First consider the baseline strategy for distributing a developing fishery. Neutral pressure of the fishery on a target stock is to apportion catch in a given area according to the proportion of the target stock in that area. This neutral pressure is then adjusted to account for local area ecosystem vulnerabilities, thereby reducing the fishery in higher risk areas. The resulting distribution is the baseline catch vector with an attendant baseline regional risk to the ecosystem.

Neutral fishing pressure ($\dot{F}_a$) is the proportions of the region-wide catch or effort that could be taken from the respective local areas and/or times that result in the same fishing pressure on the target stock in each area. For example, this fishing pressure could be according to the proportions of the stock in each area, determined from the respective measures of density, *D*, and the surface area of the area, *A*:

$$\dot{F}_a = \frac{D_a A_a}{\Sigma_{a'} D_{a'} A_{a'}} \quad 6$$

where *a*' refers here and in the following equations to all areas in the assessment.

Equation 2 provides the basis for assessing ecosystem risks and using pseudo-probabilities to assess overall risk from fishing in a local area. As the risk may not be able to be quantified directly in the first instance, we use the term vulnerability, in the interim, to reflect how, for a particular attribute, v_n, one area may vary from another in terms of its vulnerability to fishing (discussed further in the next subsection), such that:

$$R = 1 - \prod_n (1 - v_n)$$

$$\text{where } 0 \le v_n \le 1 \quad 7$$

In this case, vulnerabilities may be ranked differences between areas or some quantitative metric for each area not yet adjusted to risk. In these cases, the metrics will need to be scaled between 0 and 1, such as by using Equation 3.

The equation for determining the proportion, $\alpha_{a,t}$ (also termed *alpha* in the text), of catch or effort in each area and time, *t*, is:

$$\alpha_{a,t} = \frac{\dot{F}_{a,t}(1 - R_{a,t})}{\Sigma_{a',t'} \dot{F}_{a',t'}(1 - R_{a',t'})} \quad 8$$

where *t*' refers here and in the following equations to all time periods in the assessment.

The vector of *alphas* for all areas in the region is the distribution of catch or effort that spreads the ecosystem risk. The contribution to regional risk of the local area in a time period is the product of $\alpha_{a,t}$ and $R_{a,t}$. The baseline risk to fishing is then the catch or effort weighted risk from across the region, which is the sum of the local area contributions to risk:

$$\hat{R} = \sum_{a,t} \alpha_{a,t} R_{a,t} \quad 9$$

2.2.2. Accounting for preferred fishing patterns

Preferred fishing patterns will likely be different from the baseline *alpha* vector. The fishing industry may have preferred locations or wish to concentrate on the target species in areas of greatest value, such as greater abundances or areas where schooling occurs naturally and predictably. Other factors may influence fishing; sea ice cover is an important consideration in Antarctica. Areas may not allow fishing such as areas for purposes of biodiversity conservation, recovery of stocks, refugia, or reference areas for scientific or management purposes. A method is needed to take account of these desirable fishing patterns while ensuring baseline risk, $\hat{R}$, is not exceeded, i.e., by reducing the total catch in the overall region.

The method for accounting for desirable fishing patterns has two steps. The first is to determine an initial alternative catch vector of *alphas*, $\boldsymbol{\alpha}'$. The second step is to modify the vector if the resulting catch-weighted region-wide risk is greater than the baseline risk.

The initial vector $\boldsymbol{\alpha}'$ could be determined in many ways. One approach would be to develop an index for desirability, *D*, of the different areas and times in the same way the risk index is developed, but for desirability factors rather than risks, and include this in Equation 8, such that

$$\alpha'_{a,t} = \frac{\dot{F}_{a,t}(1 - R_{a,t}) D_{a,t}}{\Sigma_{a',t'} \dot{F}_{a',t'}(1 - R_{a',t'}) D_{a',t'}} \quad 10$$

Another approach may be to simply nominate the vector of $\hat{R}'$, if there was an identifiable preference of where to concentrate fishing.

Following Equation 9, the new region-wide risk, $\hat{R}'$, is determined by substituting $\alpha_{a,t}$ with $\alpha'_{a,t}$. If the new region-wide risk is greater than the baseline then strategies need to be employed to reduce $\hat{R}'$ until it is less than or equal to $\hat{R}$. According to the formulation in this paper, the reduction could be achieved by scaling the catch vector by $\frac{\hat{R}}{\hat{R}'}$, reducing the overall regional catch. Alternatively, consideration could be given to modifying the catch vector to offset risks by closing high risk areas or the like until equality with the baseline is achieved.

This method for distributing the fishery when only vulnerabilities are known is the focus for the remainder of the paper.

2.2.3. Including closed areas for offsetting risks or conserving biodiversity

Setting fishing to zero in closed areas is one method for offsetting risk before a reduction in overall catch limit. Closing areas of high conservation value is also important for achieving objectives for

conserving biodiversity. Incorporating closed areas into the calculations is achieved after the calculation of the baseline catch vector, by modifying each neutral fishing pressure in which there is a closed area (surface area, C) for inclusion in Equation 10:

$$\dot{F}_a = \frac{D_a\left(A_a - C_a\right)}{\Sigma_{a'} D_{a'} A_{a'}} \qquad 11$$

Care is needed in applying such offsets in order to avoid increasing risks to unacceptable levels for some factors in other areas. The effects of offsets can be determined by examining the risks for individual factors under candidate scenarios, a recommended step in all analyses.

2.2.4. Illustration

A simple example to illustrate this method is given in Table 1 and Figure 2. It has two parts. First, the calculation of the baseline catch vector and the baseline catch-weighted region-wide risk. This shows how the catch is moved away from the high risk areas and added to the lower risk (in this case, no risk) areas. Note, if the risk for any area is equal to 1 then no catch will be taken from those areas. Second, it illustrates how a preferred fishing strategy may result in lower region-wide catches than expected when the region-wide risk under the preferred strategy is adjusted to be no more than the baseline risk. This is because the catch vector needs to not exceed the risk in any one local area.

TABLE 1 Simple example of distributing catch amongst three areas (see Figure 2 for an illustration of the baseline scenario), along with assessment of risk for an example of proposed distribution of catches between areas.

	Local area			Regional risk
	1	2	3	
Data				
Local risk index (R)	0	0	0.75	
Target species abundance (S)	1	1	1	
Baseline calculation				
Numerator (S*(1-R))	1	1	0.25	
Denominator (sum all numerators)	2.25	2.25	2.25	
Alpha (Numerator/ Denominator)	0.445	0.445	0.11	
Realised risk (Alpha*R)	0	0	0.083	$\hat{R} = 0.083$
Desirable catch distribution				
Initial designated Alpha	0	0.7	0.3	
Realised risk	0	0	0.225	$\hat{R}' = 0.225$
Risk relative to baseline	–	–	2.711	2.711
Adjusted alpha	0	0.26	0.11	$\hat{R}' = \hat{R}$

Local realised risk is the catch-weighted risk in local areas.

2.2.5. Accounting for uncertainty

Most inputs will have some degree of uncertainty. Randomisation methods are suitable for estimating a catch vector to distribute the fishery. Two steps are needed: (i) randomise inputs to give a replicate set of baseline catch and local risk vectors across areas, and (ii) use the replicate vectors for establishing a catch vector for the fishery.

The first step is dependent on the values used to develop inputs to the formulae, along with their errors. The approach would be to have a large number of trials, each randomly sampling the values for undertaking the calculations from their respective statistical distributions and then determining the baseline catch vector for a trial. The second step, itself, has two parts. The estimated baseline catch vector for the fishery can simply be estimated as the mean of the replicate baseline catches for each area and ensuring the consequent proportions of the region-wide catch sum to one. Implementation of a preferred option, either wishing to apply the neutral catch vector (as the proportion of the stock in each area) or a specified fishing pattern, may require a downward adjustment of the regional catch.

In order to account for the uncertainty in a preferred option, we suggest the adjustment, if needed, is determined using the following method. First, for each randomisation trial, the regional risk is calculated from the replicate vectors of local risk combined with the estimated baseline catch vector, as well as with the preferred vector, giving replicate values of regional risk for each. As in Section 2.2.2, the adjustment for each trial is calculated as the quotient of the regional risks of baseline over preferred. The median of these adjustments could be used as the overall adjustment of the region-wide catch.

An illustration of this approach is in Table 2 and Figure 3 with the implementation in Supplementary material (SM Table 1). Results in Figure 3D show the estimated baseline catch (alpha) reduces the regional risk distribution across the trials compared to the distribution when the individual trial catch vectors are used, probably from keeping catches lower in many trials. The neutral and specified catch vectors increase the regional risk. In the latter case, the median downward adjustment of the specified catch vector is 0.54.

3. Example: Antarctic krill fishery in FAO Statistical Area 48

An important focus of ecosystem-based management of fisheries (EBFM) is to limit alteration of food webs from the cascading effects of removing target and by-catch species (Fulton et al., 2019), an especially important issue for wasp-waist fisheries where target species are important prey of many predators in the food web (Atkinson et al., 2014). Conserving predators is often not straight forward when predators interact at many different spatial scales relative to the target species, the fishery will often prefer to target the same prey aggregations as the predators, and the expansion of the fishery may be faster than the acquisition of data on the requirements for conserving predators (Constable, 2006).

A staged approach to the development of the fishery is needed for ensuring conservation of predators is achieved while gathering data and developing suitable EBFM strategies (Constable, 2006; Constable, 2011; SC-CAMLR, 2011).

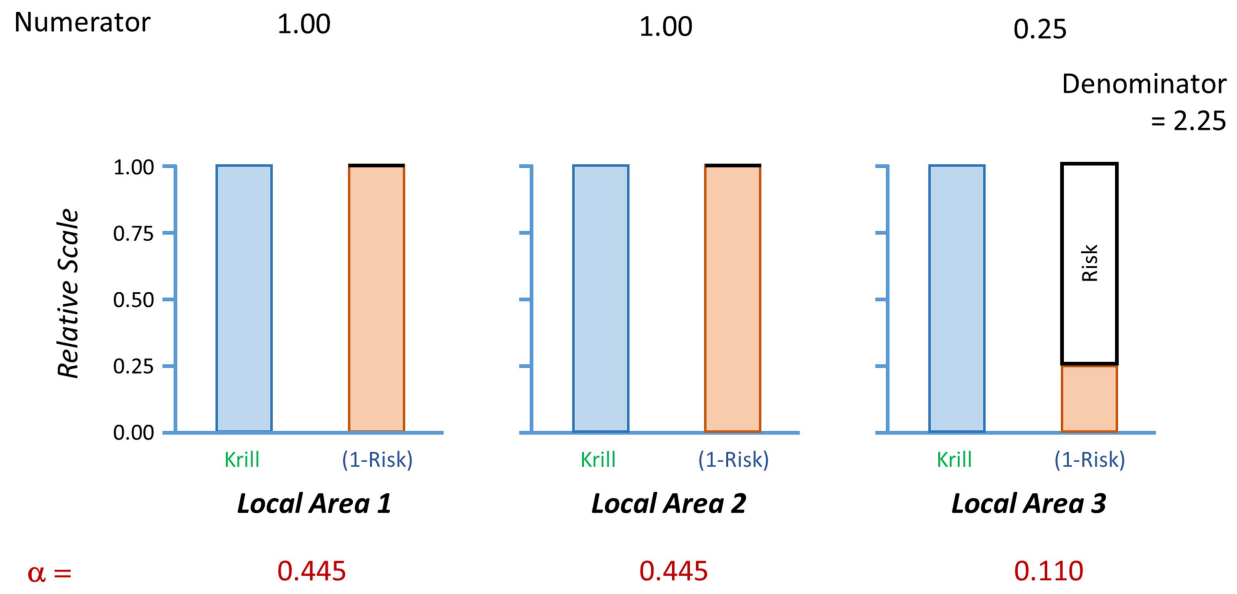

FIGURE 2
Illustration of the calculations of a baseline catch vector. In this case, the region is divided into three local areas. The ecosystem risks in each local area are shown in the solid black boxes above the orange bars. Local areas 1 and 2 have zero risks while local area 3 has ecosystem risks of 0.75. The target species (blue bars) has the same relative abundance equalling 1 in each local area. The values of the numerator show the multiplication of krill abundance times the value of one minus the risk (orange bars). The denominator is the sum of the values in the numerator. Alpha is the proportion of the regional catch limit to be assigned to each local area. Each alpha is determined by the division of the respective numerator by the denominator. A regional risk is calculated as the sum of the local realised risks, which are the multiplications of alpha times the risk. Here, the baseline regional risk is 0.083 (Table 1).

TABLE 2 Illustration for accounting for uncertainty in spreading risk amongst 8 areas.

	Local area								
	1	2	3	4	5	6	7	8	Total proportion of regional catch
Data									
Local risk index (Variance) (beta distribution)	0.2 (0.032)	0.2 (0.128)	0.4 (0.048)	0.4 (0.192)	0.6 (0.048)	0.6 (0.192)	0.8 (0.032)	0.8 (0.128)	
Target species abundance (CV) (lognormal distribution)	1 (0.5)	1 (1.0)	1 (0.5)	1 (1.0)	1 (0.5)	1 (1.0)	1 (0.5)	1 (1.0)	
Specified fishing pattern	0	0	0.11	0	0	0.18	0.36	0.36	
Estimated baseline alpha	0.22	0.19	0.16	0.14	0.11	0.09	0.05	0.04	1.00
Preferred fishing pattern but retaining baseline regional risk	0	0	0.06	0	0	0.10	0.19	0.19	0.54

Input data and results (Figure 3) for an estimated baseline catch vector, alpha. 10,000 randomised trials across uncertainty. Algorithm implemented in the Statistical Software R (R Core Team, 2022) is in Supplementary material. Median adjustment of regional risk in specified fishing pattern is 0.54.

