MANAGING FOR THE FUTURE: UNDERSTANDING THE RELATIVE ROLES OF CLIMATE AND FISHING ON STRUCTURE AND DYNAMICS OF MARINE ECOSYSTEMS

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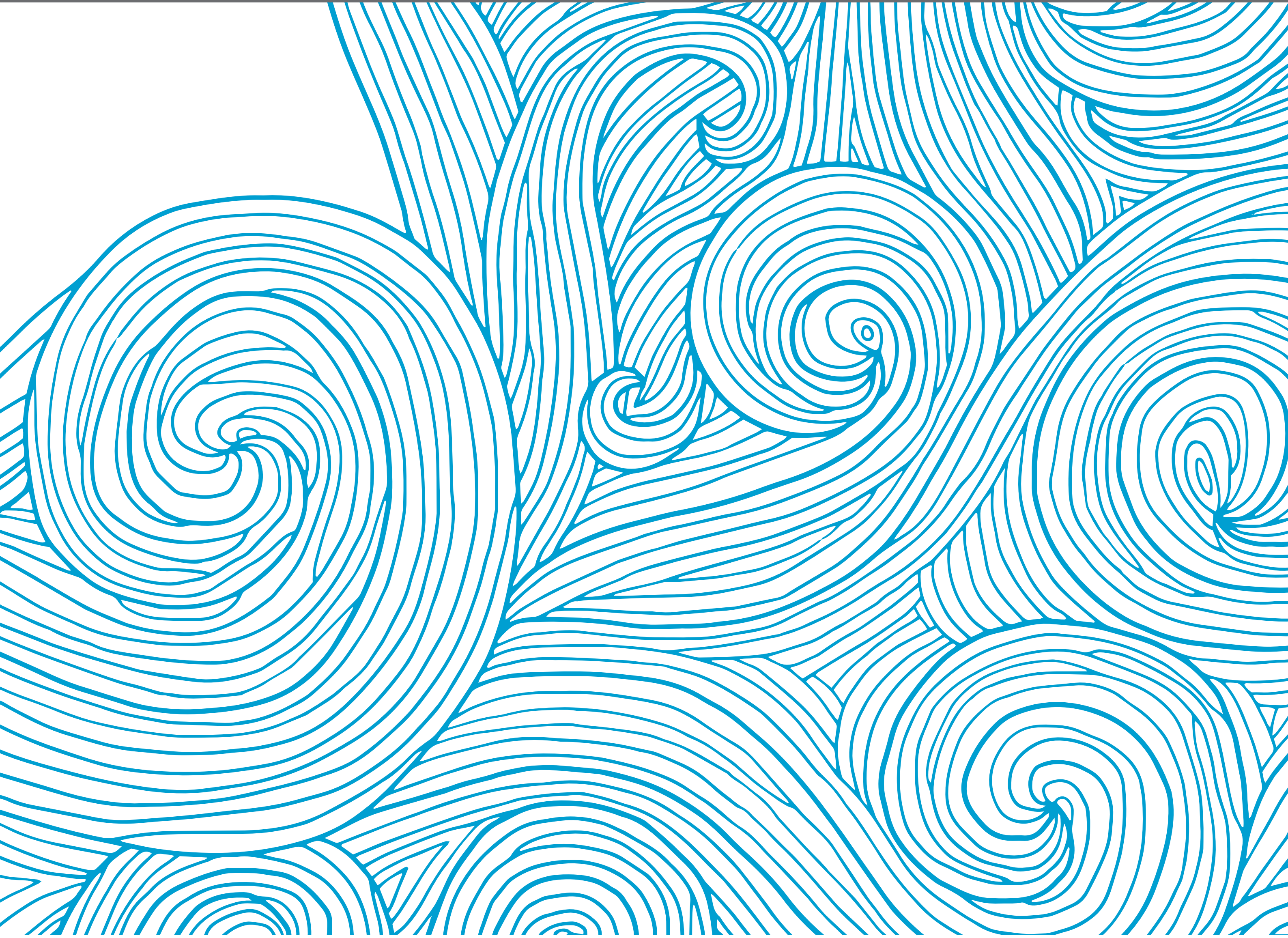
PUBLISHED IN: Frontiers in Marine Science



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ISSN 1664-8714
ISBN 978-2-88971-712-5
DOI 10.3389/978-2-88971-712-5

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Citation: Bundy, A., Coll, M., Koenigstein, S., Niiranen, S., Pennino, M. G., Renaud, P. E., Tam, J. C., Travers-Trolet, M., eds. (2021). Managing for the Future: Understanding the Relative Roles of Climate and Fishing on Structure and Dynamics of Marine Ecosystems. Lausanne: Frontiers Media SA.
doi: 10.3389/978-2-88971-712-5

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frontiers
in Marine Science

EDITORIAL
published: 08 October 2021
doi: 10.3389/fmars.2021.753459

Editorial: Managing for the Future: Challenges and Approaches for Disentangling the Relative Roles of Environmental Change and Fishing in Marine Ecosystems

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Keywords: ecosystem variability, management, multiple stressors, cumulative effects, spatial scale, climate change, fisheries

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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: *04 August 2021*
Accepted: *08 September 2021*
Published: *08 October 2021*

Citation:
Bundy A, Renaud PE, Coll M, Koenigstein S, Niiranen S, Pennino MG, Tam JC and Travers-Trolet M (2021) Editorial: Managing for the Future: Challenges and Approaches for Disentangling the Relative Roles of Environmental Change and Fishing in Marine Ecosystems. Front. Mar. Sci. 8:753459. doi: 10.3389/fmars.2021.753459

Editorial on the Research Topic

Managing for the Future: Challenges and Approaches for Disentangling the Relative Roles of Environmental Change and Fishing in Marine Ecosystems

INTRODUCTION: WHAT LIMITS OUR UNDERSTANDING OF ECOSYSTEM VARIABILITY?

In the Anthropocene era, characterized by significant human impact on Earth's systems, the old saying "*plus ça change, plus c'est la même chose*" does not apply to the natural world. The oceans, long held to be relatively stable physically, biogeochemically and ecologically, are warming, acidifying, and de-oxygenating (Gruber, 2011; IPCC, 2019; Kwiatkowski et al., 2020). In short, marine ecosystems are changing (Doney et al., 2012; Hollowed et al., 2013; Gao et al., 2019), and in some areas of the globe, the change is very rapid (Henson et al., 2017; Johnson and Lyman, 2020). At the same time, human-induced stressors such as fisheries and pollution continue, with sometimes dramatic observed and predicted declines in commercial stocks (e.g., Vasilakopoulos et al., 2014; Lotze et al., 2019). Therefore, in the 21st century, fisheries and ocean managers require science advice that accounts for the cumulative effects of multiple stressors, fisheries removals, human-induced climate change, anthropogenic stressors, environmental variability, and trophic dynamics. Ongoing climate change and increasing pressure to intensify Blue Growth and the Blue Economy highlight the immediacy of the situation. There is strong need to better understand the impacts of these stressors and ecosystem variability so that we may proactively contribute to the management process.

In parts of the world, such as the data rich northern hemisphere, over a century of monitoring marine fisheries and ecosystems has produced a substantial database from which to study ecosystem response to climate change. This has contributed to the development of policies for sustainable management of fisheries and ecosystems, and in some jurisdictions, development of ecosystem-based action plans, such as the Baltic Sea Plan (HELCOM, 2007) and the Norwegian Sea

Integrated Management Plan (Norwegian Ministry of Climate and Environment, 2017). In other parts of the world where there may be lower availability of observational data, shorter time series and fewer resources, the challenge of understanding ecosystem variability and thus managing for the future may be greater.

To date, we have had some success describing variability on multiple scales of space and time, and from the genetic to the ecosystem levels (e.g., Rijnsdorp et al., 2009; Petitgas et al., 2018). Managing for the future to mitigate the impacts of human-induced ecosystem change requires that we incorporate this variability, and its consequences, into management policies. This requires integration of empirical studies, modelling and the development of system indicators that describe relevant variability and change.

This Frontiers research topic (RT) "Managing for the future: understanding variability and the relative roles of environment, climate, fishing, and trophic dynamics in marine ecosystems" explores these questions using theoretical, empirical, and modelling approaches across a variety of spatial scales and levels of description. Here we review the contributions from these studies and identify remaining challenges.

NOVEL APPROACHES YIELD NEW KNOWLEDGE

This RT presents a range of questions, approaches, and challenges to both understand system response to various climate and human-related drivers, and to develop scenarios of response to better inform management of marine ecosystems for the future. The 21 papers address ecosystem, species, and population-level effects over broad spatial and temporal scales using modeling and statistical approaches that represent the state of the art. Effective ecosystem and fisheries management is put into the important context of multiple drivers, especially climate change and fisheries activity. The span of these studies reveals some key commonalities, as well as important sources of variability that must be considered. **Figure 1** summarizes the contributions across 5 dimensions: level of biological organization, spatial scale, research approach, stressor examined, and possibility for application of results to management. The bulk of studies address species or ecosystem levels on broader scales, with a split between empirical and modeling studies. In half the cases the combination of fisheries and climate change was studied, and most authors identified implications for management. In the following section, we highlight some of the main findings across these dimensions and how they address the theme of the RT.

Level of Organization

The level of organization considered in the suite of papers included population, species, ecosystem, and the social system, with most focusing on the species or ecosystem level (**Figure 1**). In general, studies at the ecosystem level used food-web or multi-species modelling approaches (see below) whereas those at the species and population levels used statistical approaches to explore questions such as environmental impacts on life history characteristics.

Processes at the base of ecosystems vary considerably across the year, often tracking seasonal cycles in primary production and phenology of taxa throughout the food web. Lloret-Lloret et al. linked seasonal variation in the spatial distribution of European hake (*Merluccius merluccius*) to ontogenetic changes and trophic ecology using species distribution models (SDMs) and further revealed substantial differences in trophic strategies between seasons and ontogenetic stages. Albo-Puigserver et al. used Generalized Linear and Additive Mixed Models (GLMs/GAMMs) to explore spatial/temporal variation in key life history traits of two small pelagic species (European sardine *Sardina pilchardus* and European anchovy *Engraulis encrasicolus*) from northern and southern regions of the Mediterranean Sea and concluded that the two species respond differently to environmental pressures in the north compared to the south. Véron et al., exploring the life history of European sardine in the Bay of Biscay, concluded that short term variability in length at maturation was "strongly dependent upon individual growth which is likely driven by environmental factors." In the eastern US, black sea bass *Centropristis striata* distribution has shifted north into the Gulf of Maine. McMahan et al. used multivariate analysis and GLMs to explore life-history traits of black sea bass and found that sea bass from the newly expanded range had a less diverse diet, lower condition, and reached maturity at a younger age than fish from the historic region off southern Massachusetts. This result has implications for the stock assessment of this economically valuable species. Using GLMs, GAMs and Random Forest (RF) approaches, Liu et al. investigated Japanese anchovy *Engraulis japonicus* population dynamics and found strong relationships between environmental characteristics (salinity and sea surface temperature—SST) and catch statistics. These relationships were further linked to climatic oscillation indices.