Scientists under the auspices of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) have been considering a precautionary EBFM approach for Antarctic krill predators since its inception, including developing an ecosystem monitoring program (Agnew, 1997), considering approaches to subdivide the krill catch limit for FAO Statistical Area 48 into Subareas (Hewitt and Watters, 1992), determining areas of predator demand for krill as a means of determining areas

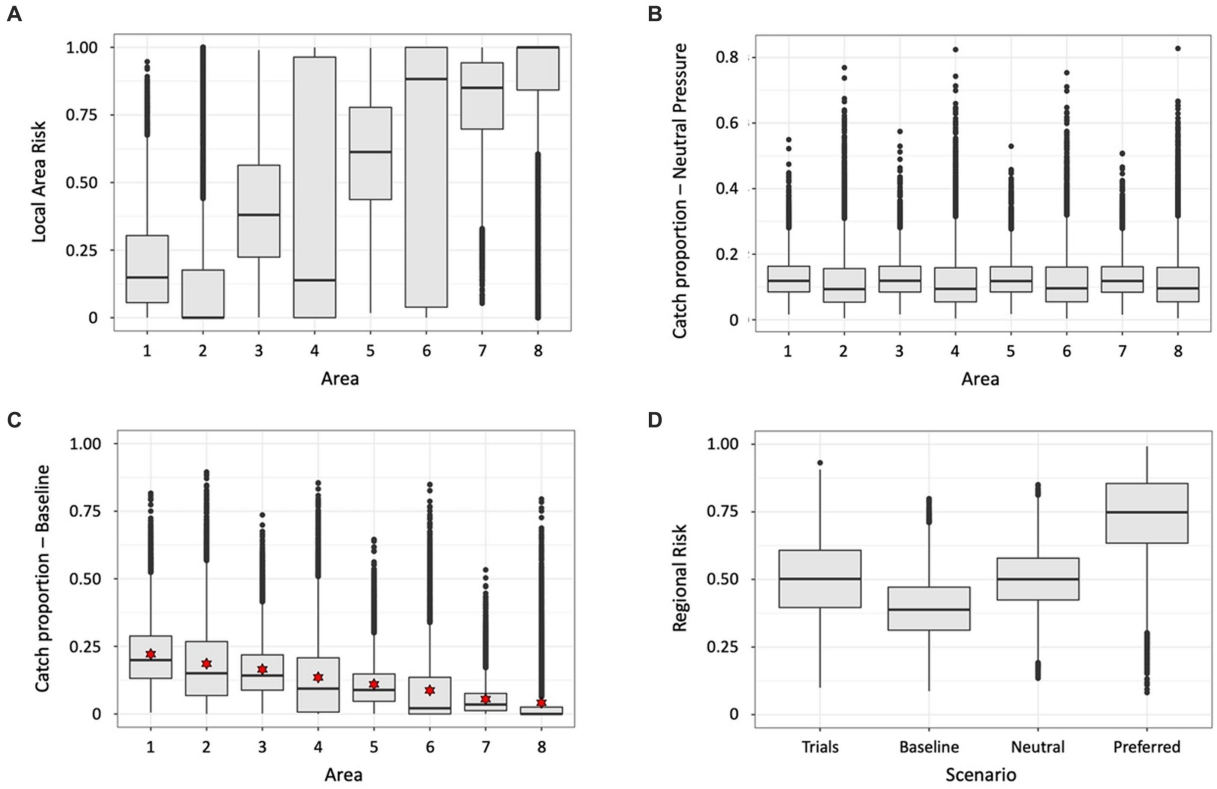

FIGURE 3
Results of illustration of estimating baseline catch vector by randomising (10,000 trials) across uncertainty, using the input parameters in Table 2. Boxplots showing the distributions across all trials of **(A)** local area risks in each of the eight illustrative local areas, **(B)** proportions of catch from each local area under neutral fishing pressure, i.e., the proportion of the target species in a local area, **(C)** proportion of catch in the baseline catch vectors calculated in each trial – red stars indicate the estimated catch vector for use as baseline, and **(D)** regional risk, as calculated using the risk vector in each trial combined with the following catch vectors – 'Trials' uses the respective catch vectors in each trial, 'Baseline' uses the estimated catch vector indicated by the stars in **(C)**, 'Neutral' uses the catch vector from proportions of the target species in each area derived using the mean abundances from each area in Table 2, 'Preferred' is the vector specified in Table 2.

where predators would be vulnerable to fishing for krill (Agnew and Phegan, 1995), and, since 2001 (Constable, 2001; SC-CAMLR, 2001; Constable, 2002), considering spatial management strategies and the use of spatially structured models to evaluate their ability to manage the food web effects of fishing (Constable, 2004; SC-CAMLR, 2004; Constable, 2005; Watters et al., 2013; Klein et al., 2018). The primary management outcomes for conserving krill predators in CCAMLR has been (i) allowing for escapement of krill to provide for predators in the decision rule used to establish catch limits for krill (Constable et al., 2000) in Conservation Measure 51–01 (CCAMLR, 2021), (ii) establishing in Conservation Measure 51–01 (CCAMLR, 2021) an interim limit, known as the 'trigger level', of 620,000 tonnes in Area 48 until a means of subdividing the krill catch into smaller management units has been determined (Constable, 2006), and (iii) subdividing the krill trigger level amongst Statistical Subareas in Area 48 in Conservation Measure 51–07 (CCAMLR, 2021). The latter was established for the 2009 season because of concerns that the trigger level might impact on krill predators if all the catch was concentrated in a small area (SC-CAMLR, 2008a; Watters et al., 2013, 2020). Of note in adopting this Conservation Measure, the Commission reiterated its objectives for krill predators in the preambular paragraphs that:

- *".the need to distribute the krill catch in Statistical Area 48 in such a way that predator populations, particularly land-based predators, would not be inadvertently and disproportionately affected by fishing activity,"*
- *".that large catches up to the trigger level from areas smaller than Subareas should be avoided," and*
- *".that the distribution of the trigger level needs to provide for flexibility in the location of fishing in order to (i) allow for interannual variation in the distribution of krill aggregations, and (ii) alleviate the potential for adverse impacts of the fishery in coastal areas on land-based predators."*

Despite this work, there remains no accepted measures for managing the food web effects of fishing at the scale of krill predator populations in CCAMLR. In the absence of being able to set local area catch limits based on local risks of ecosystem effects (Equations 1–5), we use the vulnerability assessment (Equations 7–10) to illustrate how to spread the risk of the krill trigger level. We derive data from historical literature for CCAMLR Statistical Area 48 that has been accepted for use in the Scientific Committee of the Commission for the Conservation of Antarctic Marine Living Resources (Constable et al., 2000; SC-CAMLR, 2006, 2008b, 2016a), and use these in conjunction with updated estimates of krill distribution and

abundance in the area (Krafft et al., 2021). Here, we step through the implementation of the method and conclude with available outcomes on risk based on these data.

3.1. Spatial and temporal scales for assessing risk

Antarctic krill, *Euphausia superba*, is widely distributed in the Southern Ocean (Marr, 1962; Mackintosh, 1972, 1973), with a number of recent reviews describing the factors influencing its distribution, dynamics and long-term change; 70% of the Antarctic krill stock is concentrated between 0°W and 90°W (Area 48), with 87% of the stock over deep oceanic water (>2000 m) (Atkinson et al., 2019; Meyer et al., 2020; Johnston et al., 2022). Biomass estimates at this large geographic scale are derived from three international multi-ship acoustic surveys, undertaken during the summers of 1981 (Trathan et al., 1995), 2000 (Fielding et al., 2011) and 2019 (Krafft et al., 2021). Krafft et al. (2021) reported that while variation in the distribution of krill may occur between years, there is no evidence of a general regional decline in the last 20 years. Smaller, regional acoustic surveys of krill biomass reflect high levels of intra-and inter-annual variability in stock density and biomass, but reveal no trend in abundance (Reiss et al., 2008; Reid et al., 2010; Fielding et al., 2014; Trathan et al., 2022a). However, these surveys do show differences in distribution and biomass between summer and winter (Saunders et al., 2007; Reiss et al., 2017), including with biomass occurring deeper vertically in the water column during winter (Lascara et al., 1999).

The mesoscale distribution of krill is thought to be related to sea ice, shelf bathymetry, and ocean currents, particularly the fronts in the Antarctic Circumpolar Current (ACC) (Johnston et al., 2022) or further south (Trathan et al., 2022a). Although there are no consistent environmental relationships apparent across regions in space and time (Silk et al., 2016), the ACC plays an important role in transporting krill across the region, beginning in the west Antarctic Peninsula and southern Weddell Sea (Hofmann and Murphy, 2004; Thorpe and Murphy, 2022), indicating that the 'stock' of krill extends across the south Atlantic, at least to CCAMLR Subareas 48.1, 48.2, 48.3, and 48.4, but probably more extensively.

Risks to predators occur at two main spatial scales within the region of the stock. Land-based predators, such as seals and penguins, operate at local scales near to their breeding colonies, while pelagic predators, such as whales, fish and pack ice seals, are distributed more across the region depending on their feeding grounds (Bestley et al., 2020). Subareas are likely to be insufficient to manage local scale risks. In 2002, the Scientific Committee of CCAMLR determined small-scale management units (SSMUs) in Area 48 to manage local-scale effects of krill fishing (Figure 4; Constable and Nicol, 2002; SC-CAMLR, 2002; Hewitt et al., 2004b). While it is 20 years since those SSMUs were cast and that it is time for their review, they still form a suitable basis on which to consider how to spread risk and conserve predators at their ecologically-relevant scale.

The time-period for the application of a catch limit is the overall temporal scale of the assessment, usually 1 year. For polar regions, there is extreme seasonality giving rise to production occurring in spring and summer and stasis or attrition in autumn and winter. This is exemplified by many life histories. For example, whales and many seals migrate to the north of the Antarctic region in winter and many predators tied to land in summer during the breeding season will forage more widely and away from their colonies in winter (Bestley et al., 2020).

Individual krill live for a number of years, with a plausible maximum age of around six-plus (Quetin and Ross, 2003). Somatic growth is seasonal, with an increase in body size during spring and summer with possible shrinkage over winter (Ikeda, 1985; Constable and Kawaguchi, 2017). Observations suggest winter shrinkage is most apparent in adult females but not males, based on the tracking of modal size classes over seasons and sex-ratio patterns; other explanatory factors, such as differential mortality, immigration and emigration, do not explain the observed differences (Tarling and Fielding, 2016). Growth rates are thought to be greater where primary production is higher, but with limitations imposed by sea ice and sea surface temperature (e.g., with elevated growth in spring around South Georgia; Murphy et al., 2017).

The risks to krill and predators from krill fishing are therefore not the same throughout the year. Here, we divide the year into two seasons, summer and winter, to take account of this variation and compare this to an assessment without considering season.

3.2. Neutral fishing pressure for krill

Neutral fishing pressure for krill was determined from the proportion of biomass in each area. Densities of Antarctic krill were derived from the results of two regional surveys in austral summer of Area 48: 1999–2000 (Watkins et al., 2004; Hewitt et al., 2004a) and 2018–2019 (Krafft et al., 2021). The two surveys have been analysed using the same stratification (Table 3a), with island strata (areas near to the islands) in each of Subareas 48.1 (South Shetlands), 48.2 (South Orkney), 48.3 (South Georgia), 48.4 (South Sandwich), and larger pelagic strata encompassing much of the remainder of the Subareas.

Hewitt et al. (2004a) used the densities in the island strata to represent densities in each of the neritic (non-pelagic) SSMUs. In their paper, the pelagic SSMUs were given the densities of the pelagic strata in the surveys. That approach for neritic SSMUs was used here, taken as the mean density from across the two surveys in the relevant island survey strata. The Antarctic Peninsula East SSMU was not surveyed in either survey. The density in Antarctic Peninsula East was approximated as the mean density of the Antarctic Peninsula stratum from across the two surveys. In the South Orkneys, the island stratum encompassed the neritic SSMUs of South Orkney Islands West and North East. The South East SSMU had the mean density of the pelagic stratum applied because of the substantial difference of this stratum to the other neritic strata (Krafft et al., 2018).

In order to ensure the biomass in a Subarea was consistent with estimates from the surveys, the biomass in the respective pelagic SSMUs was calculated as the mean biomass in the Subarea from across the two surveys less the summed biomass from the neritic SSMUs in that Subarea, excluding the Antarctic Peninsula East SSMU. Note the Scotia Sea stratum encompasses Subareas 48.2 and 48.3, which was accounted for in this formulation.

The derived krill densities for each SSMU and the Subareas are given in Table 3b (see also Figure 5), along with the spatial areas of each, and the consequent biomass and proportion of the region-wide stock found in each area.

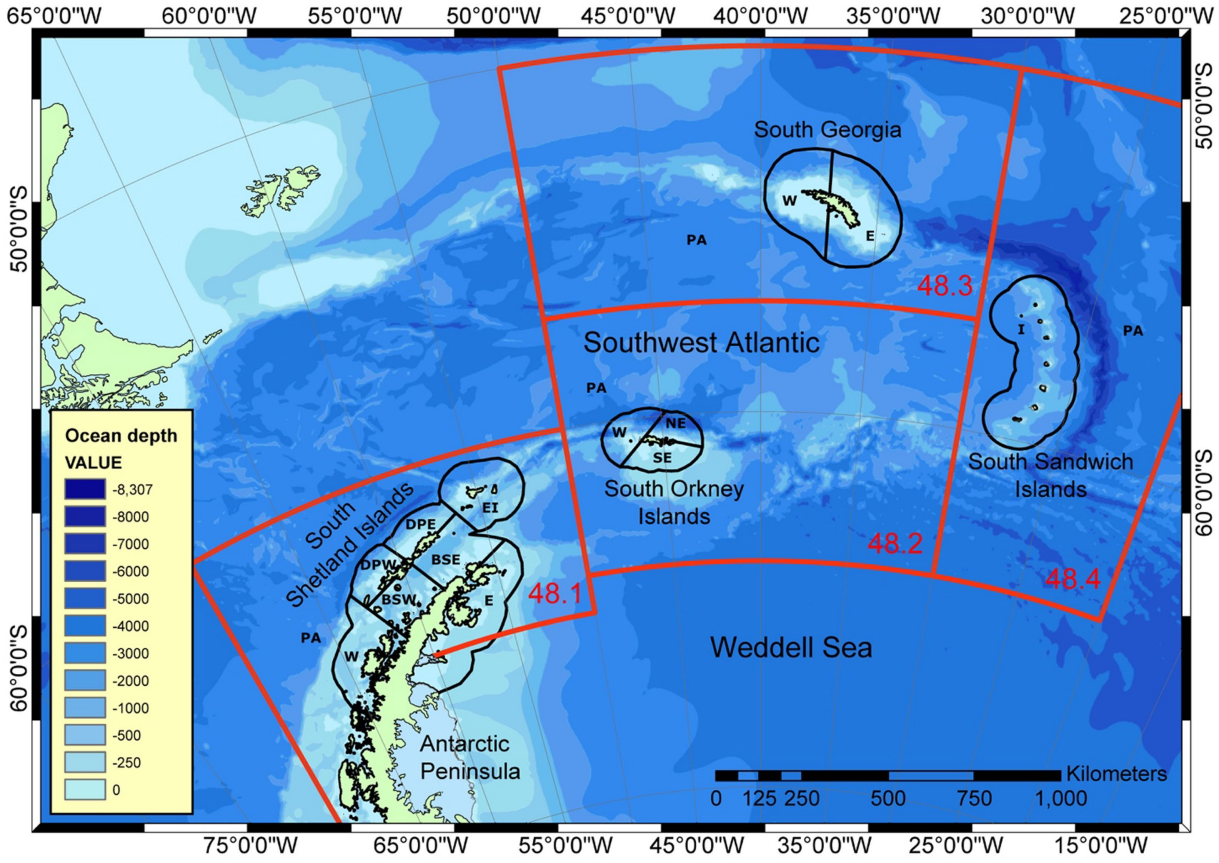

FIGURE 4
Small-scale management units in FAO Statistical Area 48 established by the Scientific Committee of CCAMLR in 2002 (SC-CAMLR, 2002). FAO Subareas (numbers shown in red) are 48.1 (Antarctic Peninsula, AP), 48.2 (South Orkney, SO), 48.3 (South Georgia, SG) and 48.4 (South Sandwich, SS). Small-Scale Management Units are shown with acronyms relating to the Subareas: PA, Pelagic Area; E, East; NE, North East; SE, South East; W, West; BSE, Bransfield Straight East; BSW, Bransfield Straight West; DPE, Drake Passage East; DPW, Drake Passage West; EI, Elephant Island; I, Islands. Full acronym for an SSMU used in later figures and tables have the Subarea acronym as the first two letters combined with the relevant SSMU acronym used here.

At present, there are no consistent estimates tracking biomass within SSMUs from summer to winter. In order to partition the year into two seasons, krill densities in winter were approximated from applying constant mortality ($M = 0.8\,yr^{-1}$) (Constable and de la Mare, 1996) giving an average biomass over winter months (May to October) of approximately 0.84 of the average over the summer months (November to April) (Constable, 2000). While this is only an approximation in the absence of other data, we multiply the summer estimates of density/biomass by 0.84 to reflect a difference in winter density/biomass.

3.3. Vulnerabilities of krill

Risks to Antarctic krill from fishing relate to the importance of areas as source areas for adults and recruitment areas for juveniles.

Advection is considered to play a central role in distributing krill across Area 48 with the Antarctic Peninsula being an important source area for krill that then move with the Antarctic Circumpolar Current along the Scotia Arc to the east. Areas where juveniles recruit follow this pattern. While early life stages may be present in most areas where krill are found (Meyer et al., 2020), the population is dependent on successful recruitment, which occurs primarily in the Antarctic Peninsula with advection from this Subarea to the other Subareas (Reiss, 2016).

Spawning is episodic, with multiple spawning events within a year (Quetin and Ross, 2003). Recruitment is episodic and regional, with models showing that the seasonal location of sea ice is the main limiting factor for successful larval recruitment (Thorpe et al., 2019). Spawning in January leads to the greatest extent of viable larval recruitment habitat, while later spawning in February, when sea ice is at a minimum, generally provides insufficient time for larvae to reach a viable developmental stage before the winter sea ice advances (Thorpe et al., 2019).

Generally krill exist within different aggregation states, with swarms, layers and individuals, but with the numbers and sizes of swarms in an area changing across space and time. Smaller, more widely dispersed swarms occur in summer, whilst larger, more infrequent swarms occur in winter, with the patterns and seasonal changes unlikely to be simply the consequence of oceanographic circulation (Lascara et al., 1999). Other behavioural aspects of krill life history also challenge our understanding; for example, it has been observed, at least along the west Antarctic Peninsula, that the length frequency distributions of krill collected by nets exhibits an

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TABLE 3 Derivation of densities of Antarctic krill for small-scale management units (SSMUs) in FAO Statistical Area 48 and consequent proportions of the region-wide biomass in each SSMU for use in the risk assessment.

(a) Densities and biomass of Antarctic krill in strata estimated from surveys in FAO Statistical Area 48 in the austral summers of 1999–2000 and 2018–2019, from Table 11 in Krafft et al. (2021).

		1999–2000		2018–2019	
Subarea	Survey stratum	Density (tonnes. km^2)	Krill biomass (million tonnes)	Density (tonnes. km^2)	Krill biomass (million tonnes)
48.1	Antarctic Peninsula (S-AP)	19.6	9.278	40.6	19.235
	South Shetland Islands (S-SShI)	136	6.615	68.3	3.325
48.2 & 48.3	Scotia Sea (S-SS)	31.5	34.928	28.5	31.585
	South Orkney Islands (S-SOI)	319.4	7.797	93.2	2.275
	South Georgia (S-SG)	33.8	0.846	6.4	0.161
48.4	Eastern Scotia Sea (S-ESS)	1.8	0.587	25	8.049
	South Sandwich Islands (S-SSaI)	4	0.247	26.8	1.672
Total			60.298		66.302

(b) Krill densities and proportion of region-wide stock in SSMUs derived from the average density for the relevant survey substratum in (a), as described in the text.

SSMU Name	SSMU	Survey Stratum	Area (km^2)	Summer Density[&] (tonnes.km^2)	Summer Biomass[&] (million tonnes)	Proportion of region-wide stock
Subarea 48.1 – South Shetland			656,452	31.91[#]	20.950	0.322
Pelagic Area	APPA*	S-AP	441,722	7.11	3.140	0.048
West	APW	S-SShI	37,219	102.15	3.802	0.058
Drake Passage West	APDPW	S-SShI	16,068	102.15	1.641	0.025
Drake Passage East	APDPE	S-SShI	16,680	102.15	1.704	0.026
Bransfield Strait West	APBSW	S-SShI	22,505	102.15	2.299	0.035
Bransfield Strait East	APBSE	S-SShI	28,317	102.15	2.893	0.044
Elephant Island	APEI	S-SShI	36,694	102.15	3.748	0.058
East	APE	S-AP	57,248	30.10	1.723	0.026
Subarea 48.2 – South Orkney			856,106	23.86[#]	20.428	0.314
Pelagic Area	SOPA*	S-SS	813,539	17.60	14.321	0.220
West	SOW	S-SOI	16,495	206.30	3.403	0.052
North East	SONE	S-SOI	10,897	206.30	2.248	0.035
South East	SOSE	S-SS	15,175	30.00	0.455	0.007
Subarea 48.3 – South Georgia			1,029,732	17.84[#]	18.368	0.282
Pelagic Area	SGPA*	S-SS	933,136	17.60	16.427	0.253
West	SGW	S-SGI	43,077	20.10	0.866	0.013
East	SGE	S-SGI	53,520	20.10	1.076	0.017
Subarea 48.4 – South Sandwich			944,681	5.59[#]	5.278	0.081
Pelagic Area	SSPA*	S-ESS	847,522	4.46	3.781	0.058
Islands	SSI	S-SSaI	97,160	15.40	1.496	0.023
Total					65.023	

*Pelagic SSMUs for which densities are adjusted to account for biomass allocated to neritic SSMUs from the respective larger Subarea-scale strata. Subarea Area and Biomass are the sums of the SSMUs. [#]Densities calculated by dividing biomass by area. [&]Summer density and biomass are converted to winter density & biomass by multiplying by survivorship term of 0.84.

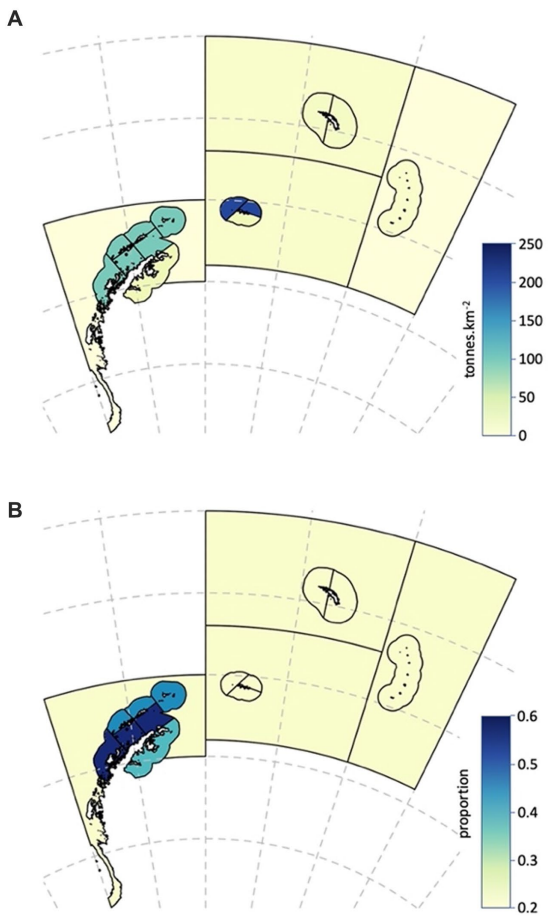

FIGURE 5
Spatial characteristics of the Antarctic krill population used in the risk assessment. **(A)** Densities of Antarctic krill (tonnes.km^{-2}). **(B)** Median annual proportion of Antarctic krill less than 35mm in length in the population.

across-shelf pattern of larger (>40 mm) krill located offshore smaller krill (<38 mm) in all seasons except winter. Such data, coupled with historical observations suggest that there is a seasonal shift in the primary habitat of krill and that changes in behaviour are an important factor in krill distribution. Similar assortative length frequency patterns are also evident within individual swarms, where differences in size between adjacent swarms are probably due to a length-dependent sorting mechanism that restricts the size range of krill in a swarm (Watkins, 1986).

The geographic domain that encompasses the life cycle of krill is unclear. However, deep water is thought to be a prerequisite for successful spawning (Hofmann and Hüsrevoğlu, 2003), as eggs need at least 700 m water depth to fulfil their development before the larvae rise again to the sea surface (Hofmann and Hüsrevoğlu, 2003; Thorpe et al., 2019). Temporal and spatial coherence in patterns of early life-history stages are evident across the Atlantic sector (Perry et al., 2019); however, mechanisms whereby adult life-history stages migrate back onto the shelf after spawning (Siegel, 1988) remain uncertain, particularly given regions of complex bathymetry and strong ocean currents. Transport in oceanographic currents has certainly been a topic of much debate (Renner et al., 2012). Nevertheless, understanding how krill behaviour, recruitment, and movement in ocean currents interact remains elusive, but a key challenge for understanding ecosystem functioning.

Resolving these issues will help increase understanding about the potential for some areas to act as krill sources, or krill sinks. So far, several studies have already begun to consider the complexity of krill movement in relation to local oceanography within the southwest Atlantic, and particularly along the west Antarctic Peninsula region. For example, Capella et al. (1992) reported that the Bransfield Strait and the South Shetland Islands receive krill larvae from the Bellingshausen Sea to the west, the Weddell Sea to the east and from north of the South Shetland Island arc (Figure 4; see also Trathan et al., 2022b). Subsequently, Piñones et al. (2011, 2013a), calculated residence times for biological hotspots using a Lagrangian model, inferring that particle (=krill) retention was aided by certain physical features, including proximity to deep depressions and shelter from wider shelf circulation. Piñones et al. (2013b) and Capella et al. (1992) noted that off-shelf transport from the west Antarctic Peninsula supports the hypothesis that spawning contributes to populations downstream across the southwest Atlantic. Further, age-dependent sea-ice associated behaviour may be important in the transport and distribution of krill populations (Thorpe et al., 2007). Diel vertical migration (DVM) over a 24 h period may also have implications for krill availability. However, Piñones et al. (2013b) noted that DVM made little (< 10%) difference in the horizontal and vertical dispersion of particles.

The relative importance of SSMUs for recruiting krill juveniles is reflected by the proportion of the population in an area comprising animals less than 35 mm in length, the length being sufficient to encompass animals in Year 1 (de la Mare, 1994). The U.S. AMLR program provides a time series of length frequency data from regular surveys in Subarea 48.1, data from which these proportions can be derived.[1] We use the surveys in early summer (January–February; Leg 1) for the period 1996 to 2011 to calculate the proportion of the population in their strata that comprise juveniles. The importance of an SSMU as a recruitment area is determined as the median of the time series of observations from the survey stratum in which the SSMU resides (Table 4 and Figure 5). Juvenile krill have been observed in the other Subareas but only sporadically (e.g., Krafft et al., 2018). For this reason, we apply a recruitment value from the Antarctic Peninsula Pelagic SSMU to the SSMUs of the other Subareas.

3.4. Vulnerabilities of krill predators

Risks to krill predators include the removal of krill from feeding grounds and the potential disruption of krill availability to predators.

A broad guild of predators feed on krill (Croxall et al., 1985; Trathan and Hill, 2016), made possible by its wide geographic distribution and its various aggregation states. A corollary of this is

1 KRILLBASE at https://doi.org/10.5285/8b00a915-94e3-4a04-a903-dd4956346439

TABLE 4 Median annual proportion of Antarctic krill less than 35mm in length in the population in Antarctic Peninsula SSMUs derived from time series of length frequencies in survey strata from early summer by the US AMLR program from 1996 to 2011.

SSMU	US AMLR survey stratum	Median proportion of krill juveniles in population
APPA	3	0.22*
APW	#	0.58
APDPW	2	0.46
APDPE	2	0.46
APBSW	1	0.58
APBSE	1	0.58
APEI	2	0.46
APE	4	0.39

*Indicates value used for SSMUs in Subareas 48.2, 48.3, and 48.4. #Indicates the SSMU further west than the annual survey but takes account of the result of Conroy et al. (2020) and adopts the value from the Bransfield Strait stratum.

that krill swarm structure is also thought to be a fundamental response for avoiding predation, whilst krill themselves continue to mate, spawn and feed (Tarling and Fielding, 2016). The dominance of smaller krill swarms in summer along the west Antarctic Peninsula (Lascara et al., 1999) coincides with the feeding activity of numerous central-place foraging seabirds and seals provisioning offspring. The reduction in this concentrated foraging pressure after these land-based predators complete breeding also coincides with the emergence of larger krill swarms in autumn and winter (Lascara et al., 1999). As such, the interplay between predators and krill may be important, even though the actions of individual predators might be relatively minor, the cumulative impacts of many predators may generate significant effects on local prey aggregation states. In this context, the recovery of baleen whales after historical over-exploitation might now have implications for krill aggregation states, given baleen whales feed in differing ways to those of penguins and seals.

Further, there is now also growing recognition that the demands made by land-based predators are likely to be eclipsed by other taxa (Hill et al., 2007; Warwick-Evans et al., 2022). Currently, a number of humpback whale stocks are thought to be close to pre-exploitation levels (Cooke, 2018c), yet other baleen whale species remain well below historical numbers (Cooke, 2018a; Cooke, 2018b). As these also recover, competitive effects are likely to change as species endeavour to re-occupy their historical niches, although whether such niches now remain the same is uncertain, given ecological change (Nicol et al., 2010; Atkinson et al., 2019; Constable et al., 2022). Certainly, in recent years, some penguin species have shown shifts in population abundance, the causes of which have been attributed to climate, but which may equally be (at least partially) a result of changes in inter-specific competition for krill (Ainley et al., 2007; Trivelpiece et al., 2011). Determining how predator dominance changes as baleen whales recover, will be a key topic for future research.

Central-place foraging predators are constrained by the need to provision offspring during the summer breeding season (Figure 6). However, other predators considered to have an ideal-free distribution (Fauchald, 2009), such as baleen whales, fish and squid are not so constrained and so are more likely to track shifting prey resources. Outside the breeding season, central-place foragers are also no longer constrained and may go to regions with more abundant or predictable prey resources. This means that there are distinct spatial patterns of consumption which are predictable within and between years (Trathan et al., 1998; Warwick-Evans et al., 2018, 2019). However, in addition to apparent spatial differences in consumption, all krill-dependent predators also show temporal patterns of consumption across the annual cycle. For example, macaroni penguins, *Eudyptes chrysolophus*, show different profiles of demand during the year compared with Antarctic fur seals, *Arctocephalus gazella*, (Boyd, 2002), whilst within a given species, different demographic categories can show subtly different annual profiles across the year (e.g., Adélie penguins, *Pygoscelis adeliae* – Southwell et al., 2015). Baleen whales may also have different periods of feeding intensity, with particularly hyperphagic periods when they first return to their summer feeding grounds (Baines et al., 2022).

While clear examples exist of spatial overlap between the fishery and various predators (Trathan et al., 2018; Warwick-Evans et al., 2018; Trathan et al., 2022b), there is no evidence as yet on the potential for fishing to interfere with the local availability of krill to predators. Predators have a variety of feeding behaviours, probably arising from the variable aggregation states of krill. Some predator species may feed off individual krill, some skim, whilst some lunge and require krill swarms to feed efficiently. Removal of krill by fishing vessels, or disturbance so that swarm-structure is disrupted into a different aggregation state may displace predators from preferred predictable areas. However, to date little work has been undertaken to assess predator (or fishery) krill aggregation preferences, but the fact that vessels periodically move (SC-CAMLR, 2016b Annex 6, paragraphs 2.215 to 2.221; Santa Cruz et al., 2018) suggests that the potential exists for disturbance competition.

3.4.1. Spatial distribution of krill predation

Predator demand for krill is a product of the abundance of a population (colony) and the *per capita* consumption of the population. The distribution of predator demand for a population will vary between times of year and between years, particularly for species tied to colonies during breeding, and will depend on the foraging behaviour of the species.