One study directly addressed the critical level of the social system in determining the effects of fishing and climate change on marine ecosystems. Using social network analysis of results from semi-structured interviews, Obregón et al. identified the importance of communication flow among stakeholders, and the imbalance in this communication in managing a small-scale fishery. In this example, the public and academic stakeholders were the least connected. This study highlights structural barriers in the information-sharing network necessary for fully informed management decisions. Heymans et al. in an opinion piece, highlight such communication barriers between stakeholders as a major challenge for the Ocean Decade.

Scale of Study

Most papers in this RT were focused within national boundaries, including bays, shelves and seas, reflecting management mandates that rarely extend past national boundaries. However, large-scale studies are required when managing highly migratory populations/species, or when addressing general questions of broader trajectories of ecosystem response to changing pressures. Cleeland et al. used spatially resolved demographic modelling to isolate the effects of climate change, oceanography, fisheries effort, and habitat degradation on the demographic rates of multiple threatened albatross species. Results illustrated the need to integrate fisheries, oceanographic, and also

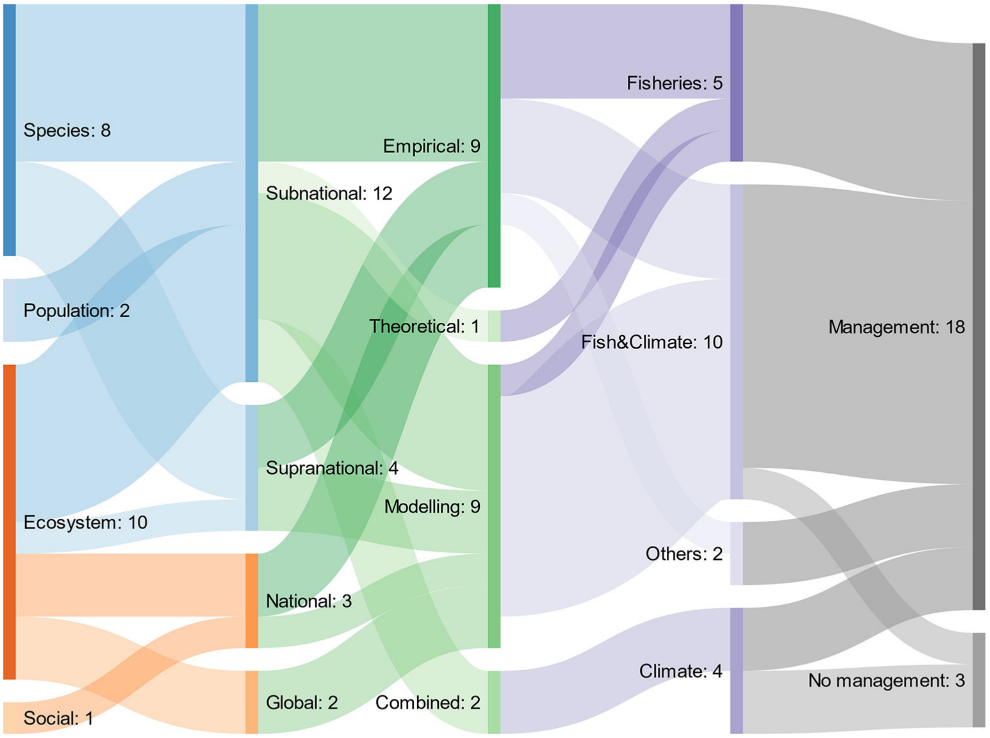

FIGURE 1 | Sankey diagram summarizing the articles contributed to this research topic (source: http://sankeymatic.com/build/). Distribution of articles across (from left to right) level of organization, spatial scale, research approach, type of stressor studied, and whether there was an application to management discussed. Numbers represent the number of papers in each category.

terrestrial processes when assessing demographic variability and formulating the appropriate management response. Considering such a wide range of processes over broad scales and multiple ecosystems clearly shows the complexity of managing species with wide ecological ranges and habitat use. Coll et al. developed a global ecological model coupling climate, ocean conditions, and food-web dynamics (EcoOcean) which was used to assess the individual and combined effects of climate and fisheries in the global ocean. They concluded that fisheries overall exacerbates the negative impact of climate change, and weakens the positive consequences. Such "whole-ecosystem" models and their development are key steps toward an integrated approach to projecting ecosystem variability and developing plausible ocean-based solutions to mitigate and adapt to climate change.

Selection of spatial scales within which to study migratory species is complicated by residency patterns, and the exposure to different environmental and human-induced pressures, including climate change effects, encountered during migration. Papers by Lloret-Lloret et al. and Albo-Puigserver et al. (discussed above) demonstrate that temporal and spatial patterns of variability are often confounded, representing a challenge to management.

Research Approach

Approximately half the studies used one or more models to produce their results and half used empirical data, with two papers combining approaches (**Figure 1**). In this section we focus on the insights derived from novel modeling approaches.

The importance of spatial scale and variability in space was underscored by the use of spatial modelling approaches to address key ecological questions. Shannon et al., in an update of their temporal EwE model of the Benguela upwelling system, highlighted the need to consider various environmentally-driven changes, including upwelling effects on phytoplankton availability to zooplankton and small pelagic fish and geographic shifts in sardine distribution, in addition to trophic interactions and fishing effects. It concluded that spatially explicit ecosystem models would provide further mechanistic understanding of variability in the ecosystem. The spatially-explicit version of the Ecopath with Ecosim (EwE) marine ecosystem model, Ecospace, was used by Hernvann et al. to identify the relative importance of drivers of change in determining the structure and functioning of the Celtic Sea ecosystem. They found that integrating a spatial perspective helped explain the changing spatial distributions of commercial fish species, and the strong role of bottom-up processes (primary productivity) in the system. Fu et al. used the OSMOSE (Object-oriented Simulator of Marine ecOSystEms) model to understand how stressors interactively and cumulatively affect commercially important fish species. They simulated favorable and unfavorable conditions based on varying food supply at the base of the food web and different levels of fishing pressure, and found synergistic effects of the two drivers, with more pronounced negative effects. Travers-Trolet et al. used OSMOSE to assess the performance of fisheries management tools under climate change. They explored the management-relevant response of two main biological reference points, Maximum Sustainable Yield (MSY) and fishing mortality at MSY (FMSY), to two contrasting climate change scenarios, and showed that both MSY and FMSY of overexploited cold-water species were likely to decline with climate warming.

In a creative use of bio-energetic models, Koen-Alonso et al. "transplanted" cod from the Barents Sea to the Newfoundland-Labrador model and vice-versa by switching estimated key parameters between models and then following spatial dynamics in cod stocks. They concluded that the stocks were biologically similar and that differences in their trajectories were due to lack of prey (capelin) in Newfoundland. In a more general sense, this highlights a message in the RT: the need to integrate food-web perspectives into dynamic models that integrate climate and other drivers.

Ensemble modeling was advocated by Pethybridge et al., who demonstrated that this is a robust means of exploring ecosystem responses to climate change in the face of uncertainty about the structure, function, and change in marine ecosystems. The ensemble approach enabled them to include confidence intervals in their results and account for uncertainty in model structure. Their results indicate that demersal systems appear to be more susceptible to climate change than pelagic systems. This perspective is central in the work of Horn et al., who reviewed the modeling literature on climate change effects on coastal ecosystems. They conclude that models that couple deterministic ocean models and food-web models will be essential tools for providing scenarios to guide ecosystem-based management.

Stressors and Multiple-Stressor Effects

Analysis of cumulative effects, using both modelling and statistical approaches, was a common theme in this RT. Stressors examined mainly included fishing and climate change, and results clearly demonstrate the negative cumulative effects of both (e.g., Coll et al., Fu et al., Pennino et al., Travers-Trolet et al.). Hernvann et al., (described above) for example, demonstrated the predominance of fisheries impacts over climate change. Subramaniam et al. using EwE, found the opposite: climate change effects much greater than those from fishing in the Southern Ocean region of the Kerguelan Plateau. Here the authors suggest current management strategies are sustainable, but fishing effort here is relatively low to other areas studied, including the Celtic and Yellow Seas. Stenson et al. investigated three harp seal populations in the North Atlantic and identified an interactive effect between climate conditions and hunting pressure. Importantly, trends and responses among the three populations varied, with important consequences for management now and in the future. These results complement the studies of Fu et al. and Coll et al. who also found synergistic effects between fishing and climate change.

The main pathway explored for climate impacts was through bottom-up action. This was exemplified by Friedland et al. for the northeast coast of the US, one of the most rapidly warming marine ecosystems. Using time series analyses and GLMs, these authors explored the changes in SST, salinity, and chlorophyll concentration (chl) in 5 areas and their impacts on higher trophic levels. They showed that a decrease in chl and a shift to smaller species of phytoplankton has been observed with warming temperatures. Declines in fish and benthic invertebrate populations were linked to lower chl or increased temperature. Whereas, it is logical that climate effects through potential resource availability (chl) and energetics (SST) should be a dominant driver of ecosystem variability, it is interesting to note that Shannon et al.'s EwE study from Benguela indicated specific climate-sensitive trophic links as being decisive in how the ecosystem responds to climate change.

In a study of the robustness and sensitivity of fish community structure indicators, Li et al. investigated the response of 22 indicators of fish community structure to 3 types of pressures, fishing, large-scale climate change, and regional environmental variables in the Yellow Sea. Using INDperform (Otto et al., 2018), they showed that most indicators were more sensitive to fishing than climate change, with some notable exceptions (e.g., temperature of catch, functional evenness of thermally defined fish groups).