The average annual density (tonnes.km^{-2}) of predator demand for krill in small areas was developed from Hill et al. (2007), given the publication of the *per annum* estimates of summer demand by SC-CAMLR (2011); see Annex 4, Table 3. The winter and summer demand was estimated for all predators combined (fish, whales, fur seals and penguins) in each small-scale management unit according to the parameters and calculations of Hill et al. (2007). Krill-eating fish included in those calculations were nototheniid and channichthyid species in the on-shelf areas and myctophid species in off-shelf areas. Hill et al. (2007) provide the details of these calculations. Table 5a gives the population size of fish, whales, penguins and fur seals in each SSMU along with *per capita* consumption of krill (g) in each SSMU for summer and winter.

The data to calculate predator demand for the SSMUs in Subarea 48.4 were not available except as provided by Trathan et al. (2008) for the numbers of penguins. Trathan et al. (2008) provide a census of fur seal pups, showing only a low abundance of seals on the islands. Without an estimate of abundance of adults, the population of seals was assumed to be zero. For the purposes of developing this example of the risk assessment, we approximated

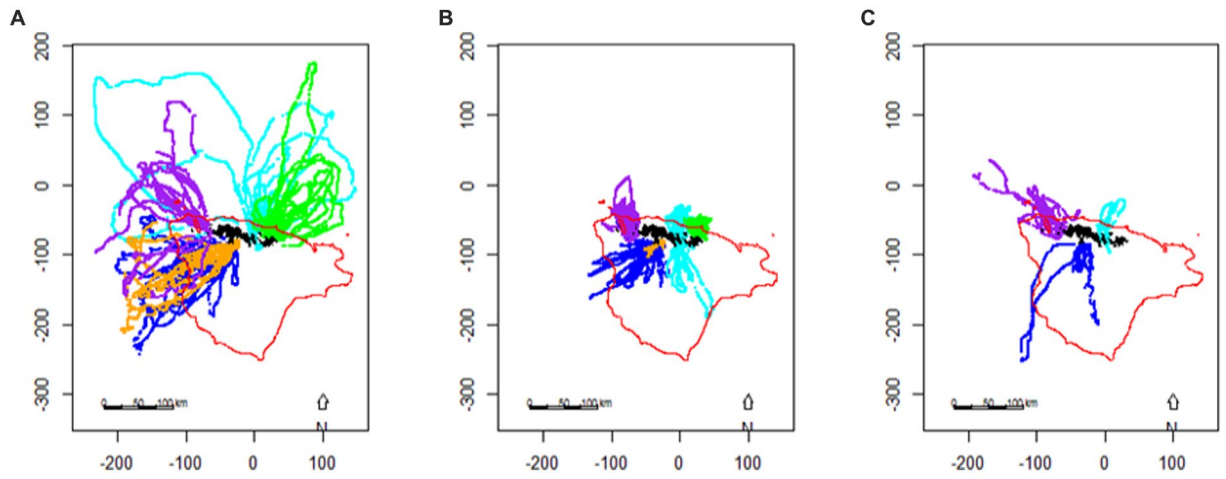

FIGURE 6
The location of foraging dives made by chinstrap penguins, *Pygoscelis antarctica*, breeding on the South Orkney Islands during **(A)** incubation, **(B)** brood, and **(C)** crèche based on telemetry data (from Warwick-Evans et al., 2018), axes are shown with units of km (see Figure 4 for location). Colours represent different sites/years: Powell Island (pale blue), Monroe Island (purple), Laurie Island (green), Signy Island 2013 (orange), and Signy Island 2015 (blue). The 500m isobath, representing the shelf-edge, is indicated in red.

the abundance of whales and fish using proxy methods. The densities of mesopelagic fish and the general attributes of the ocean environment are of similar characteristics between Subarea 48.2 and the area around the South Sandwich Islands (Dornan et al., 2022). We therefore applied the same density of fish and whales in the pelagic and north east SSMUs in Subarea 48.2, along with the consumption rates, to the pelagic and island SSMUs, respectively, in Subarea 48.4. For penguins, we applied the consumption rates from the north east SSMU in Subarea 48.2.

Annual krill consumption by pack ice seals in the SSMUs of Area 48 are available in Forcada et al. (2012) (Table 5b). These are included in the calculations of total predator demand by allocating 60% to summer and 40% to winter, following the partition of demand by fur seals between summer and winter.

These calculations do not include the consumption of krill by flying seabirds. Warwick-Evans et al. (2022) show that flying seabirds consume ~2% during summer around the Antarctic Peninsula. Methods for including flying seabirds in future calculations will be important as predator demand is currently underestimated.

3.4.2. Risks

For Antarctic krill predators, fishing will have the highest risk in areas where there is naturally greater pressure for krill. Predation pressure is the ratio of the predator demand density for krill and the available krill density in an area, i.e., an indicator of the potential for competition amongst predators. Areas with higher predation pressure would be expected to be more vulnerable to the effects of fishing than areas with lower pressure. Here, we evaluate predation pressure for land-based predators and other predators that are more likely to forage according to an 'ideal-free' distribution. Data in Tables 3b, 5 are used to calculate predation pressure in each SSMU (Table 6 and Figure 7). Note that winter predation pressure is based on summer krill densities adjusted for expected survivorship after 6 months (Table 3b). The annual predation pressure is an average of the summer and winter pressures.

3.5. Baseline catch distribution and region-wide risk

Baseline Alphas as proportions of the catch limit and the consequent baseline region-wide risks were calculated for two examples: local catches distributed across the SSMUs (i) for the whole year, and (ii) for when the fishery is separated into summer and winter. These examples applied Equations 6–8. The examples developed here are provided in an Excel spreadsheet in Supplementary Material Table 2.

The local risks, $R_{a,t}$, arising from applying Equation 7 are presented in Table 6 for the two examples, along with the data on the three vulnerabilities – krill recruits, and predation pressure for each of land-based predators and 'ideal free' foragers. Krill recruits remained unscaled. Predation pressure was scaled between 0 and 1 using the logistic function in Equation 3 ($h = 3$; $v = 3$; $X_{50} = 0.5$; $X_0 = 0$; $X_1 = 4$; $Y_0 = 0$; $Y_r = 1$,illustrated as the black line in Figure 1).

The neutral fishing pressure, $\dot{F}_{a,t}$, used for calculating the baseline alpha levels, $\alpha_{a,t}$, (Equation 8) is the proportion of the region-wide stock in each SSMU shown in Table 3b. The Baseline Alphas for the two examples are presented in Table 7.

The local risks and baseline alphas for the whole year example and for the summer-winter examples are illustrated in Figure 8. The baseline regional risk (Equation 9) for the whole year assessment was 0.559 (Table 7).

3.6. The krill fishery and managing preferred fishing patterns

The vast majority of the krill stock occurs in deep oceanic water but is unpredictable in location and often at low density in this habitat (Figure 5). Therefore, over time, the fishery has coalesced into areas where krill are more predictable and at levels of abundance that are desirable to fishery operators. These areas tend to be over shallower

TABLE 5 Data for calculating predator demand for krill.

(a) Abundance (numbers) and per capita demand for krill (g) for fish, whales, penguins and fur seals, from Hill et al. (2007).						
	Number	*Per capita* Krill (g)		Number	*Per capita* Krill (g)	
SSMU		Summer	Winter		Summer	Winter
	Fish			Whales		
APPA	8.403E+09	897	125	9,233	54,942,525	0
APW	8.344E+08	1,558	310	767	54,942,525	0
APDPW	3.019E+08	1,325	227	330	54,942,525	0
APDPE	3.220E+08	1,384	245	341	54,942,525	0
APBSW	4.389E+08	1,405	252	460	54,942,525	0
APBSE	5.747E+08	1,407	253	600	54,942,525	0
APEI	6.797E+08	992	144	773	54,942,525	0
APE	1.553E+09	1,628	342	1,284	54,942,525	0
SOPA	6.906E+10	140	24	6,808	60,444,604	0
SOW	3.201E+08	827	112	131	60,444,604	0
SONE	1.969E+08	1,035	153	86	60,444,604	0
SOSE	3.893E+08	1,616	336	126	60,444,604	0
SGPA	2.488E+11	43	16	7,737	60,444,604	0
SGW	1.141E+09	659	176	354	60,444,604	0
SGE	1.478E+09	631	165	452	60,444,604	0
SSPA	7.233E+10##	140**	24**	7,130##	60,444,604**	0
SSI	1.866E+06#	1,035*	153*	815#	60,444,604*	0
	Penguins			Seals		
APPA	0	0	0	0	0	0
APW	253,873	311,307	221,278	0	0	0
APDPW	74,798	255,235	205,329	12,204	1,613,386	1,039,700
APDPE	1,084,367	251,591	206,643	211	1,613,386	1,039,700
APBSW	1,160,224	251,988	206,499	0	0	0
APBSE	298,817	314,812	223,652	0	0	0
APEI	1,413,511	251,228	206,775	1,002	1,613,386	1,039,700
APE	823,403	366,713	243,211	0	0	0
SOPA	0	0	0	0	0	0
SOW	2,286	251,065	206,833	0	0	0
SONE	584,507	364,280	242,398	0	0	0
SOSE	1,003,958	273,603	213,599	0	0	0
SGPA	0	0	0	0	0	0
SGW	6,642,811	227,304	225,304	611,054	1,613,386	1,039,700
SGE	564,496	246,586	215,006	6,090	1,613,386	1,039,700
SSPA	0	0	0	0	0	0
SSI	3,394,200[1]	364,280*	242,398*	0[1]	0	0

(b) Annual predator demand for krill (tonnes) in SSMUs for pack ice seals (Forcada et al., 2012).					
APPA	APW	APDPW	APDPE	APBSW	APBSE
59E3	154E3	0	0	6E3	113E3

Number prorated from SONE (#) or SOPA (##) and *per capita* krill consumption assumed from SONE (*) or SOPA (**) (see text for details). [1]From Trathan et al. (2008)—see text for details.

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TABLE 6 Vulnerabilities (krill recruitment and predation pressures) and consequent local area risk in each SSMU for a 'whole year' assessment and an assessment with seasons – summer (S) and winter (W).

	Krill recruits	Predation pressure land-based foragers			Predation pressure 'Ideal free foragers'			Local risk		
SSMU		S	W	Year	S	W	Year	S	W	Year
APPA	0.22	0	0	0	2.57	0.41	1.49	0.999	0.559	0.970
APW	0.58	0.02	0.02	0.02	0.37	0.11	0.24	0.756	0.633	0.695
APDPW	0.46	0.02	0.02	0.02	0.26	0.05	0.15	0.619	0.500	0.560
APDPE	0.46	0.16	0.16	0.16	0.27	0.06	0.16	0.686	0.578	0.632
APBSW	0.58	0.13	0.12	0.13	0.28	0.06	0.17	0.748	0.659	0.704
APBSE	0.58	0.03	0.03	0.03	0.31	0.08	0.20	0.732	0.627	0.680
APEI	0.46	0.10	0.09	0.09	0.19	0.03	0.11	0.616	0.531	0.573
APE	0.39	0.18	0.14	0.16	1.51	0.37	0.94	0.982	0.686	0.911
SOPA	0.22	0	0	0	0.70	0.14	0.42	0.758	0.337	0.569
SOW	0.22	0	0	0	0.08	0.01	0.05	0.288	0.231	0.259
SONE	0.22	0.10	0.08	0.09	0.09	0.02	0.05	0.370	0.295	0.333
SOSE	0.22	0.60	0.56	0.58	1.40	0.34	0.87	0.985	0.792	0.934
SGPA	0.22	0	0	0	0.68	0.29	0.48	0.744	0.464	0.617
SGW	0.22	2.88	2.93	2.91	0.89	0.28	0.59	1.000	1.000	1.000
SGE	0.22	0.14	0.14	0.14	0.89	0.27	0.58	0.869	0.533	0.732
SSPA	0.22	0	0	0	2.79	0.55	1.67	0.999	0.661	0.982
SSI	0.22	0.83	0.66	0.74	1.32	0.23	0.78	0.989	0.796	0.941

TABLE 7 Baseline Alpha (proportion of total catch limit) for each SSMU for a 'whole year' assessment and an assessment with seasons – summer (S) and winter (W).

	Baseline Alpha			Fishing pattern			
SSMU	S	W	Year	Neutral	Adjusted	Desirable	Adjusted
APPA	0.000	0.026	0.004	0.048	0.040	0	0
APW	0.021	0.026	0.051	0.058	0.035	0	0
APDPW	0.014	0.015	0.032	0.025	0.012	0.111	0.102
APDPE	0.012	0.014	0.027	0.026	0.014	0.111	0.102
APBSW	0.013	0.015	0.030	0.035	0.021	0.111	0.102
APBSE	0.017	0.020	0.040	0.044	0.026	0.111	0.102
APEI	0.032	0.033	0.070	0.058	0.029	0.111	0.102
APE	0.001	0.010	0.007	0.026	0.021	0	0
SOPA	0.078	0.179	0.269	0.220	0.108	0	0
SOW	0.055	0.049	0.110	0.052	0.012	0.111	0.102
SONE	0.032	0.030	0.065	0.035	0.010	0.111	0.102
SOSE	0.000	0.002	0.001	0.007	0.006	0	0
SGPA	0.094	0.166	0.275	0.253	0.134	0	0
SGW	0.000	0.000	0.000	0.013	0.011	0.111	0.102
SGE	0.003	0.009	0.013	0.017	0.010	0.111	0.102
SSPA	0.000	0.024	0.003	0.058	0.049	0	0
SSI	0.000	0.006	0.004	0.023	0.019	0	0
Regional risk			0.559	0.648		0.608	
Proportion of catch limit to reduce regional risk to baseline of 0.491					0.862		0.919

Note that the seasonal assessment is for both summer and winter over the year and that the sum of the alphas for summer and winter combined will equal 1.0. For the whole year assessment, two alternative fishing patterns are analysed – (i) the consequences of applying the neutral fishing pattern as a preferred pattern, and (ii) a possible pattern desirable to the fishing industry. In both latter cases, the adjusted proportions to keep the regional risk at the baseline level are also shown.

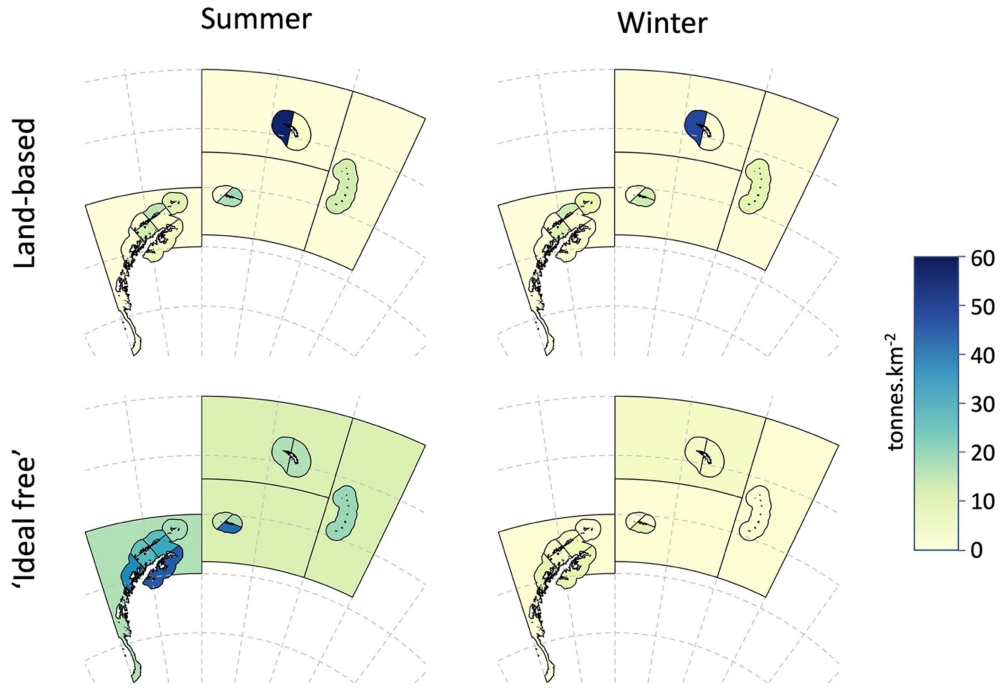

FIGURE 7
Demand density for Antarctic krill (tonnes.km^{-2}) in summer and winter, aggregated for land-based predators and predators that are likely to concentrate foraging in areas of higher densities of krill, termed 'ideal-free' foragers.

shelf waters, or at the shelf edge, such that the fishery now generally operates close to island archipelagos within the southwest Atlantic (Santa Cruz et al., 2018). Recent studies have highlighted the potential for the krill fleet to locally deplete levels of krill (or disturb the swarm structure) such that vessels relocate, with catch rates per hour in fishing hotspots gradually declining over four or 5 days (SC-CAMLR, 2016b Annex 6, paragraphs 2.215 to 2.221). Such a result highlights the potential for the fishery to compete with predators. At these scales of operation, managers need to understand the critical levels of krill density preferred by different predators, and the time taken for an area to recover to a given density level after depletion (Trathan et al., 2022b).

We illustrate how to manage preferred fishing patterns if the baseline alphas do not seem satisfactory. First, we examine the unweighted fishing pattern of neutral fishing pressure based on krill densities might be managed. Table 7 shows how the regional risk (Equation 9) is increased to 0.648, greater than the baseline risk of 0.559. The proportion of catches in each SSMU need to be adjusted downward by 0.138 in order to retain the regional risk at the baseline level. The second scenario was for a pattern with a desirability of the fishery to operate around the Antarctic Peninsula and adjacent to islands. In this case, we set equal catches to be taken from the SSMUs near to land (Table 7). The consequent regional risk is 0.608, requiring an adjustment of catches downwards by 0.081 to satisfy the baseline risk.

4. Concluding remarks

The risk assessment procedure presented here provides a method for combining risks to conservation from fisheries into a single metric and to use this to identify areas of higher overall risk. The procedure then has mechanisms to spread the fishery away from higher risk areas, to adjust catch limits to reduce risks if the fishery cannot avoid such areas, and to also allow for closed areas to help compensate for higher risks in other areas. It also includes the rationale for how adjustments to fishing patterns can be implemented to appropriately spread risks arising from fisheries when a full risk assessment is not possible. We used the Antarctic krill fishery as a case study but this framework can be readily applied to other fisheries. The method allows for the seamless inclusion of new data when they become available, but can be implemented with existing data. A further feature of this method is that the risk of impacts can be assessed for individual areas of interest based on more detailed information for that area whilst including it in a wider assessment across many areas, thereby enabling broader ecological considerations to be incorporated. In conclusion, spatial ecosystem-based management strategies for fisheries can proceed from the outset of a fishery using suitable proxies for ecosystem vulnerabilities within a risk framework.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material (Table 1 - code for undertaking the uncertainty simulation; Table 2 - the data and working of the Antarctic krill fishery example), further inquiries can be directed to the corresponding author.

Author contributions

AC conceived of the project, developed the framework, undertook the simulations, and led the writing of the manuscript. SK, PT, and

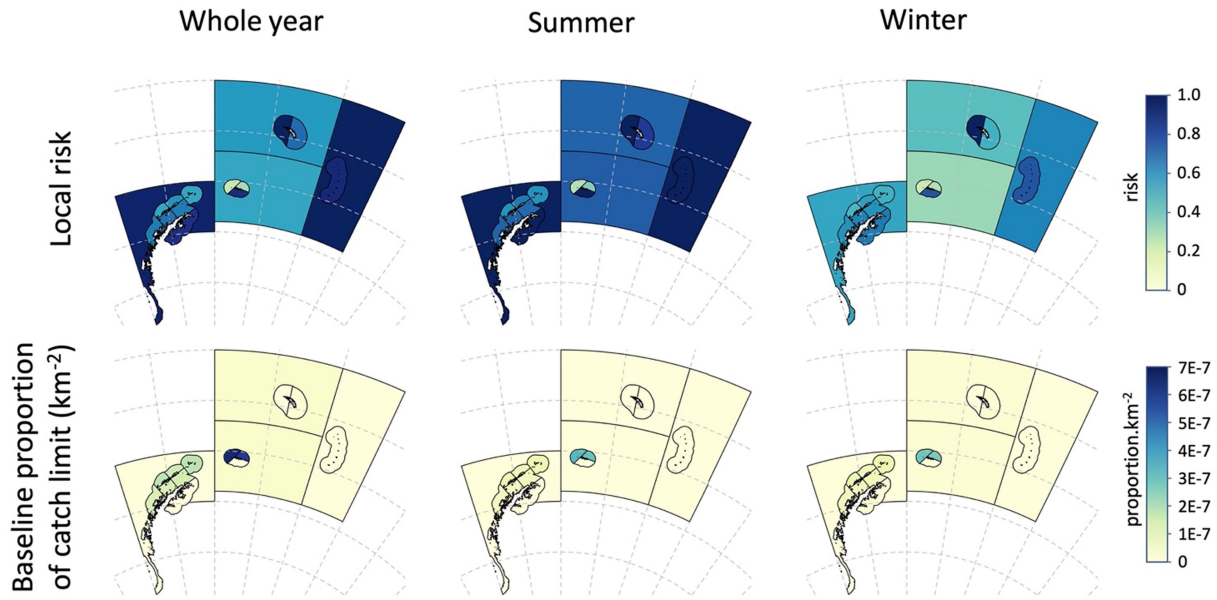

FIGURE 8
Local risk in each assessment area (Table 6) and the baseline proportion of the catch (alpha) (Table 7) displayed as proportion per km^2 for the whole year, and for the seasonal assessment splitting the year into summer and winter (see Table 7 and the text for details).

VW-E contributed to detailing the Antarctic marine ecosystem, trialling the framework, and writing the manuscript. MS contributed to analytical support and mapping. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1043800/full#supplementary-material

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Opportunities and limitations of large open biodiversity occurrence databases in the context of a Marine Ecosystem Assessment of the Southern Ocean

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The Southern Ocean is a productive and biodiverse region, but it is also threatened by anthropogenic pressures. Protecting the Southern Ocean should start with well-informed Marine Ecosystem Assessments of the Southern Ocean (MEASO) being performed, a process that will require biodiversity data. In this context, open geospatial biodiversity databases such as OBIS and GBIF provide good avenues, through aggregated geo-referenced taxon locations. However, like most aggregated databases, these might suffer from sampling biases, which may hinder their usability for a MEASO. Here, we assess the quality and distribution of OBIS and GBIF data in the context of a MEASO. We found strong spatial, temporal and taxonomic biases in these data, with several biases likely emerging from the remoteness and inaccessibility of the Southern Ocean (e.g., lack of data in the dark and ice-covered winter, most data describing charismatic or well-known taxa, and most data along ship routes between research stations and neighboring continents). Our identification of sampling biases helps us provide practical recommendations for future data collection, mobilization, and analyses.

KEYWORDS

OBIS, GBIF, sampling bias, biodiversity data, spatial bias, temporal bias, taxonomic bias

1 Introduction

The Southern Ocean is a highly productive region that provides a large variety of ecosystem services (e.g., climate regulation, natural resources – including for food provision – and tourism; Grant et al., 2013). Exploration and exploitation of the Southern Ocean is relatively recent (starting with small research and whaling expeditions at the end of the 19th century) but interest and human activities have since increased dramatically, along with associated stressors – e.g., exploitation of fishing resources, disturbances by human visitors, pollution, invasive species, but also global warming and ocean acidification (Petrou et al., 2019; Rogers et al., 2020; Grant et al., 2021). Changes induced by these stressors can be profound and are expected to become more important (e.g., changes in primary productivity, ecosystem structure and functions, carbon uptake, species migrations, etc.; Henley et al., 2020; Morley et al., 2020; Brasier et al., 2021; Caccavo et al., 2021). For these reasons, maintaining the Southern Ocean in good health by minimizing the impact of human activities and climate change on ecosystem services should be a major priority for governance and policy bodies (Kennicutt et al., 2014; Rogers et al., 2020).

In this context, a marine ecosystem assessment of the Southern Ocean (MEASO) aims to provide managers with consolidated information about the status and trends of Southern Ocean habitats, species and ecosystems, to better support management and conservation planning activities. This information includes summaries of current knowledge from experts and peer-reviewed literature as well as biodiversity-related data and model outputs that can inform specific aspects of policy development. The specific requirements of such data will vary according to the particular objectives of a given assessment exercise. Ideally, however, biodiversity data should include abundances or densities from a phylogenetically and functionally wide variety of species, have a circumpolar coverage and allow comparison of the present state with a past benchmark (Brasier et al., 2019). As a starting point, the Census of Antarctic Marine Life (Schiaparelli et al., 2013) had as its main objective to understand the biodiversity of the Southern Ocean and set reference baselines to allow subsequent measurements of change (Van de Putte et al., 2021). The resulting Biogeographic Atlas of the Southern Ocean (de Broyer and Koubbi, 2014) provided an initial benchmark of the Southern Ocean biogeography knowledge. However, to inform policy, such complex ecological data are best summarised in a few easily understandable statistics which can be used to track changes through time. These include Essential Biodiversity Variables (EBV; cooperatively defined by the Group on Earth Observations Biodiversity Observation Network, or GEO BON, http://geobon.org) and Essential Ocean Variables (EOV; proposed by the Global Ocean Observing System, or GOOS, http://goosocean.org). These summary variables range from species-level distributions and biomass to measures of community composition and taxonomic or trait diversity (Pereira et al., 2013; Constable et al., 2016; Miloslavich et al., 2018; Muller-Karger et al., 2018; Jetz et al., 2019, Van de Putte et al., 2021). At the regional scale, monitoring frameworks and essential variables are being developed concurrently. For the Southern Ocean the Southern Ocean Observing System (SOOS) is leading the creation of Southern Ocean-specific ecosystem Essential Ocean Variables (eEOVs; Constable et al., 2016).

The remoteness, difficulty of access, and harsh weather conditions of the Southern Ocean pose particular challenges to the collection of biodiversity data in the region. Individual studies are limited in their spatial and temporal extent, but thankfully, initiatives have emerged to aggregate these individual studies into larger biodiversity research data infrastructures. These provide opportunities to leverage the knowledge generated by these individual independent efforts to obtain a wider understanding of ocean biodiversity (Van de Putte et al., 2021). The Global Biodiversity Information Facility (GBIF, https://www.gbif.org) and the Ocean Biodiversity Information System (OBIS, https://obis.org) were created at the start of the 21st century to provide open access biodiversity data. At the regional level of the Southern Ocean, the Scientific Committee on Antarctic Research (SCAR) Antarctic biodiversity portal (www.biodiversity.aq) acts as their regional node. These biodiversity research data infrastructures are in line with the current guidelines of many funding agencies, and with the spirit of the Antarctic Treaty, that "Scientific observations and results from Antarctica shall be exchanged and made freely available" (Antarctic Treaty 1959, Article 3), and therefore with the FAIR principles of "Findability, Accessibility, Interoperability, and Reusability" (Wilkinson et al., 2016). GBIF and OBIS follow the Darwin Core (DwC) data standard (Wieczorek et al., 2012), an international standard - ratified and maintained by the Biodiversity Information Standards (TDWG) - that facilitates the sharing of information about biological diversity. Through a Darwin Core Archive (DwC-A), it is possible to share metadata (using the ecological metadata language, eml), species (taxonomic) checklists, occurrence and sampling event data. In addition, additional data such as DNA derived data (Nilsson et al., 2022), or extended measurements or facts (De Pooter et al., 2017) can be included in various extensions. The requirement to follow these standards provide advantages over general purpose data portals (e.g. figshare.com, pangea.de) in terms of Interoperability and Reusability. Highly FAIR compliant data could allow the development of analytical workflows to automatise the calculation of EBVs or eEOVs (Van de Putte et al., 2021). Finally, GBIF and OBIS put the emphasis on data with geospatial information, which is not the case of, e.g., portals dedicated to molecular data such as GenBank. These biodiversity research data infrastructures therefore represent a promising avenue for understanding large-scale diversity patterns and the long-term state of Southern Ocean ecosystems.

Whether these promising data have the quality and spatial, temporal and taxonomic coverage to support the calculation of essential variables for a MEASO, however, remains unknown. Assessing the quality and biases of GBIF data in European seas, (Ramírez et al., 2022) found severe biases towards waters closer to well-funded institutions (around the United Kingdom and in the North Sea), recent years (with a peak in the 2010s), and the most conspicuous and abundant taxa (e.g., crustaceans, echinoderms or fish). However, environmental and socio-economic factors make the Southern Ocean a very different system to European seas (e.g., remote and inaccessible with extreme seasonality caused by winter darkness and seasonal sea ice), making repeating the exercise for the Southern Ocean a necessity. In a first Southern Ocean case study, Moudrý and Devillers (2020) found issues with the quality and coverage of a number

of records from GBIF and OBIS on marine mammals (e.g., missing collection dates, varying geographic accuracy, and known mammal biodiversity hotspots with no available records). Here, we extend this exercise to all biodiversity records from the Southern Ocean. We assess overall quality and geographical, temporal, and taxonomic coverage of GBIF and OBIS records for the region. We examine these potential sources of bias and formulate recommendations should these data be used for a MEASO. Finally, the tools for data cleaning, as well as the cleaned dataset, are made available for future use.

2 Materials and methods

2.1 Data access

Biodiversity data from the Southern Ocean was sourced from GBIF (http://www.gbif.org, interpreted data downloaded on November 10, 2022; GBIF.org, 2022) and OBIS (https://obis.org, downloaded on November 10, 2022) with the R package *robis* (Provoost and Bosch, 2021) and from the GBIF data portal and R package *rgbif* (Chamberlain et al., 2023). The data was queried using a polygon combining all MEASO regions, obtained through the *measoshapes* package (Sumner, 2020). The MEASO regions divide the Southern Ocean into five longitudinal sectors that are further subdivided in three longitudinal zones.

2.2 Data integration and quality control

Raw data from GBIF and OBIS were combined and subjected to a quality control procedure largely based on the approach outlined by Moudrý and Devillers (2020) and Vandepitte et al. (2015). The series of filters that were used to flag (and subsequently remove) problematic data are described below.

2.2.1 Spatial filters

As in Moudrý and Devillers (2020), coordinates were rounded to four decimal places, and occurrences located on land were flagged for further removal, based on shorelines from the Global Self-consistent, Hierarchical, High-resolution Geography database (GSHHG full resolution L1 – for sub-Antarctic islands – and L6 – for Antarctica, Version 2.3.7 Released June 15, 2017, downloaded from www.soest.hawaii.edu/pwessel/gshhg/). Although shoreline maps can sometimes be inaccurate in the Southern Ocean, no buffer was used to avoid removing too many coastal records. Note that coordinate precision was not taken into account here, which might lead in a few cases to the undue removal of records (e.g. for gridded data, the center point for the grid cell could be on land even if the recorded occurrence was in the water - a problem which might be more prevalent for benthic species). Contrary to Moudrý and Devillers (2020), occurrences with identical values for latitude and longitude were not filtered out as we had no means to distinguish between erroneous and correct cases (some locations with identical latitude and longitude fall within a highly sampled area of the Southern Ocean, and locations with inverted latitude and longitude can be hard to detect in the region).