Management Applications

Over 80% of the studies in this RT indicate that their research results are relevant to management. In the long view, this is certainly true, but as Obregón et al. pointed out, the academic community is one of the least interactive stakeholders in the decision-making process. Indeed, this is a well-known disconnect in the process of policy development (Stephenson et al., 2021). We identify five results from studies in this RT that can likely be transferred directly to managers for integration into policy. Fu et al., Cleeland et al. and Travers-Trolet et al. provide specific population and demographic parameters and fisheries indicators that can be integrated into management strategies. As just mentioned, Shannon et al. identified sensitive trophic links that could be monitoring or mitigation targets. Finally, Pennino et al. used the results from their RF analysis of environmental drivers of European sardines and anchovies in the Northwestern Mediterranean to test the past and future impact of different climate change scenarios using species distribution models. They identified specific locations that could serve as future refuges for these species in the face of climate change. Clearly, these areas can become immediate targets for conservation/protection to secure the species for the future within a regional context of overexploitation. Coll et al.'s global modelling results are part of a larger ensemble of model projections initiative (Tittensor et al., 2018) that informs global scientific initiatives within the Intergovernmental Panel on Climate Change (IPCC) context to motivate management action to halt climate change (Lotze et al., 2019).

Other studies have produced relevant tools and findings for management, but work remains if these results are to be immediately useful in development of management, mitigation, and adaptation policies.

MAIN CHALLENGES

The studies outlined in this RT demonstrate excellent, innovative science with the potential of being used by managers. However, challenges remain and we must continue to work to address knowledge gaps and needs for methodological improvements and developments. Below we include a short, non-prioritized and non-exhaustive discussion of the challenges in incorporating marine ecosystem variability into assessment and management.

Tractability of Multiple Stressors

At any time, an ecosystem is affected by multiple climate-related, human-induced and natural drivers, each with direct and indirect pathways of action on target response variables. This makes interpreting impacts of specific stressors, including such multi-faceted stressors as climate change, challenging. Some recent approaches to explore cumulative effects that were not covered in this RT include statistical and dynamical modeling, such as path analysis (Tenenhaus et al., 2005; Fu et al., 2015; Selim et al., 2016), empirical dynamic modelling (Perretti et al., 2013; Munch et al., 2020), ecosystem dynamic programming (Brias and Munch, 2021) and Gaussian graphical models (Liang et al., 2021). Existing knowledge of system dynamics gained from decades of scientific study provides a solid baseline from which to explore the effects of multiple stressors, but the challenge increases as we enter a period without historical (or prehistorical) precedent. Experimental studies and mathematical simulations can shed light onto the process behind the observed pattern, and determining interactions of multiple stressors can be simplified through reduced factorial designs (Boyd et al., 2018).

Studying Processes Over Relevant Spatial and Temporal Scales

Climate change occurs over decadal and multi-decadal scales, time scales beyond most empirical studies. It also changes baselines for comparison and control. Long time-series exist and are often used in empirical studies to test for effects of different drivers on ecosystem variability; and these offer interesting insights. However, observational data on ecosystem drivers (e.g., fishing effort, pollution, pH) are not always collected in comparable ways over long temporal scales, making analysis of its effects challenging. Migrations and species range extensions can complicate evaluating processes taking place in a single region as these organisms are affected by changes elsewhere. Understanding these limitations/challenges when designing studies and interpreting results is critical.

Model Development Needs and Quantification Uncertainty

Statistical and mechanistic modeling techniques are probably the best options for integrating climate, human impacts, environmental variability, and ecosystem interaction in a meaningful way. As the studies above point out, increased use of spatially-explicit models, multiple spatio-temporal scales and coupling of ecosystem and trophic models are key elements for explaining ecosystem variability that need further development. However, current challenges include validation and fitting models to data, which is especially problematic for more complex models that require both more high-quality data for validation and supercomputer access. Quantifying uncertainty in models is also key and includes measurement uncertainty, parameter uncertainty and structural uncertainty (Payne et al., 2016). Methods to account for measurement and parameter uncertainty include Monte Carlo analysis and Bayesian approaches (Dilks et al., 1992; Spiegelhalter and Best, 2003), and ensemble modelling is one approach to account for structural uncertainty (Pethyridge et al.; Lotze et al., 2019).

On smaller spatial scales, relevant downscaling methods and incorporation of local factors that can have significant structuring impacts (e.g., variation in flow from small rivers) are important to consider. At some levels of organization, seasonal data are needed to fully understand the (varying) links within the ecosystem, and thus their sensitivity to change (Lloret-Lloret et al.).

In their opinion piece, Heymans et al. point out that we also need to enhance research and modeling impact through capacity building and co-design of models with different forms of knowledge and working "together to achieve the ensemble of well-parameterized, calibrated and validated ecosystem models needed to address the questions asked of us in the Ocean Decade."

Integrating Social Dimensions

Humans are part of what has been termed a socio-ecological system (SES, Berkes et al., 2000; Colding and Barthel, 2019). SES are complex, integrated systems consisting broadly of humans (social) and ecological (biophysical) subsystems, between which there exist two-way feedback relationships. This RT did not explicitly discuss SES, but human activity affects and is affected by ecosystem structure and function, and variability in these parameters. Climate change produces yet another nested network of impacts and effects that are embedded in decisions about resource extraction, protection of natural systems, and adaptation strategies for sustainable activities. Environmental management is a socio-political decision, where academic science may be detached from decision making processes. Thus, co-generation of goals and strategies of scientific study with multiple stakeholders is urgently needed.

Communication of Results to Management

It is a well-acknowledged point of frustration for empiricists and ecosystem modelers that scientific results are often not directly integrated into management plans. In this RT, Heymans et al. challenged the marine ecosystem modelling community to address how we: (i) enable ocean managers and decision-makers to use our science, (ii) communicate our science, and most importantly (iii) ensure co-design of our science to achieve sustainable development. Five papers were identified to contain very specific advice, ready to integrate into policy (see above). These examples can offer a roadmap for successfully bridging the gap between science and management. Concrete targets for protection or monitoring and use of accepted, robust, and easily defined indicators make implementation of advice more straightforward. Dialogue between scientists and managers defining specific study questions and contexts for presenting findings can also help.

CONCLUSIONS

The studies presented in this RT provide new knowledge and perspectives on impacts of fisheries and climate change on marine ecosystems and species. In addition, they demonstrate use of new methods and combinations of methods, and offer complementary results from different systems to investigate generalities in findings. The importance of spatial and temporal scale is woven through many of the papers and must be integrated to address important management questions. However, translating science into advice for management remains a frontier that was not fully explored here. The nature and type of science advice required for management will differ across issues and spatial/jurisdictional scales. For the former, it is perhaps more straightforward to provide advice when dealing with single species issues rather than ecosystem concerns. Similarly, science advice is required at multiple scales (local, regional, national international), and while it may be most straightforward at the local scale, stated goals of ecosystem-based management, which are context specific, require consideration of multiple species and scales. Regardless, the current climate crisis creates a pressing need for better communication of research findings to end-users.

AUTHOR CONTRIBUTIONS

AB and PR conceived the idea for the RT and led the writing of the editorial. MC created **Figure 1**. All authors reviewed manuscripts in the RT and contributed ideas and text.

ACKNOWLEDGMENTS

This RT originated from a session led by the CoArc project at the IMBeR 2019 Open Science Conference, Future Oceans2, held in Brest, France on 17-21 June 2019. This is a contribution of the CoArc project, which received funding from the Norwegian Foreign Ministry and its Arctic 2030 program. PR acknowledges support from the Research Council of Norway through 'The Nansen Legacy project' (RCN no. 276730). MC acknowledges funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 817578 (TRIATLAS project) and the Institutional Support of the 'Severo Ochoa Centre of Excellence' accreditation (CEX2019-000928-S) to the Institute of Marine Science (ICM-CSIC; Barcelona, Spain).

REFERENCES

Berkes, F., Folke, C., and Colding, J., (Eds.). (2000). *Linking Social and Ecological Systems: Management Practices and Social Mechanisms for Building Resilience*. Cambridge: Cambridge University Press.

Boyd, P. W., Collins, S., Dupont, S., Fabricius, K., Gattuso, J. P., Havenhand, J., et al. (2018). Experimental strategies to assess the biological ramifications of multiple drivers of global ocean change—a review. *Glob. Chang. Biol.* 24, 2239–2261. doi: 10.1111/gcb.14102

Brias, A., and Munch, S. B. (2021). Ecosystem based multi-species management using Empirical Dynamic Programming. *Ecol. Model.* 441:109423. doi: 10.1016/j.ecolmodel.2020.109423

Colding, J., and S. Barthel. (2019). Exploring the social-ecological systems discourse 20 years later. *Ecol. Soc*. 24:2. doi: 10.5751/ES-10598-240102

Dilks, D. W., Canale, R. P., and Meier, P. G. (1992). Development of Bayesian Monte Carlo techniques for water quality model uncertainty. *Ecol. Model.* 62, 149–162. doi: 10.1016/0304-3800(92)90087-U

Doney, S. C., Ruckelshaus, M., Emmett Duffy, J., Barry, J. P., Chan, F., English, C. A., et al. (2012). Climate change impacts on marine ecosystems. *Annu. Rev. Mar. Sci.* 4, 11–37. doi: 10.1146/annurev-marine-041911-111611

Fu, C., Large, S., Knight, B., Richardson, A. J., Bundy, A., Reygondeau, G., et al. (2015). Relationships among fisheries exploitation, environmental conditions, and ecological indicators across a series of marine ecosystems. *J. Marine Syst.* 148, 101–111. doi: 10.1016/j.jmarsys.2015.01.004

Gao, K., Beardall, J., Häder, D. P., Hall-Spencer, J. M., Gao, G., and Hutchins, D. A. (2019). Effects of ocean acidification on marine photosynthetic organisms under the concurrent influences of warming, UV radiation, and deoxygenation. *Front. Marine Sci.* 6:322. doi: 10.3389/fmars.2019.00322

Gruber, N. (2011). Warming up, turning sour, losing breath: ocean biogeochemistry under global change. *Philos. Transac. R. Soc. A* 369, 1980–1996. doi: 10.1098/rsta.2011.0003

HELCOM (2007). "HELCOM baltic sea action plan," in *Proceedings of the Adopted by the HELCOM Ministerial Meeting* (Krakow).