2.2.2 Temporal filters

Temporal filters were applied based on the *eventDate* and *year*, *month*, and *day* fields. When there was a range of dates in the *eventDate* field, only the first date was considered. When there was a conflict between information in the *eventDate* field and data in the *year*/*month*/*day* fields, priority was given to the *year*/*month*/*day* fields. Records with missing or incomplete dates were flagged for further removal. Dates prior to 1773 (first recorded crossing of the Antarctic circle by captain Cook) and after 2022 were also flagged for further removal.

2.2.3 Taxonomic filters

Records with no information in the *scientificName* field were flagged for further removal. For all other records, taxon names present in the *scientificName* field (or in the *species* field when there was no match with *scientificName*) were matched with the World Register of Marine Species (WoRMS; www.marinespecies.org), the reference taxonomic database for marine wildlife. We did so using the *worrms* package (Chamberlain, 2020) and retaining only exact matches. For each taxon that matched, a unique WoRMS identifier (i.e., *aphiaID*) – favouring accepted names when multiple matches were found – could be assigned to it, along with the corresponding valid name, that was used in further analyses. Higher level categorisations (e.g., families for taxa identified at the genus level) imported from WoRMS were also added to the working dataset. In a few cases, a *scientificName* matched multiple accepted entries from WoRMS belonging to different phyla (e.g., the genus *Nitzschia* can be a member of either phyla Platyhelminthes or Ochrophyta; similarly, members of the genus *Gardnerella* can be either Actinobacteria or Mollusca). In these cases, priority was given to the WoRMS entry whose phylum matched the original phylum entered in OBIS and GBIF, and no WoRMS entry was kept when there was no phylum match. Taxa with no match were flagged for further removal.

2.2.4 Observation type filters

Absence data were flagged for further removal, as not all biodiversity survey datasets include a list of taxa that were not observed at a given time and place (absence data represent a marginal fraction of all data present on GBIF and are absent by default from OBIS downloads).

Fossil data were also flagged for further removal, as only extant data was of interest for this study. The remaining data was further separated into 'machine observations' (using the MachineObservation tag in the *basisOfRecord* field – defined by Darwin Core as "an output of a machine observation process", e.g. photographs, videos, audio recordings, remote sensing images, telemetry, etc. – https://dwc.tdwg.org/terms/#machineobservation) and 'human observations' (all remaining data). These two sub-datasets were separated for further analysis (see *Evaluation of biases* section), because occurrences associated with various types of tracking of individual movements (e.g., Argos or GPS systems) artificially inflate the relative importance of the tracked species in the data.

2.2.5 Potential duplicates

Following these steps (i.e., after matching taxonomic names with WoRMS), records that were duplicated between and/or within

databases were flagged for further removal. Records that had identical values (including NAs) in the fields *decimalLatitude*, *decimalLongitude* (rounded to 4 decimals), *year*, *month*, *day* – or *eventDate* – and WoRMS-matched *scientificName* were considered as potential duplicates. Potential duplicates could be multiple entries of a species at the same geographic location and time within or between databases or could be records that are duplicated with changes to the *occurrenceID* field, for instance when data is uploaded again as part of an extended dataset.

2.3 Evaluation of biases

A working dataset – in which all flagged data were removed, and valid taxonomic names were associated using WoRMS – was used for the evaluation of geographical, temporal, and taxonomic biases. Biases were visualised either for the whole working dataset, or for machine or human observations only, for certain abundant phyla, or for other groups of interest (see *Analysis of focal groups* for details).

Temporal biases were explored by calculating the number of records per month of year, per year or per decade.

Spatial biases were visualised on a reference square grid, using a Polar Stereographic projection and a 100km x 100km resolution, by plotting the number of records in each grid cell. Spatial coverage for the groups of interest was estimated by creating a 3° x 3° grid covering the whole MEASO region (origin set at 180°W and 90°S, as in Griffiths et al., 2014) and counting the percentage of cells that contained at least one record.

The depth of taxonomic identifications was assessed by calculating the proportion of records that were described up to the phylum, class, order, family, genus, or species level.

Following Ramírez et al. (2022), we also built taxa accumulation curves for each major MEASO sector (Atlantic, Central Indian, East Indian, East Pacific, West Pacific). For this we used the 3° x 3° grid mentioned above, and calculated, in each grid cell, the number of records and the number of genera. We used genera and not species, to increase the number of records that could be used in this analysis. The relationship between the number of records and the number of genera was modelled using a Michaelis-Menten fit, with the rationale that if the relationship plateaus, the cells on the plateau can be considered as well sampled (i.e., increasing the number of records should not increase the number of recorded genera).

2.3.1 Analysis of focal groups

Benthic vs. pelagic species were identified following (Griffiths et al., 2014). Information was only retained for taxa with unambiguous matching. Seventeen other focal groups were defined: 1. Birds and mammals, 2. Crustacea, 3. Microzooheterotrophs, 4. Mollusca, 5. Tunicata, 6. Echinodermata, 7. Bacteria, 8. Eukaryote primary producers, 9. Gelatinous zooplankton, 10. Pisces, 11. Plantae, 12. Annelida, 13. Bryozoa, 14. Porifera, 15. Protozoa, 16. Tintinnid ciliates, 17. Macroalgae. These groups were defined by extending the definitions of Ramírez et al. (2022) and the list of corresponding taxa can be found in Supplementary Table S1. Finally, records were considered as zooplankton or phytoplankton (to estimate the amount of data in the EOV categories – see Table 1) based on functional groups associated with WoRMS entries, accessed using the worrms package and a modification of a code available from https://github.com/tomjwebb/WoRMS-functional-groups. For benthic, pelagic, zooplankton, and phytoplankton groups, taxa were considered as belonging to a group if at least one life stage was recorded as belonging to it.

2.4 Suitability of the available data for a MEASO

Based on definitions provided by GEO BON and GOOS (see Table 1 for details), we identified, for each relevant EBV and EOV, the data necessary for their calculation. We then evaluated how appropriate data from OBIS and GBIF are for this exercise, based on qualitative evaluation of biases as well as quantitative evaluations of the percentage of records containing the required information. Note that our evaluation of the availability of abundance data was focused on the *organismQuantity(Type)* and *individualCount* columns, and excluded information that may have been recorded in extension tables (Extended Measurement or Fact), as only occurrence data was included in this analysis. This may underestimate to a certain extent the availability of abundance data.

2.5 Code availability

All analyses were performed in R-studio (R version 4.4.1; R Core Team, 2021). The R-code of the analyses has been extensively documented and is freely available at GitHub (https://github.com/asbonnetlebrun/measo_gap_analysis).

3 Results

3.1 Data availability and overall quality

The search criteria matched 5,993,533 records on OBIS and 5,579,904 on GBIF. Of these, 547,944 records appeared to be situated on land (Figure 1). In total, 1,478 records had no *scientificName* (0.01% of the data), and 467,966 records had a *scientificName* with no match in WoRMS (4.04% of the data). Note that for records from DNA sequence reads, the number without a scientificName match in WoRMS increased substantially to 40.56%.

5.04% of records had incomplete date information (year missing for 2.84% of records, month for 4.55% and day for 5.04%). In addition, 5,369 records prior to 1773 (first recorded crossing of the Antarctic circle), and 6 records after 2022, were flagged as erroneous for further removal (e.g. 5,353 records supposedly in year 0). 141,966 records (1.23% of all data) referred to species absences (all from GBIF; Figure 1).

7,002,899 (60.51% of the total) records were potential duplicates of other records (2,118,495 within OBIS, 1,373,050 within GBIF, and 3,511,354 between the two databases, leaving 4,570,538 unique records in the database. Machine observations accounted for 39.89% of all records (before quality controls), and human

TABLE 1 List of Essential Biodiversity and Essential Ocean Variables, and the availability of suitable data in OBIS and GBIF to calculate them.

Essential Biodiversity Variables (EBVs)		Definition source: GeoBON	Required quantity	Availability
	Species population EBVs			
1	Species distribution	The species occurrence probability over contiguous spatial and temporal units addressing the global extent of a species group.	Geo-referenced presences that can be used in species distribution models.	Available, but species distribution models would need to take spatial and temporal sampling biases into account. Only 1.23% of all OBIS-GBIF records for the region are absence data.
2	Species abundance	Predicted count of individuals over contiguous spatial and temporal units addressing the global extent of a species group.	Reliable abundance data (here in the *organismQuantity* and *organismQuantityType* fields, potentially in the *individualCount* field).	Only 17.56% records (34.92% when considering only human observations) may be considered trustworthy abundance data (defined by the *organismQuantity* and *organismQuantityType* field explicitly mentioning unit taxa per unit space and/or time). 18.99% of records (38.93% when considering only human observations) have *individualCount* provided, but without information on the area sampled. Note that extension tables were not evaluated here.
	Community composition EBVs			
3	Community abundance	The abundance of organisms in ecological assemblages.	Reliable abundance data (if communities are assumed to be homogeneous over a certain area and time period).	See EBV2 for data on abundance in OBIS-GBIF.
4	Taxonomic/ phylogenetic diversity	The diversity of species identities, and/or phylogenetic positions, of organisms in ecological assemblages.	Geo-referenced presences and phylogenies that can be matched based on taxonomic names.	Geo-referenced presences available in OBIS-GBIF, providing biases are taken into account. Phylogenetic information not available in OBIS-GBIF - need for external phylogenetic database(s), e.g., the "tree-of-life" databases (see http://tolweb.org/tree/phylogeny.html).
5	Trait diversity	The diversity of functional traits of organisms in ecological assemblages.	Geo-referenced presences and a trait database that can be matched based on taxonomic names.	Geo-referenced presences available in OBIS-GBIF, providing biases are taken into account. Trait information not available in OBIS-GBIF - need for external functional traits database(s).
6	Interaction diversity	The diversity and structure of multi-trophic interactions between organisms in ecological assemblages.	Geo-referenced presences and an interaction database that can be matched based on taxonomic names.	Geo-referenced presences available in OBIS-GBIF,providing biases are taken into account. Interaction information not available in OBIS-GBIF - need for external interactions database(s).
	Ecosystem structure EBVs			
7	Live cover fraction	The horizontal (or projected) fraction of area covered by living organisms, such as vegetation, macroalgae or live hard coral.	Data on cover.	Not available from OBIS/GBIF
8	Ecosystem distribution	The horizontal distribution of discrete ecosystem units.		
9	Ecosystem vertical profile	The vertical distribution of biomass in ecosystems, above and below the land surface.	Depth information related to geo-referenced presences.	Depth information only available for 30.72% of the dataset, skewed towards shallow depths (50.08% of the records with depth information in the top 10 meters of the ocean). Of these records with depth information, 62.21% % have a measure of biomass (*organismQuantity(Type)* fields).

(Continued)

TABLE 1 Continued

Essential Ocean Variables (EOVs)		source: GOOS		
1	Phytoplankton biomass and diversity		Geo-referenced presences and reliable abundance data (in the *organismsQuantity (Type)* fields, potentially in the *individualCount* field)	82,466 (1.98% of total) records for phytoplankton, of which 68.46% contain info in the *organismQuantity(Type)* fields and 16.92% in the *individualCount* field.
2	Zooplankton biomass and diversity			60,5491 (14.54% of total) records for zooplankton (based on functional groups from WoRMS), of which 68.68% contain info in the *organismQuantity*(Type) fields and 23.28% in the *individualCount* field.
3	Fish abundance and distribution			24,858 (0.60% of total) records for fish (defined as in Table S1), of which 15.16% contain info in the *organismQuantity(Type)* fields and 12.85% in the *individualCount* field.
4	Marine turtles, birds and mammals abundance and distribution			2,906,071 (69.80% of total) records for birds, and mammals (defined as in Table S1), of which 1.83% contain info in the *organismQuantity(Type)* fields and 15.74% in the *individualCount* field.
5	Microbe biomass and diversity			No clear taxonomic definition of microbes to estimate the amount of available data.
6	Invertebrate abundance and distribution			3,910,534 (93.92% of total) records for invertebrates (defined here as the kingdom Animalia minus the phylum vertebrates), of which 14.04% contain info in the *organismQuantity*(*Type)* fields and 19.51% in the *individualCount* field.
7	Seagrass cover and composition		Data on cover and representative geo-referenced presences to estimate composition.	Data on cover not available from OBIS/GBIF; seagrasses absent from the Southern Ocean (0% of the data in the families Zosteraceae, Hydrocharitaceae, Posidoniaceae or Cymodoceaceae).
8	Macroalgal canopy cover and composition			Data on cover not available from OBIS/GBIF; no clear taxonomic definition of macroalgae to estimate amount of available data.

Unless explicitly mentioned, percentages are expressed as percentages of the working dataset (after quality control and removal of duplicates).

observations for 60.11%, with the remaining ~3400 records being unclassified or fossil records.

Only 19.39% of all (i.e., presence and absence) records contained information on the number of individuals observed (*individualCount* field), and 26.27% of all records contained abundance information (i.e., explicit mention of number of individuals per unit of space and/or time in the *organismQuantity* and *organismQuantityType* fields). Note that absence records could be considered as carrying abundance information (i.e., null abundance) but the *individualCount* and *organismQuantity* fields were filled in for respectively only 3.46% and 68.17% of absence records. An *occurrenceID* was missing for 953,954 records (8.24%), probably pre-dating the implementation of *occurrenceID* as an obligatory field.

Records originated from 3,484 individually identified datasets (based on unique value in the *datasetName* field) and 570 institutions (*institutionCode* field) - but note that 10,751,553 records had no data in the *datasetName* field and 5,582,236 records had no data in the *institutionCode* field. The contributions of individual datasets were highly variable: 2,929 datasets had less than 10 records, while 6 datasets had more than 50,000 records (including "The

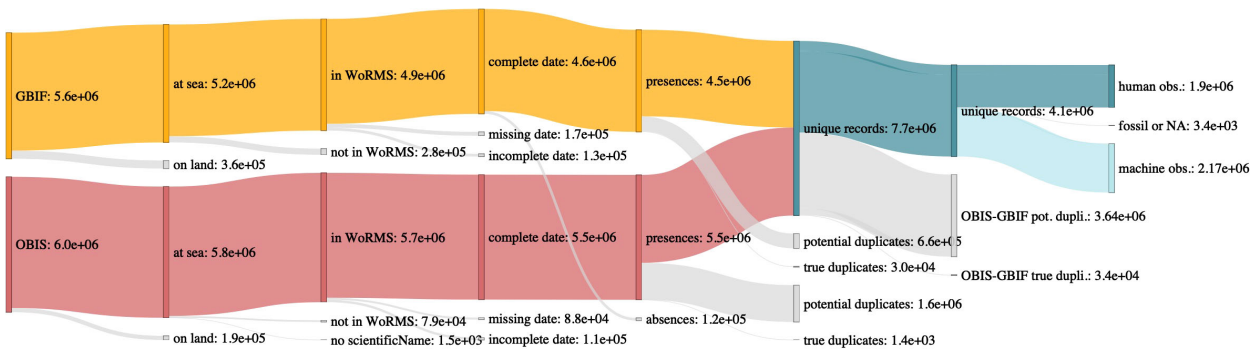

FIGURE 1
Sankey diagram of quality control steps: removing records on land, records with no match in WoRMS for their scientificName, records with incomplete or missing dates, absences, potential within-database duplicates, potential between-databases duplicates, and fossil records. Each category is followed by the number of records that fits in it. Orange: data from GBIF, red: data from OBIS, blue: unique records across the two combined databases, grey: discarded data.

Retrospective Analysis of Antarctic Tracking (Standardised) Data from the Scientific Committee on Antarctic Research" and "Southern Ocean Continuous Zooplankton Recorder (SO-CPR) Survey"). Molecular data ("DNA sequence reads" in the *organismQuantityType* field, as recommended in Andersson et al., 2021) represented 2.76% of the whole dataset.

Only 54.88% of all records contained information in the *samplingProtocol* field. When present, information in this field was not always recorded in a standardised manner, resulting in 4,885 unique values in this field, making a systematic study of the impact of sampling protocols on spatial and temporal biases impractical.

3.2 Exploration of distributions and biases

All subsequent results will refer to the filtered dataset (no terrestrial records, presences only, unique records, complete and realistic dates, machine or human observations).

3.2.1 Temporal distribution

Most observations were collected during the 20th and 21st centuries (only 0.04% of records prior to 1900, 63.9% of which classified as *preserved specimen*), with an increase starting around the 1950s and a decrease in the last decade – for both machine and human observations (Figure 2A). There was also a consistent seasonal bias in the data, particularly for human observations, which showed higher sampling intensity during the austral summer months (Figure 2B). Note that the peak in human observations in May in the last decade is dominated by what seems to be one campaign collecting and analyzing environmental DNA (i.e., "DNA sequence reads" in the *organismQuantityType* column) in 2016 in the West Pacific MEASO sector (70.37% of the 2000-2019 May peak; Supplementary Figure 1A, B). Overall, molecular data only started to represent a significant amount of data in the last decade (2010-2019; Supplementary Figure 1A).

3.2.2 Geographic distribution

Human observations were highly clustered (Figure 3A), with high record densities around Sub-Antarctic islands, and visible cruise tracks, e.g., between the Antarctic continent and New-Zealand or Australia. The number of human observation records per unit area was highest – and increased the most in recent years – in the Sub-Antarctic zone of the Central Indian sector, the Antarctic zone of the East Pacific sector, and the sub-Antarctic and Northern zones of the East Indian sector (Figure 4). High numbers of human observations were found around sub-Antarctic Islands, and along routes leading to research stations (Supplementary Figure 2A). In winter, human observations were almost absent from large areas

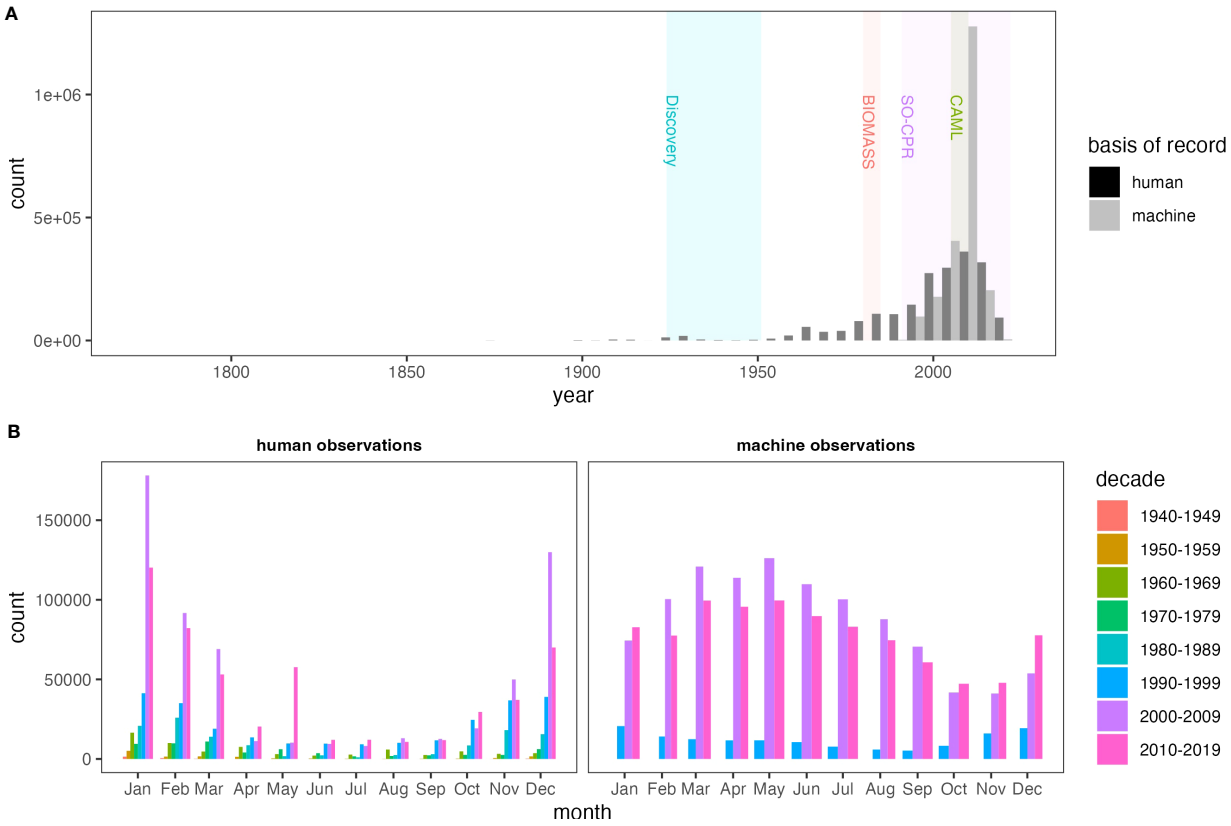

FIGURE 2
Temporal distribution of the data (after quality control): **(A)** number of records per year, along with some key expeditions (Discovery Investigations, Biological Investigations Of Marine Antarctic Systems and Stocks (BIOMASS) survey, Southern Ocean Continuous Plankton Recorder surveys (SO-CPR) and Census of Antarctic Marine Life (CAML); **(B)** number of records per month, separated into decades and human vs. machine observations.

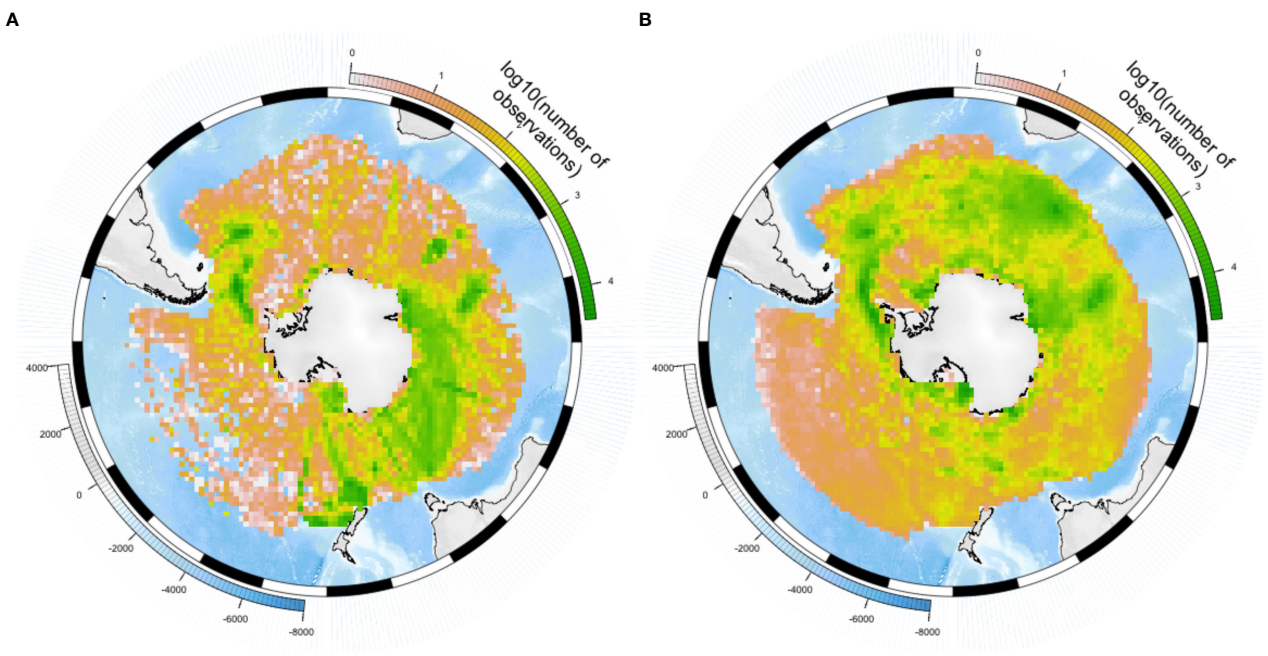

FIGURE 3
Geographic distribution of the number of records. **(A)** Human observations, **(B)** Machine observations.

covered by sea ice (Supplementary Figure 3), although areas in the Central Indian Ocean remained sampled in winter despite the presence of sea ice. In contrast, although most abundant around research stations (Antarctic Peninsula, sub-Antarctic islands, some areas on the Antarctic coast; Supplementary Figure 2B), machine observation data covered a larger part of the Southern Ocean and appeared not to be confounded by ship movement (Figure 3B, Supplementary Figures 2B, 4). However, in the case of tracking data from central-place foragers (a large part of the dataset), they will likely be biased by sampled colonies.

3.2.3 Taxonomic composition

Overall, the data included 23,947 different taxonomic units, based on values from the *scientificName* field, after matching with the WoRMS taxonomic backbone. These units ranged from (sub-)species to kingdom-level identifications. After matching with the WoRMS taxonomic backbone, we identified 93 individual phyla in the data. The 10 best represented phyla for the whole working dataset (machine and human observations) were Chordata (3,146,356 records), Arthropoda (506,936), Mollusca (70,372), Echinodermata (66,693), Foraminifera (57,147), Ochrophyta (56,567), Cnidaria (36,977), Proteobacteria (28,092), Bryozoa (25,822), and Annelida (25,512). The evolution of the number of records through time varied across phyla, with several phyla increasing until 2001-2010 and then plateauing or decreasing in the last decade, while Proteobacteria, which were absent from the databases until the decade 1980-1989, showing a very marked increase continuing in the last decade, making them to the 3rd currently most-sampled phylum (Supplementary Figure 5).

The depth of taxonomic identification varied with observation types: while 99.95% of machine observations were identified at the genus level, and 99.93% at the species level, only 83.96% of human observations were identified at the genus level, and only 70.48% at the species level. The depth of taxonomic identification also varied among phyla, with large and morphologically easily identifiable phyla such as Chordata (but also Mollusca, up to genus level) identified more precisely than phyla such as Radiozoa, Chaetognatha, Foraminifera and Proteobacteria (Supplementary Figure 6), those phyla often requiring microscopy to reach fine level identifications or DNA-based techniques, which often identify currently undescribed taxonomic units (Andersson et al., 2021). As an illustration of this, only 6.99% of molecular data were identified at the species level.

86.3% of filtered records could be unambiguously matched to benthic/pelagic categories. Overall, pelagic species appeared better sampled than benthic species, with a higher number of records and higher spatial coverage (Figure 5). There were large disparities in the number of human observations covering each focal group (Figure 5A), as well as in the spatial coverage of each group (Figure 5B). Birds and mammals were by far the most sampled group, followed by Crustacea. Birds and mammals, and Crustacea were also the groups with the best spatial coverage. However, some groups had relatively low sampling but relatively good coverage (e.g., Mollusca, Gelatinous zooplankton, or Annelida). No group had a spatial coverage higher than 65%. Both the distribution of records among groups and spatial coverage also varied across MEASO areas (Supplementary Figures 7, 8). In addition, when considering molecular data only, the four dominant phyla were all micro-organisms (by order of data quantity: bacteria, microzooheterotrophs, eukaryote primary producers, and protozoa; Supplementary Figure 1C).

In most sectors, no plateau was reached in the genus accumulation curves (Supplementary Figures 9-11), and even in

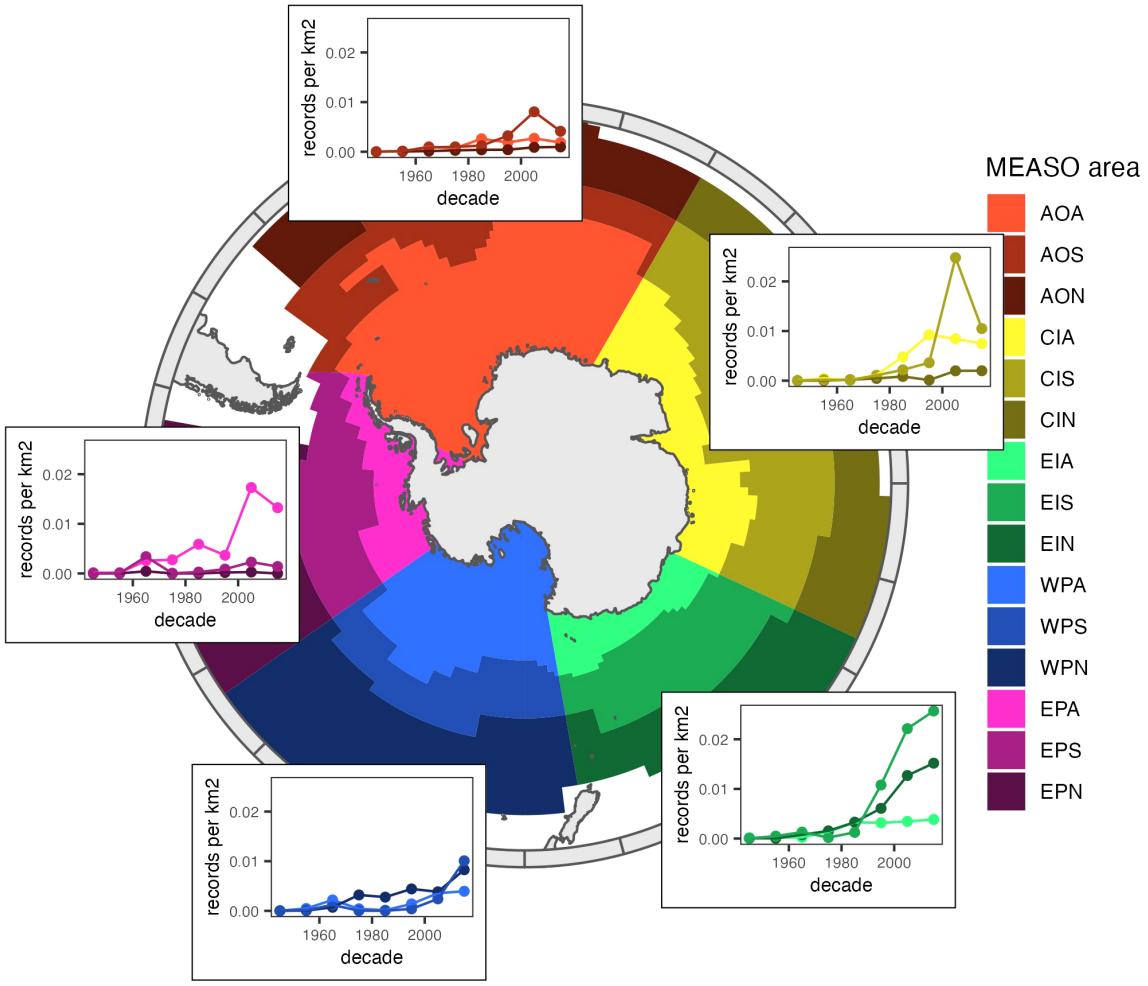

FIGURE 4
Number of human observations per km^2 per decade for each MEASO area. The MEASO areas divide the Southern Ocean into five longitudinal sectors: the West Pacific (WP), East Pacific (EP), Atlantic (AO), East Indian (EI), and Central Indian (CI). Each of these sectors is further subdivided into three longitudinal zones (from South to North): Antarctic (WPA, EPA, AOA, EIA and CIA), Sub-Antarctic (WPS, EPS, AOS, EIS and CIS), and Northern (WPN, EPN, AON, EIN and CIN).

the sector where a plateau was reached, there were very few cells that appeared to be sampled enough. In addition, the fit was poor for most sectors.