Henson, S. A., Beaulieu, C., Ilyina, T., John, J. G., Long, M., Séférian, R., et al. (2017). Rapid emergence of climate change in environmental drivers of marine ecosystems. *Nat. Commun.* 8:14682. doi: 10.1038/ncomms14682

Hollowed, A. B., Barange, M., Beamish, R. J., Brander, K., Cochrane, K., Drinkwater, K., et al. (2013). Projected impacts of climate change on marine fish and fisheries. *ICES J. Mar. Sci*. 70, 1023–1037. doi: 10.1093/icesjms/fst081

IPCC (2019). "IPCC special report on the ocean and cryosphere in a changing climate," in *Working Group II Technical Support Unit Intergovernmental Panel on Climate Change*, eds H.- O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, et al. Available online at: https://www.ipcc.ch/site/~assets/uploads/sites/3/2019/12/SROCC_FullReport_FINAL.pdf

Johnson, G. C., and Lyman, J. M. (2020). Warming trends increasingly dominate global ocean. *Nat. Clim. Change* 10, 757–761. doi: 10.1038/s41558-020-0822-0

Kwiatkowski, L., Torres, O., Bopp, L., Aumont, O., Chamberlain, M., Christian, J. R., et al. (2020). Twenty-first century ocean warming, acidification, deoxygenation, and upper-ocean nutrient and primary production decline from CMIP6 model projections. *Biogeosciences* 17, 3439–3470. doi: 10.5194/bg-17-3439-2020

Liang, D., Nesslage, G. M., Wilberg, M. J., and Miller, T. J. (2021). Ranking ecosystem impacts on Chesapeake Bay blue crab (*Callinectes sapidus*) using empirical Gaussian Graphical Models. *Can. J. Fish. Aquat. Sci.* 78, 245–254. doi: 10.1139/cjfas-2019-0439

Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. L., Galbraith, E. D., et al. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc. Natl. Acad. Sci. U.S.A.* 116, 12907–12912.

Munch, S. B., Brias, A., Sugihara, G., and Rogers, T. L. (2020). Frequently asked questions about nonlinear dynamics and empirical dynamic modelling. *ICES J. Marine Sci.* 77, 1463–1479. doi: 10.1093/icesjms/fsz209

Norwegian Ministry of Climate and Environment. (2017). *Update of the integrated management plan for the Norwegian Sea*. Oslo: St. Meld. 35. Norwegian Parliament.

Otto, S. A., Kadin, M., Casini, M., Torres, M. A., and Blenckner, T. (2018). A quantitative framework for selecting and validating food web indicators. *Ecol. Indic*. 84, 619–631. doi: 10.1016/j.ecolind.2017.05.045

Payne, M. R., Barange, M., Cheung, W. W., MacKenzie, B. R., Batchelder, H. P., Cormon, X., et al. (2016). Uncertainties in projecting climate-change impacts in marine ecosystems. *ICES J. Marine Sci.* 73, 1272–1282. doi: 10.1093/icesjms/fsv231

Perretti, C. T., Munch, S. B., and Sugihara, G. (2013). Model-free forecasting outperforms the correct mechanistic model for simulated and experimental data. *Proc. Natl. Acad. Sci. U.S.A.* 110, 5253–5257. doi: 10.1073/pnas.1216076110

Petitgas, P., Huret, M., Dupuy, C., Spitz, J., Authier, M., Romagnan, J. B., et al. (2018). Ecosystem spatial structure revealed by integrated survey data. *Prog. Oceanogr.* 166, 189–198. doi: 10.1016/j.pocean.2017.09.012

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., and Pinnegar, J. K. (2009). Resolving the effect of climate change on fish populations. *ICES J. Marine Sci.* 66, 1570–1583. doi: 10.1093/icesjms/fsp056

Selim, S. A., Blanchard, J. L., Bedford, J., and Webb, T. J. (2016). Direct and indirect effects of climate and fishing on changes in coastal ecosystem services: a historical perspective from the North Sea. *Reg. Environ. Change* 16, 341–351. doi: 10.1007/s10113-014-0635-7

Spiegelhalter, D. J., and Best, N. G. (2003). Bayesian approaches to multiple sources of evidence and uncertainty in complex cost-effectiveness modelling. *Stat. Med.* 22, 3687–3709. doi: 10.1002/sim.1586

Stephenson, R. L., Hobday, A. J., Allison, E. H., Armitage, D., Brooks, K., Bundy, A., et al. (2021). The quilt of sustainable ocean governance: Patterns for practitioners. *Front. Marine Sci.* 8:120. doi: 10.3389/fmars.2021.630547

Tenenhaus, M., Vinzi, V. E., Chatelin, Y. M., and Lauro, C. (2005). PLS path modeling. *Comput. Stat. Data Anal.* 48, 159–205. doi: 10.1016/j.csda.2004.03.005

Tittensor, D. P., Eddy, T. D., Lotze, H. K., Galbraith, E. D., Cheung, W., Barange, M., et al. (2018). A protocol for the intercomparison of marine fishery and ecosystem models: Fish-MIP v1.0. *Geosci. Model Dev*. 11, 1421–1442. doi: 10.5194/gmd-2017-209-supplement

Vasilakopoulos, P., Maravelias, C. D., and Tserpes, G. (2014). The alarming decline of Mediterranean fish stocks. *Curr. Biol.* 24, 1643–1648. doi: 10.1016/j.cub.2014.05.070

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 24 July 2020
doi: 10.3389/fmars.2020.00622

Current and Future Influence of Environmental Factors on Small Pelagic Fish Distributions in the Northwestern Mediterranean Sea

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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: *27 May 2020*
Accepted: *07 July 2020*
Published: *24 July 2020*

Citation:
Pennino MG, Coll M, Albo-Puigserver M, Fernández-Corredor E, Steenbeek J, Giráldez A, González M, Esteban A and Bellido JM (2020) Current and Future Influence of Environmental Factors on Small Pelagic Fish Distributions in the Northwestern Mediterranean Sea. Front. Mar. Sci. 7:622. doi: 10.3389/fmars.2020.00622

In the Northwestern Mediterranean Sea, the European sardine (*Sardina pilchardus*) and the European anchovy (*Engraulis encrasicolus*) are the most important small pelagic fish in terms of biomass and commercial interest. During the last years, these species have experimented changes in their abundance and biomass trends in the Northwestern Mediterranean Sea, in addition to changes in growth, reproduction and body condition. These species are particularly sensitive to environmental fluctuations with possible cascading effects as they play a key role in connecting the lower and upper trophic levels of marine food webs. It is therefore essential to understand the factors that most profoundly affect sardine and anchovy dynamics. This study used a two-step approach to understand how the environment influences the adult stages of these species in the Northwestern Mediterranean Sea. First, we explored the effects of environmental change over time using Random Forests and available datasets of species occurrence, abundance, biomass and landings. We then applied species distribution models to test the impact of the extreme pessimistic and optimistic Intergovernmental Panel on Climate Change (IPCC) pathway scenarios, and to identify possible climate refuges: areas where these species may be able to persist under future environmental change. Findings from the temporal modeling showed mixed effects between environmental variables and for anchovy and sardine datasets. Future pathway projections highlight that both anchovy and sardine will undergo a reduction in their spatial distributions due to future climate conditions. The future climate refuges are the waters around the Rhone River (France) and the Ebro River (Spain) for both species. This study also highlights important knowledge gaps in our understanding of the dynamics of small pelagic fish in the region, which is needed to progress towards an ecosystem approach to fisheries management.

Keywords: climate changes, climate refuges, futures scenarios, NW Mediterranean, small pelagic fishes, species distribution model

INTRODUCTION

Small pelagic fish species (SPF) are sensitive to environmental fluctuations, which can be amplified from climate variability, with cascading effects up and down the food web, due to their high biomass at intermediate levels and their potential wasp-waist control of the food web (Cury and Roy, 1989; Cury et al., 2000; Bakun, 2006; Checkley et al., 2009; Fauchald et al., 2011). In the Mediterranean Sea, SPF species such as European sardine (*Sardina pilchardus*, Walbaum, 1792; hereafter sardine), and European anchovy (*Engraulis encrasicolus*, Linnaeus, 1758; hereafter anchovy) have been shown to be key elements in the transfer of energy from lower to higher trophic level organisms (Palomera et al., 2007; Coll et al., 2008; Albo-Puigserver et al., 2016). Historically, they showed an important bulk of biomass and production and played a key ecosystem role due to a strong coupling between the pelagic and the demersal environments (Coll et al., 2008), acting as important prey of pelagic predators such as tunas (Navarro et al., 2017), cetaceans (Gómez-Campos et al., 2011) and pelagic seabirds (Navarro et al., 2009; Cury et al., 2011), and of demersal predators (Recasens et al., 1998; Mellon-Duval et al., 2017; Saraux et al., 2019).

Recent changes in SPF have been observed in the Mediterranean Sea, in parallel with an overall increase of fishing effort, changes in environmental variability and a decline of primary productivity (Piroddi et al., 2017). Specifically, in the Northwestern Mediterranean Sea we have observed declines in biomass and landings of anchovy and, especially important, of sardine in parallel with a spatial expansion of round sardinella (Sabatés et al., 2006; Palomera et al., 2007; Van Beveren et al.,