3.3 Suitability of the available data for a MEASO

Table 1 shows, for each relevant EBV or EOV, the data required for its calculation, and the fit for purpose of OBIS and GBIF data. In general, geo-referenced data are available for a range of taxa but (as discussed below) their suitability for a MEASO is hindered by the spatial, temporal, and taxonomic biases identified above. For variables that require abundance, biomass, trait, or depth data, large proportions of records do not contain suitable information.

4 Discussion

By exploring the temporal, spatial and taxonomic distributions of open biodiversity data in the SO, we found a strong seasonal and spatial bias, as well as an unbalanced representation of the different taxa. These limitations, along with limited information on certain variables of interest (e.g., absences, abundance, depth) might constrain the utility of such data for a MEASO. We also found consistent differences between human and machine observations, highlighting the need to treat these two data types separately when using these to calculate EBVs or EOVs.

4.1 Opportunities arising from open biodiversity databases for a MEASO

By providing enormous amounts of geo-referenced data (millions of records), on a large taxonomic diversity (thousands of taxonomic units) and with large spatial extent, OBIS and GBIF represent promising data infrastructures for mapping distributions in the Southern Ocean. These data aggregators are continuously growing, due to increased data collection and incentives to submit data to publicly accessible repositories, while standards for publishing these data are also constantly improving (Van de Putte et al., 2021). Several

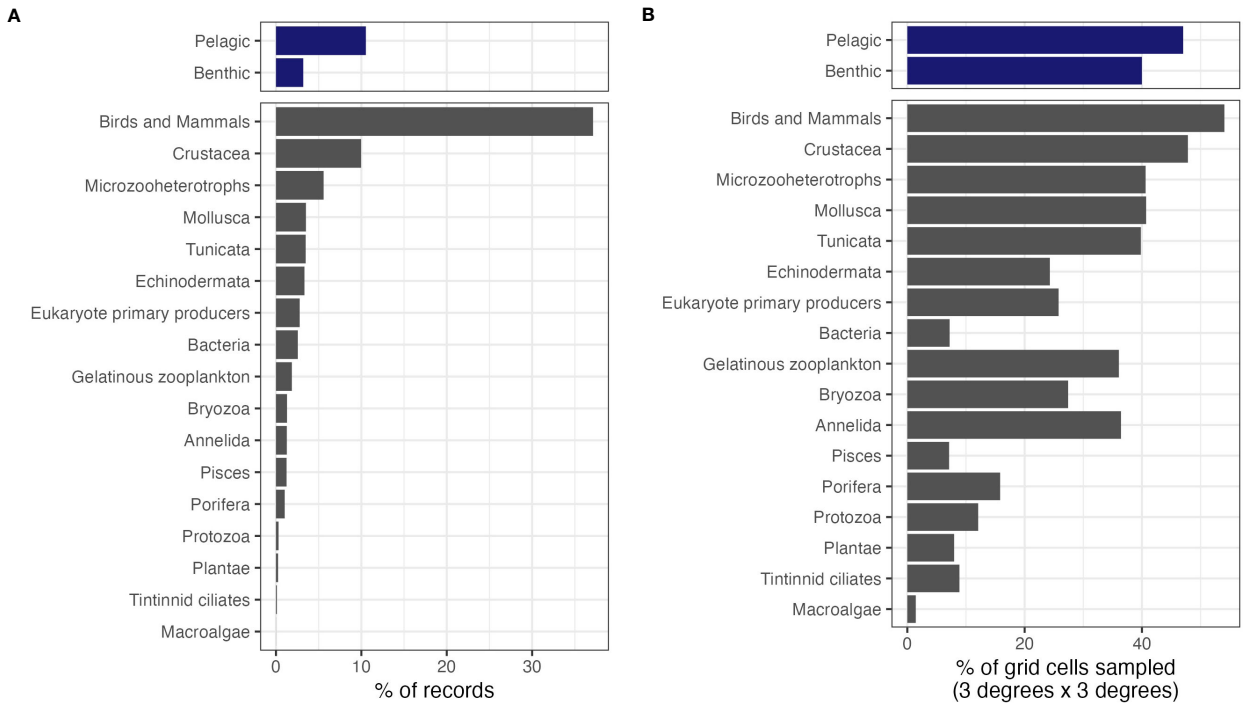

FIGURE 5
Data and spatial coverage for a range of focal groups, for human observations only. **(A)** Percentage of records belonging to each focal group; **(B)** for each focal group, percentage of cells of a 3° x 3° grid covering the MEASO area with at least one record.

key expeditions and joint efforts can be related to periods with increased data collection visible in Figure 2 – e.g., the Discovery Investigations (1924-1951), the Biological Investigations Of Marine Antarctic Systems and Stocks (BIOMASS) survey (1980-1985), the Southern Ocean Continuous Plankton Recorder surveys (SO-CPR, 1991-), or the Census of Antarctic Marine Life (2005-2010) (see Griffiths, 2010 for a more detailed perspective). The rate of data accumulation has also increased drastically until the last decade – probably due to a delay between data collection and publication, and increased interest in certain (until recently under-sampled) taxa, suggesting that the utility of the database could keep increasing. This delay is often caused by the fact that samples need to be collected in the field, transported to a research institute and identified by experts who may only have limited time and resources. Here machine based observation can help close this temporal gap between observation and publication of data. Guidance on how to implement this exists for DNA derived data, GPS data (van der Kolk et al., 2022) and imaging devices (Mortelmans et al., 2019)

4.2 Challenges with using open biodiversity databases for a MEASO

However, the strong biases we highlighted in the data, severely limit their direct and widespread use for a MEASO. First, the data (particularly human observations) were strongly seasonally biased, because of sea-ice and prolonged darkness in the winter, complicating accessibility and work in the Southern Ocean. Second, the data were strongly biased towards certain regularly sampled sectors of the ocean. Most concerning is the spatial bias in human observations, with more data in recurrently visited areas – mostly around research stations of the Antarctic Peninsula and sub-Antarctic Islands, and along routes between other continents and these stations. Note that the environmental and socio-economic drivers of spatial sampling bias differ between the Southern Ocean and other systems [with the importance of, e.g., proximity to settlements or to well-funded research institutions (Meyer et al., 2016; Ramírez et al., 2022)]. But care also needs to be taken with machine observations, because of potentially stronger spatial autocorrelation in data such as animal tracking data (e.g., GPS), potential limitations in the types of taxa that can be observed by machine methods (e.g. tracking tags can only be deployed on certain animals), and other biases that might differ from those affecting human observations. Third, there was a strong imbalance in the representation of different taxa, with birds and mammals largely dominating the database, followed by other widespread and conspicuous taxa [e.g., Crustacea, as in (Ramírez et al., 2022)]. This taxonomic bias is also evolving, with certain taxa becoming comparatively increasingly sampled – e.g., some microbes, due to developing technologies. Finally, missing relevant information – such as limited records of absences, or missing abundance or depth information for many records – can also strongly limit the utility of such data for a MEASO.

4.3 Recommendations for using open biodiversity databases for a MEASO

There are two avenues for enhancing the utility of open biodiversity databases for a MEASO: (1) improvements in the available data, and (2) corrections for the above-mentioned biases by using appropriate models.

As mentioned above, there is a strong need for additional data in under-sampled areas (e.g., in the Pacific), in the winter, and for less charismatic and smaller taxa. This can be achieved both by data collection and data mobilization. Indeed, if we strongly encourage data collection programs to fill in the gaps, we must be conscious of the costs involved in collecting and publishing those data. To complement new collection activities, there are existing data that are not yet in GBIF or OBIS – either because they have not yet been made publicly available, or because they have been submitted to other (often more local) databases not linked to GBIF or OBIS. Encouragements to publish data in public databases linked to GBIF or OBIS (possibly extending existing requirements by funding agencies to make data openly available) should be reinforced, and particularly target those key missing taxa, areas, and season. Some data types, e.g., molecular data or data from autonomous observation devices, are becoming more and more important and allow access to under sampled organisms or areas. However, these data are currently found only in limited amounts in GBIF and OBIS, while geospatial information is often missing in the databases in which they are published (e.g., consistently low percentage of georeferenced data on NCBI GenBank, Gratton et al., 2017). Encouraging linking between databases, following good practices (including efforts to address shortcomings related to taxonomic reliability and lack of standardized metadata vocabulary; Andersson et al., 2021), would enhance their discovery and use in a spatial context. In general, making more data available through GBIF and OBIS, the most widely used biodiversity research data infrastructures in the Southern Ocean would comply with the FAIR principles (Wilkinson et al., 2016), which aim to increase the Findability, Accessibility, Interoperability and Reusability of digital datasets. Indeed, the two portals are recognized as the key repositories by many international instances – e.g. the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES; see https://assets.ctfassets.net/uo17ejk9rkwj/6ddNMnbw7CiSIkusowkS4e/f5fd21478e21f984b6276709eca31b3b/IPBES_memorandum.pdf, https://www.ipbes.net/sites/default/files/factsheet_gbif_growth_in_species_occurrence_records.pdf), the Convention on Biological Diversity (CBD), or the International Panel for Climate Change (IPCC; see Johnson et al., 2023) – and follow common data standards (DwC standards). Finally, encouragement by data aggregators to fill in certain fields that are not currently mandatory (e.g., fields related to abundance or depth) or to also publish absence records (to provide information on the distribution of sampling effort) could increase the utility of the data.

The collection and mobilization of additional data is a process that takes time and money. Modelling techniques cannot replace primary data collection, but might provide complementary approaches that can go some way towards correcting for biases – particularly spatial biases. Modelling is a potential avenue for obtaining improved information and derived products such as species distributions, both in the shorter term as more data is collected but also as a means of maximizing the value of larger data collections. However, there are multiple precautionary steps to correctly apply species distribution models (SDMs) to these data. First, data should be rigorously quality controlled before any application. This involves basic quality control steps as those carried out in this study, but should ideally be more thorough, and more specific to the study taxa, involving experts to remove other potentially erroneous records (e.g., likely misidentifications, errors in coordinates). This was done for example in the Biogeographic Atlas of the Southern Ocean (de Broyer and Koubbi, 2014). Second, caution should be taken when extrapolating results to environmental conditions absent from the data (Guillaumot et al., 2020), which is likely to occur across such large scales considering the large gaps in the data. Additionally, and most importantly, there are a whole range of modelling difficulties that can impact model performance. An obvious example of this is spatial sampling bias (Beck et al., 2014; Pender et al., 2019). Correcting for sampling bias in species distribution models requires some layer representing sampling effort, used for example to guide the selection of background locations (Guillaumot et al., 2021) or as a control variable (e.g., Warton et al., 2013). Contrary to certain cases where sampling completeness can be known (e.g., when there is some reference of species ranges, e.g. Meyer et al., 2015, 2016), in other cases it must be estimated or modelled (e.g., as a function of other spatial variables (Zizka et al., 2021), or based on records of similar species – sampled with similar protocols (Guillaumot et al., 2019)). Other forms of sampling bias can be introduced when combining datasets collected with different survey designs, sampling protocols or gear (e.g. human vs. machine observations, or different net types and sizes), recording methodology (e.g. presence-only, presence-absence, abundance), seasonal timing, or other factors. Some information about these factors may be provided in the aggregated records, for example in the *samplingProtocol* field. However, as noted above, we found this field to be inconsistently populated and with varying terminology. Adoption of stricter requirements in this field might improve this situation. However, bias correction is an active field of research and methods can be non-trivial (Renner et al., 2019; Matthiopoulos et al., 2022). While the Darwin Core standard has the capability to include the detailed metadata that would be necessary to support these kinds of advanced analyses, it is perhaps impractical to expect such a degree of metadata to be consistently populated in large, aggregated data infrastructures like GBIF and OBIS. However, even for such specialized applications, these data infrastructures provide a valuable service by indexing available datasets that might be provided in other, more detailed forms elsewhere, including as primary data from the author's institutional data repository. Data collected specifically for MEASO activities might reasonably be published through multiple data networks (e.g. as in Andrews-Goff et al., 2022), and this can potentially be done using dedicated packages, e.g., *movepub* package (Desmet, 2023) to publish data from Movebank (movebank.org) to GBIF. The above-mentioned modelling difficulties inherent to biased data, along with others that go beyond the scope of this discussion, need to be carefully considered (for more recommendations on applying SDMs to data from global open biodiversity databases, see for example Anderson et al., 2016) and highlight the fact that modelling should not be considered as a replacement for more primary data collection.

In conclusion, although open biodiversity databases offer promises for MEASOs, care must be taken when using these data

because of their inherent spatial, temporal, and taxonomic biases. There is a considerable need for additional data in under-sampled regions, in the winter, and for less conspicuous taxa, as well as reliable abundance or depth data, along with improvements in modelling techniques that can better account for the biases and limitations of Southern Ocean marine biodiversity data and thereby support balanced and informative ecosystem assessments.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: Data are available from OBIS (https://obis.org) and GBIF (http://www.gbif.org, https://doi.org/10.15468/dl.8w7bux). Codes to clean and analyze the data are available at https://github.com/asbonnetlebrun/measo_gap_analysis.

Ethics statement

There are no ethical considerations for this work, which entirely re-uses openly available data collected for other purposes.

Author contributions

A-SB-L analyzed the data and led the writing of the manuscript. MaS, PP, MiS, AV, and BR assisted with analysis. YR-C and AV provided overall supervision. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1150603/full#supplementary-material

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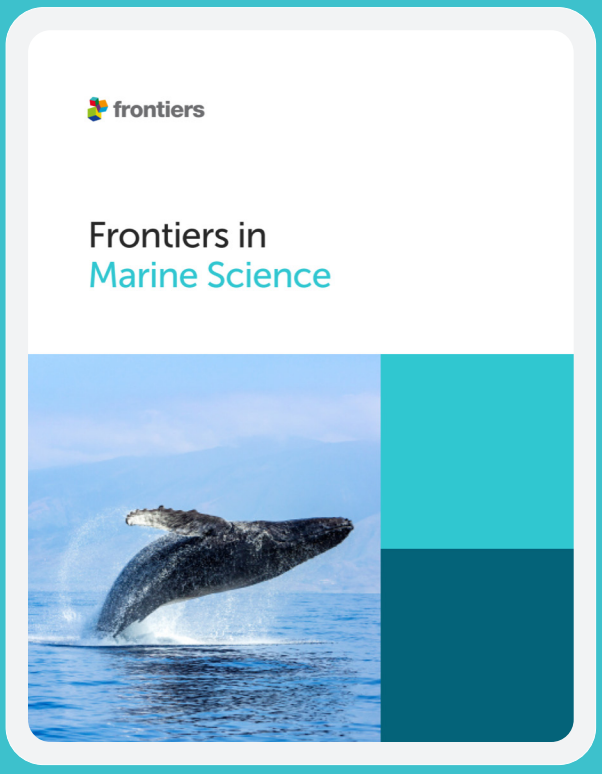

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