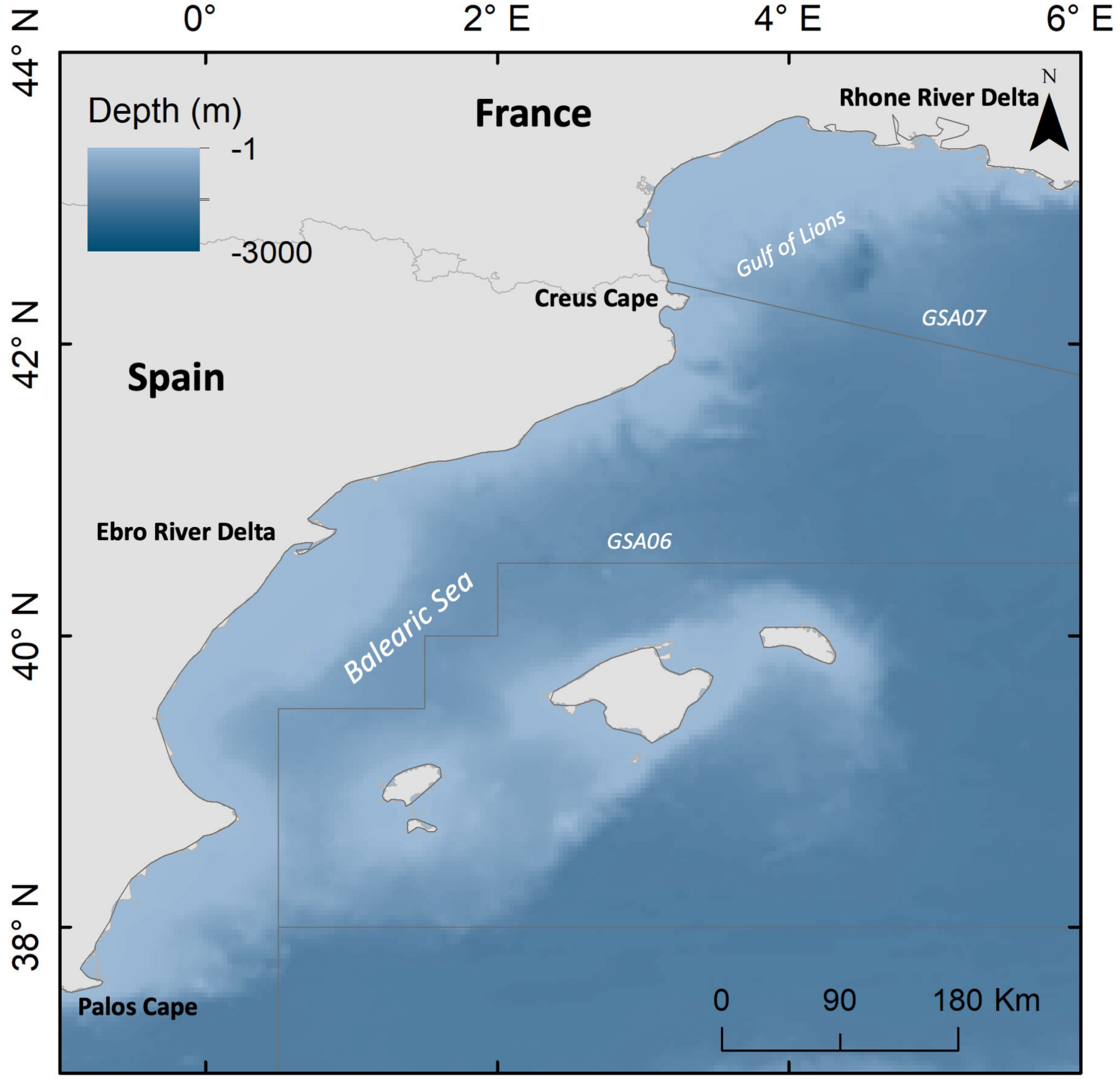

FIGURE 1 | Map of the study area.

2016). Changes in anchovy and sardine landings and abundances have also been related with increases in fishing impact and recent high rates of exploitation (Palomera et al., 2007; Scientific Technical and Economic Committee for Fisheries [STECF], 2016; FAO, 2018; Ramirez et al., 2018).

These changes have been also linked to environmental shifts that can directly influence annual recruitment, growth and the general condition of organisms, for which several hypotheses have been formulated (e.g., Palomera et al., 2007; Martín et al., 2008; Van Beveren et al., 2014; Brosset et al., 2017; Coll et al., 2019). For example, the impact of higher sea surface temperature (SST) could negatively affect some species, such as sardine that prefers cold waters to reproduce, and positively others, such as round sardinella, that prefers warm waters to reproduce (Sabatés et al., 2006; Palomera et al., 2007; Maynou et al., 2014).

Within this context, and in order to provide an exhaustive insight into the environmental influence on SPF, we developed a two-step approach to (1) explore the effect of the environment from a historical temporal perspective and to (2) spatially predict the distribution of SPF species under different future environmental scenarios to identify possible climate refuges.

The temporal perspective was explored applying Random Forests (RFs) (Breiman, 2001) to different historical datasets regarding presence/absence, abundance, biomass, and landings of (mostly adult) sardine and anchovy, with the aim to test the impact of different environmental parameters and temporal lags.

We based the spatial perspective on the Species Distribution Models (SDM) framework. The various algorithms within this framework link spatial species occurrences to environmental variables with the aim to predict if species are likely to occur in unsampled locations or future time periods (Martínez-Minaya et al., 2018). We used residuals autocovariate Boosted Regression Trees (RAC-BRT) (Elith et al., 2008; Crase et al., 2012; Escalle et al., 2016; Barcala et al., 2020) to test different environmental future pathway scenarios as defined by the Intergovernmental Panel on Climate Change (IPCC, 2013) to identify possible *climate refuges*. The term *climate refuges* refers to areas where species retreat to, and can persist, under increasing environmental stress with the potential to re-expand once the stress abates (Bennett and Provan, 2008; Keppel et al., 2012). Such areas can act as sources of re-colonization when environmental conditions improve and often have long-lasting imprints on species distributions. We argue that identifying *climate refuges* can provide essential knowledge to improve the SPF management by identifying key areas for conservation of these species and potential for re-expansions both today and in the future (Monsarrat et al., 2019).

MATERIALS AND METHODS

Study Area and Species Data

This study covers Geographical Sub-Areas (GSAs) 06 and 07 of the Northwestern Mediterranean Sea, located, respectively, in Northern Spain (between Cabo de Creus and Cabo de Palos), and the Gulf of Lions (France) (**Figure 1**). This is a highly productive area within the Mediterranean Sea due to the presence of two large rives (Rhone and Ebro) and a counter-clock oceanographic circulation that brings nutrients to the upper slope and shelf areas (Estrada, 1996; Bosc et al., 2004).

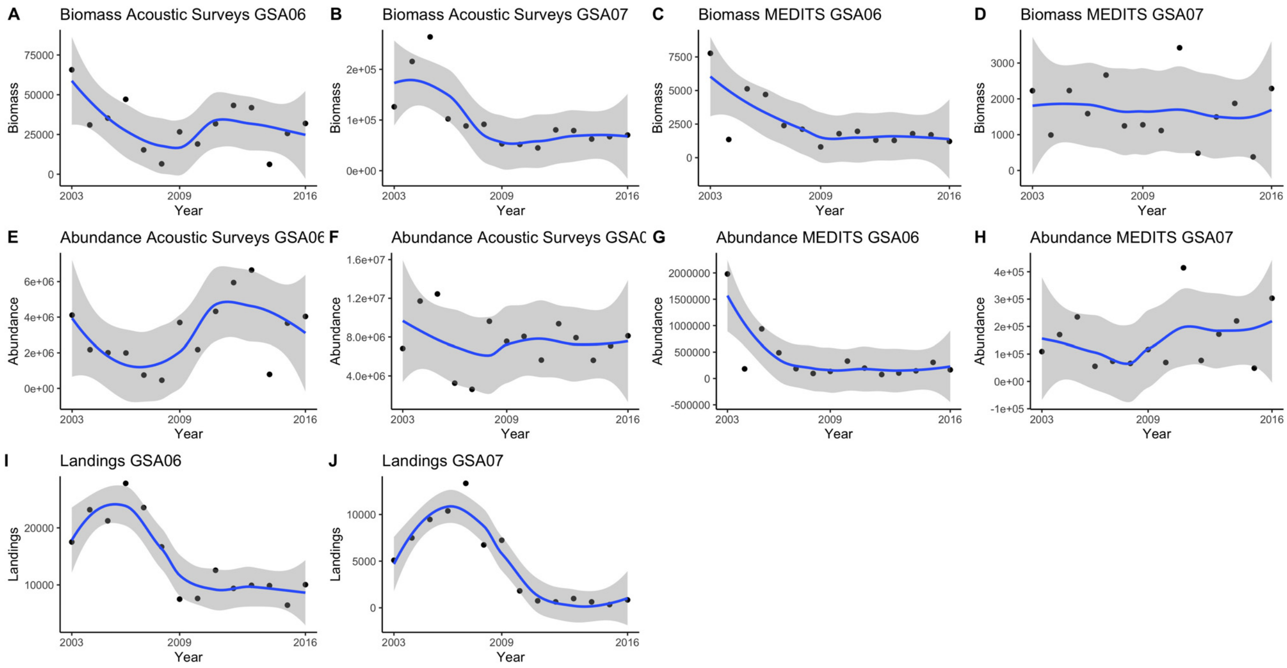

FIGURE 2 | Biomass **(A–D)**, abundance **(E–H)**, and landings **(I,J)** temporal trends from acoustic (ECOMED, PELMED, MEDIAS) and demersal (MEDITS) surveys and official countries landings for European sardine (*Sardina pilchardus*) in the Geographical Sub-Area 06 and 07 from 2003 to 2016.

Data of occurrence (presence/absence), biomass (metric tons) and abundance (number of individuals) of anchovy and sardine from 2003 to 2016 were retrieved from different sources such as EU-funded MEDIterranean Trawl Survey (MEDITS), EU-funded MEDIterranean International Acoustic Survey (MEDIAS), the Spanish Acoustic Survey "Eco-MEDiterranean" ECOMED and the French Acoustic Survey "Pelagiques MeDiterraneìe" PELMED.

Regarding MEDITS data (Bertrand et al., 2002), species data were collected during demersal trawl surveys carried out during daytime from spring to summer (April to September depending on the country). The months in which the MEDITS survey is carried out (June–July) coincide with the recruitment of sardine, and the spawning activity in anchovy (Palomera et al., 2007). The MEDITS project uses a stratified sampling design based on five depth ranges: 10–50, 51–100, 101–200, 201–500, and 501–700 meters, and GSAs. The surveys in GSA06 were performed by the Spanish Oceanographic Institute (Instituto Español de Oceanografía, IEO), while the French Research Institute for Exploration of the Sea (Institut Français de Recherche pour l'Exploitation de la Mer, IFREMER) conducted the surveys in GSA07.

Pelagic acoustic surveys sampling design in the Mediterranean Sea was homogenized in 2009 under the MEDIAS project (Anonymous, 2008). Prior to 2009, sampling design differed per Mediterranean country. In particular, in the Spanish Mediterranean coast (GSA06) from 2003 to 2008 annual acoustic ECOMED surveys were performed by the IEO during November–December. While acoustics prospections were performed during the day, pelagic trawls were deployed during night time to assess the species composition. The months in which the ECOMED survey was carried out

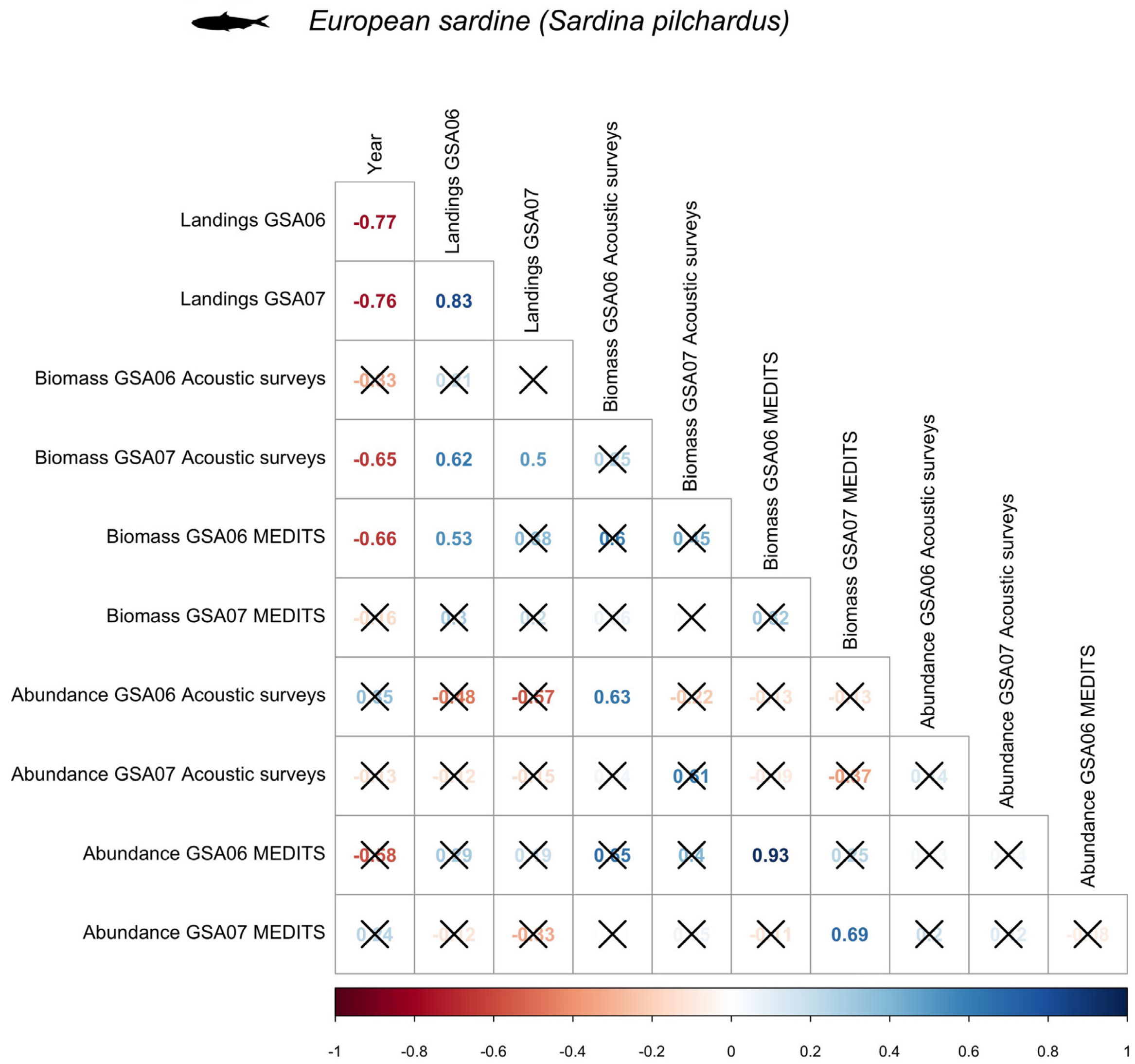

FIGURE 3 | Spearman's correlation for European sardine (*Sardina pilchardus*) among biomass and abundance collected during acoustic (ECOMED, PELMED and MEDIAS) and demersal (MEDITS) surveys, as well as official countries landings, in the Geographical Sub-Area 06 and 07 from 2003 to 2016.

(November–December) coincide with the recruitment of anchovy, and the earliest signs of spawning activity in sardine (Olivar et al., 2001). It worth to be mentioned that fishing during the night or the day does not imply significant differences in surveys catches (Machias et al., 2013). The ECOMED surveys were developed with a systematic design of transects perpendicular to the coastline covering the continental shelf approximately between the 30 and 200 m (Bellido et al., 2008). The PELMED surveys were conducted by IFREMER over the continental shelf of the Gulf of Lions during the summer season (most of the times in July) from 2003 to 2008. All cruises were performed using regularly spaced (12 nautical miles) inshore offshore transects. Acoustic sampling was performed with scientific split-beam echo sounders operating at 38 kHz and calibrated following standard techniques (Foote, 1987). Data were recorded at a constant speed of 8 knots. When the echosounder detected sufficiently long fish traces (≥2 nm) or a change in the echotrace characteristics, a pelagic trawl was deployed to assess the species composition (Van Beveren et al., 2014). The minimum sampling depth varied between 10 and 20 m depending on the area (Ospina-Álvarez et al., 2013). The MEDIAS dataset for both species and the two studied areas (GSA06 and 07) was collected through acoustic samplings from 2009 to 2017 performed during daytime each July by means of scientific split-beam echosounders working at 38 kHz (Saraux et al., 2014). As for the PELMED project, pelagic trawls were performed when the echosounder detected sufficiently long fish traces or a change in the echotrace characteristics. Acoustic data were recorded in both areas following the MEDIAS regular sampling design (parallel transects perpendicular to the coastline) at a constant speed of 8–10 nmi^{h-1} (Doray et al., 2010).

All these datasets were available through a European Data Call to the SPELMED project (Coll and Bellido, 2018). It worth mentioning that the only the MEDITS dataset was geo-referenced.

Landing datasets, collected for the fishery harbors located in the studied area, were provided by the General Secretariat of Fisheries of the Spanish Ministry of Agriculture, Food and Environment (MAPAMA) in the GSA06, while for the GSA07 the data was available through a European Data Call to the SPELMED project (Coll and Bellido, 2018).

Environmental Data

For the temporal modeling, three different possible predictors were used to model the habitats of adult anchovy and sardine: Sea Surface Temperature (SST in °C), Sea Surface Salinity (SSS in PSU) and Net Primary Productivity (NPP in mg/m^3). They were selected as the most commonly used variables to explain the variability of anchovy and sardine dynamics in the Mediterranean Sea (Fernández-Corredor, 2018).

Monthly averages of oceanographic variables covering the entire study period (2003–2016) were extracted from the Copernicus Marine Environment Monitoring Service[1] for both GSA06 and GSA07.

Bathymetry was obtained from the MARSPEC dataset[2] with a spatial resolution of 1×1 degree.

To model future scenarios, we extracted different IPCC pathway predictions with a spatial resolution of 1×1 degree

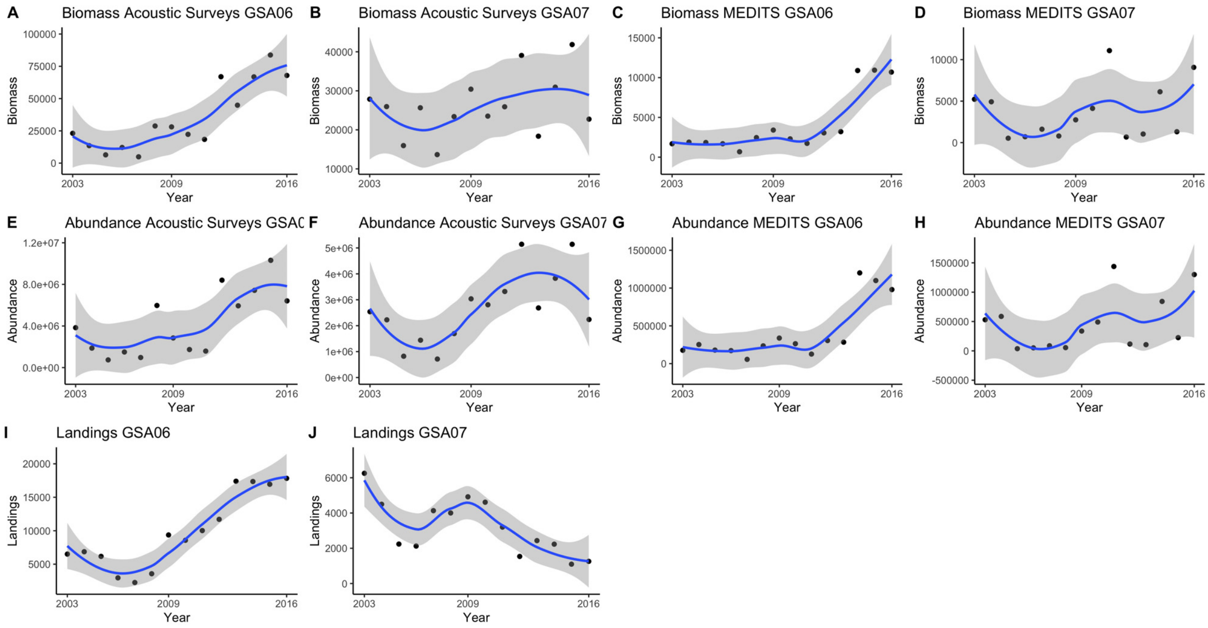

FIGURE 4 | Biomass **(A–D)**, abundance **(E–H)**, and landings **(I,J)** temporal trends from acoustic (ECOMED, PELMED, MEDIAS) and demersal (MEDITS) surveys and official countries landings for European anchovy (*Engraulis encrasicolus*) in the Geographical Sub-Area 06 and 07 from 2003 to 2016.

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[1] https://marine.copernicus.eu

[2] http://www.marspec.org

from Bio-ORACLE[3]. In particular, we used the Representative Concentration Pathway (RCP) 2.6 and 8.5 for 2050 and 2100 for SSS and SST.

The RCP2.6 projection scenarios assume least change, with an increase in temperature of 1°C degree in 2050 and 2°C degree in 2100 and of an increase of 0.5 PSU and 1 PSU units for salinity. On the contrary, the RCP8.5 scenarios presume most severe change with an increase in temperature of 1°C degree in 2050 and almost 3°C degrees in 2100, and of 1 and 1.5 PSU units for the salinity, respectively.

Temporal Trends and Correlation Analysis

As preliminary analysis with the attempt to capture the general patterns in the temporal trends of biomass, abundance and landings of the two studied species, we used the "ggplot" package (Wickham, 2011) of the R software (R Core Team, 2019) to plot these indexes. Additionally, in order to assess the complementarity and difference among these different analyzed indexes collected from different oceanographic surveys, we performed a Spearman correlation using the "corrplot" R-package (Wei et al., 2017).

Temporal Modeling

Random Forests (RFs) were applied to assess which environmental variables had influenced the indexes of biomass, abundance and landings of the two studied species historically. We run RFs using data from the different oceanographic surveys (ECOMED, PELMED, MEDIAS, and MEDITS) and landings for both areas (GSA06 and GSA07), using both total values of aforementioned indexes and with the application of a Gaussian distribution. Biomass and abundance data were log-transformed

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[3] http://www.bio-oracle.org

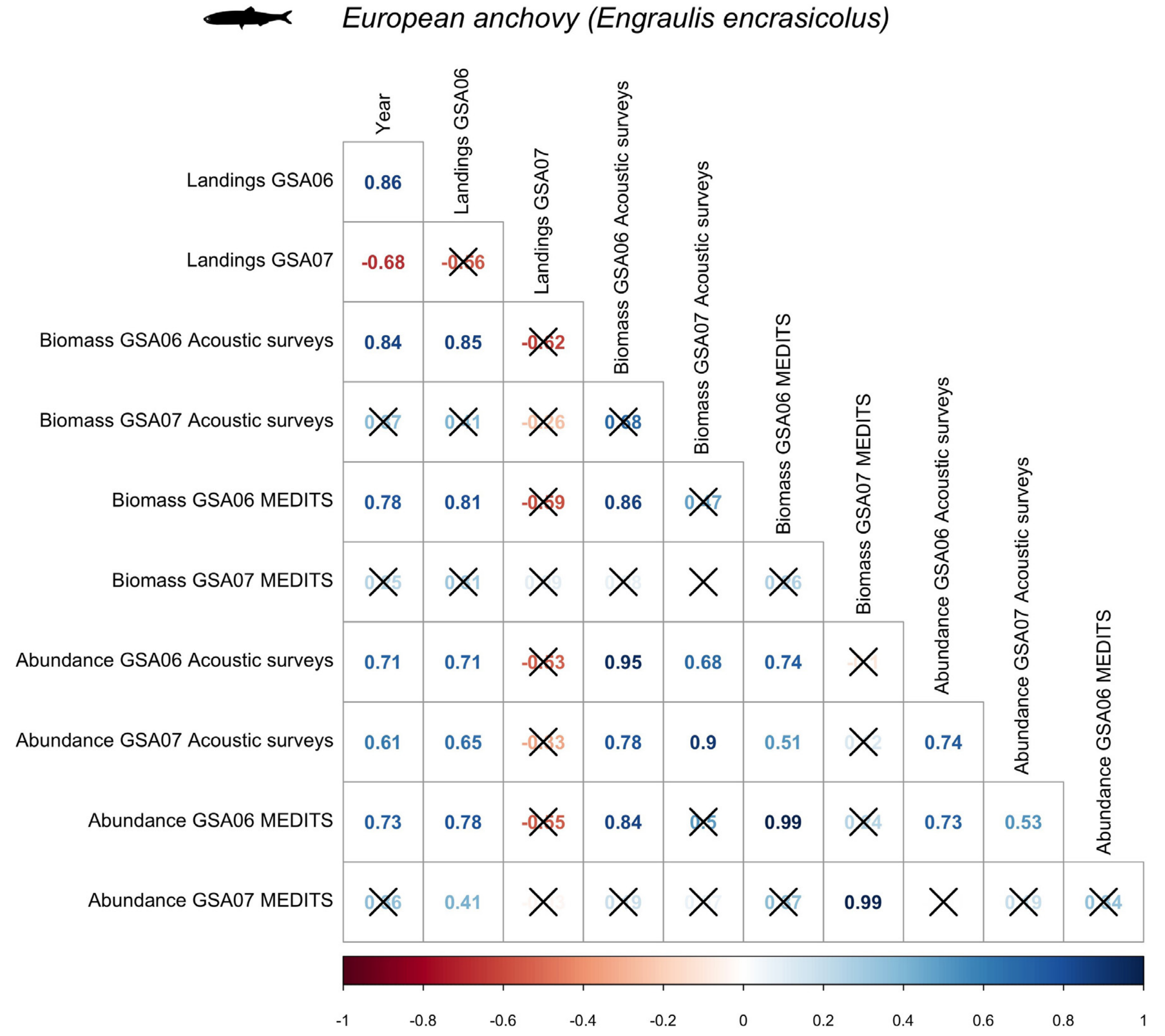


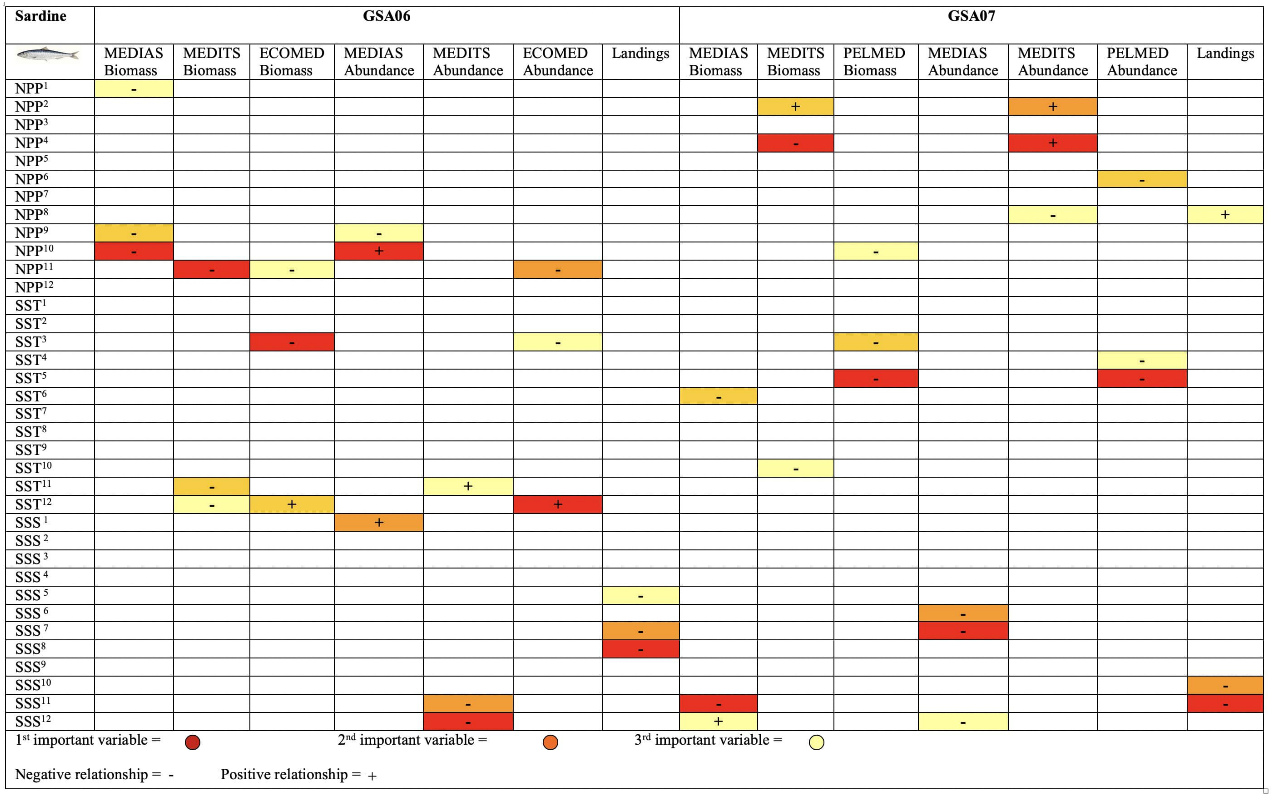
FIGURE 5 | Spearman's correlation for European anchovy (*Engraulis encrasicolus*) among biomass and abundance collected during acoustic (ECOMED, PELMED, and MEDIAS) and demersal (MEDITS) surveys, as well as official countries landings, in the Geographical Sub-Area 06 and 07 from 2003 to 2016.

before being introduced in RFs to ensure a normal distribution, as well as to reduce the weight of extreme values. In addition, we tested 12 temporal lags (from January to December) in independent model to assess if anchovy and sardine were significantly influenced by environmental conditions of the months previous to surveys.

RFs are particularly suitable for this task as they do neither require any prior assumptions about the data, nor is their classification accuracy affected by correlations or interactions between variables (Vilela and Bellido, 2015). RFs involve fitting an ensemble of regression trees, first selecting many bootstrap samples from the data, each of which contains ~63% of the original observations (Strobl et al., 2009). Observations that are not selected in each bootstrap sample are referred to as out-of-bag observations. A regression tree is then fitted to each bootstrap sample, but only a subset of randomly selected variables is used at each node. The trees are fully grown without pruning, and then each tree is used to predict the out-of-bag observations. The out-of-bag estimates are considered a cross-validation of the accuracy of estimates because they are not used in the fitting of trees. The relative importance of each predictor variable is then determined from the misclassification rate for the out-of-bag observations. A sufficiently large number of trees (10,000) were used, and different random seeds were applied to ensure stability in variable importance. The mean squared error (MSE) statistic was computed to measure variables importance (Breiman, 2001). RFs were performed using the "dismo" R-package (Hijmans et al., 2017).

Species Distribution Models

Boosted Regression Trees (BRTs) were used to model the spatial habitat of anchovy and sardine, as this technique deals with non-linear and non-monotonic relationships between response and explanatory variables. BRTs combine regression trees and boosting methods to fit complex non-linear relationships between predictors and a response variable (Elith et al., 2008). BRT parameters were selected to optimize the model using the "caret" (Kuhn, 2008) and "dismo" packages of the R software. The optimal number of boosting trees was assessed with the "gbm.step" function, while the tree complexity of the model was fixed at 2 and the learning rate at 0.01. To account for the spatial autocorrelation in the data, we implemented the residuals autocovariate (RAC) approach (Crase et al., 2012). Spatial autocorrelation was included by adding another term to the model, which represents the influence of neighbor observations on the response variable at a particular location (Escalle et al., 2016; Barcala et al., 2020). For each model, the RAC approach was implemented as follows: first, the model was computed



Sardine	GSA06							GSA07						
	MEDIAS Biomass	MEDITS Biomass	ECOMED Biomass	MEDIAS Abundance	MEDITS Abundance	ECOMED Abundance	Landings	MEDIAS Biomass	MEDITS Biomass	PELMED Biomass	MEDIAS Abundance	MEDITS Abundance	PELMED Abundance	Landings
NPP^1	🟨 -													
NPP^2									🟧 +			🟧 +		
NPP^3														
NPP^4									🟥 -			🟥 +		
NPP^5														
NPP^6													🟧 -	
NPP^7														
NPP^8												🟨 -		🟨 +
NPP^9	🟧 -			🟨 -										
NPP^{10}	🟥 -			🟥 +						🟨 -				
NPP^{11}		🟥 -	🟨 -			🟧 -								
NPP^{12}														
SST^1														
SST^2														
SST^3			🟥 -			🟨 -				🟧 -				
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SSS^{12}					🟥 -			🟨 +			🟨 -			

1st important variable = 🔴 2nd important variable = 🟠 3rd important variable = 🟡

Negative relationship = - Positive relationship = +

FIGURE 6 | Summary of the Random Forests results for European sardine (*Sardina pilchardus*) temporal index trends in the Geographical Sub-Area 06 and 07 from 2003 to 2016.This figure shows the ecological and statistical weight of each variable. (+) symbol indicates a positive relationship of the variable with the biomass, abundance or landings and (-) symbol indicates a negative relationship. The colors represent the range, from most to least important variable within the model (red the most relevant, orange medium relevancy and yellow the least relevant) based on the per cent increase in mean squared error- MSE).

with the selected environmental variables; second, residuals from the selected model were calculated for each grid cell and were used to compute the spatial component by a focal calculation. This allowed cells from a selected neighbor to have a weight of 1 and all other cells a weight of 0. Finally, the spatial component was considered as an explanatory variable in the previous model (Crase et al., 2012). Spatial autocorrelation was tested for each model by calculation of Moran's index and the Moran statistical test (R package "spdep," see Bivand et al., 2015), which indicates a correlation between observations depending on the distance between them.

A binomial distribution was implemented to model the response variables of occurrence of the MEDITS dataset. We used these response variables as the only available geo-referenced variables, as well as the large stand most consistent time-series for both areas and species. In addition, temporal trends obtained from MEDITS dataset showed significant correlations with several other available data (ECOMED, PELMED, and MEDIAS; see below).

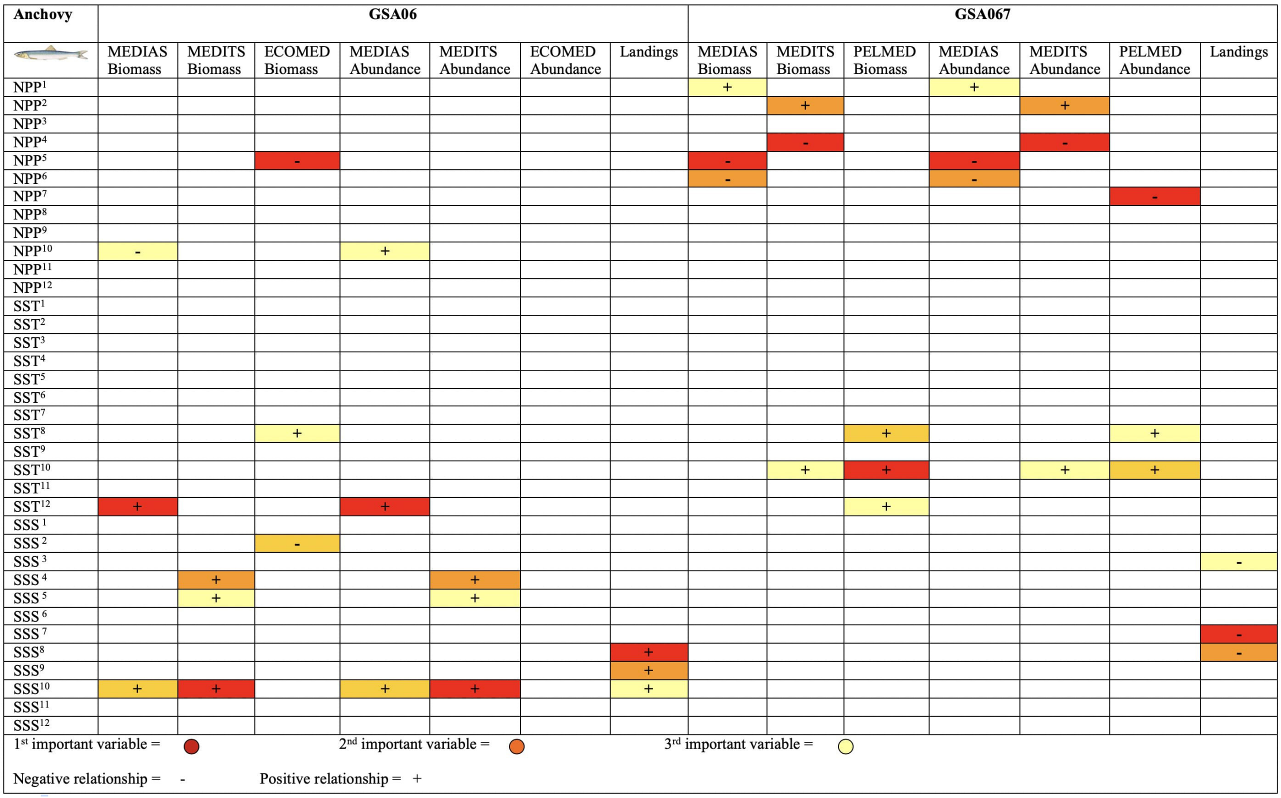
Validation of the binomial models was conducted through an internal 10-fold cross-validation in which the relationship between occurrence data and environmental variables was modeled using a training dataset (created by a random selection of 75% of the data) and the quality of predictions was then assessed using a validation dataset (created by a random selection of 25% of the data), as advised by Fielding and Bell (1997). The model performance was assessed using the Pearson's r coefficient, which measures the correlation between predicted and observed values. This coefficient can vary from −1 to 1, with 1 representing a perfect positive correlation between the 2 data sets.

Four future scenarios (RCP2.6 and RCP8.5 for 2050 and 2100) were computed for each species and area (GSA06 and GSA07). Finally, in order to identify potential *climate refuges*, areas with a probability of occurrence higher than 0.70 (where there is the bulk of occurrence of the species) were selected and mapped.

RESULTS

Temporal Trends and Correlation Analysis

Temporal trends of sardine biomass in the acoustic datasets showed a negative trend for both GSA06 and GSA07 (**Figure 2**), which was significant in case of GSA07 (rho = −0.65) (**Figures 2**, **3**). Sardine abundance showed positive but non-significant increase in GSA06 and a negative but non-significant decline in GSA07 (**Figures 2**, **3**). Trends of abundance and



Anchovy	GSA06							GSA067						
	MEDIAS Biomass	MEDITS Biomass	ECOMED Biomass	MEDIAS Abundance	MEDITS Abundance	ECOMED Abundance	Landings	MEDIAS Biomass	MEDITS Biomass	PELMED Biomass	MEDIAS Abundance	MEDITS Abundance	PELMED Abundance	Landings
NPP¹								+			+			
NPP²									+			+		
NPP³														
NPP⁴									-			-		
NPP⁵			-					-			-			
NPP⁶								-			-			
NPP⁷													-	
NPP⁸														
NPP⁹														
NPP¹⁰	-			+										
NPP¹¹														
NPP¹²														
SST¹														
SST²														
SST³														
SST⁴														
SST⁵														
SST⁶														
SST⁷														
SST⁸			+							+			+	
SST⁹														
SST¹⁰									+	+		+	+	
SST¹¹														
SST¹²	+			+						+				
SSS ¹														
SSS ²			-											
SSS ³														-
SSS ⁴		+			+									
SSS ⁵		+			+									
SSS ⁶														
SSS ⁷														-
SSS⁸							+							-
SSS⁹							+							
SSS¹⁰	+	+		+	+		+							
SSS¹¹														
SSS¹²														

1st important variable = ● 2nd important variable = ● 3rd important variable = ○

Negative relationship = - Positive relationship = +

FIGURE 7 | Summary of the Random Forests results for European anchovy (*Engraulis encrasicolus*) temporal index trends in the Geographical Sub-Area 06 and 07 from 2003 to 2016. This figure shows the ecological and statistical weight of each variable. (+) symbol indicates a positive relationship of the variable with the biomass, abundance or landings and (-) symbol indicates a negative relationship. The colors represent the range, from most to least important variable within the model (red the most relevant, orange medium relevancy and yellow the least relevant) based on the per cent increase in mean squared error- MSE).

biomass for sardine were positively correlated in both areas (**Figure 3**), but significant only in GSA06 (rho = 0.63, **Figure 3**).

Temporal trends of sardine abundance and biomass using the MEDITS dataset showed a negative decrease in GSA06, with a significant correlation for the biomass (rho = −0.66) (**Figures 2**, **3**). In GSA07 the biomass trend presented a negative trend while the abundance a positive one, but neither trend was significant (**Figures 2**, **3**). Trends of abundance and biomass for sardine in GSA06 and GSA07 were positively significantly correlated (rho = 0.93 and 0.69, respectively; **Figure 3**).

The declines in landings were large and significant in both areas, with a Spearman correlation value of −0.77 in GSA06 and −0.76 in GSA06 (**Figures 2**, **3**).

Overall, when comparing the three datasets used to describe the temporal trends of sardine in GSA06 and GSA07 (acoustic surveys, trawl surveys and landings), using biomass data from acoustic surveys and from bottom trawling, we observed that in all cases and for both areas sardine showed decreasing trends (**Figures 2**, **3**). These trends were significant for landings in both areas, and for acoustic surveys in GSA07 and trawl surveys in GSA06. It is also interesting to notice that, in all cases, time series were positively correlated. This correlation was significant between landings and acoustic surveys in GSA07 (with rho = 0.50) and between landings and trawl surveys in GSA06 (with rho = 0.53). Between GSAs, we found a significant and positive correlation between landings of sardine (with rho = 0.83) (**Figure 3**).

Temporal trends of anchovy biomass using the acoustic datasets showed positive increases (**Figure 4**), significant in the case of GSA06 (rho = 0.84) (**Figure 5**). Anchovy abundance showed a positive and significant increase with time in GSA06 and GSA07 (rho = 0.71 and rho = 0.61, respectively, **Figures 4**, **5**). Temporal trends of anchovy abundance using the MEDITS dataset showed a positive significant increase in GSA06 (rho = 0.73) and a positive but non-significant decrease in GSA07 (**Figure 5**). The trends of biomass showed a positive increase in both areas (**Figure 4**), which was significant in case of GSA06 (rho = 0.78) (**Figure 5**). Trends of abundance and biomass for anchovy in GSA06 and GSA07 were positively significantly correlated (**Figure 5**).

When comparing the three datasets used to describe the temporal trends of anchovy in GSA06 and GSA07 (acoustic

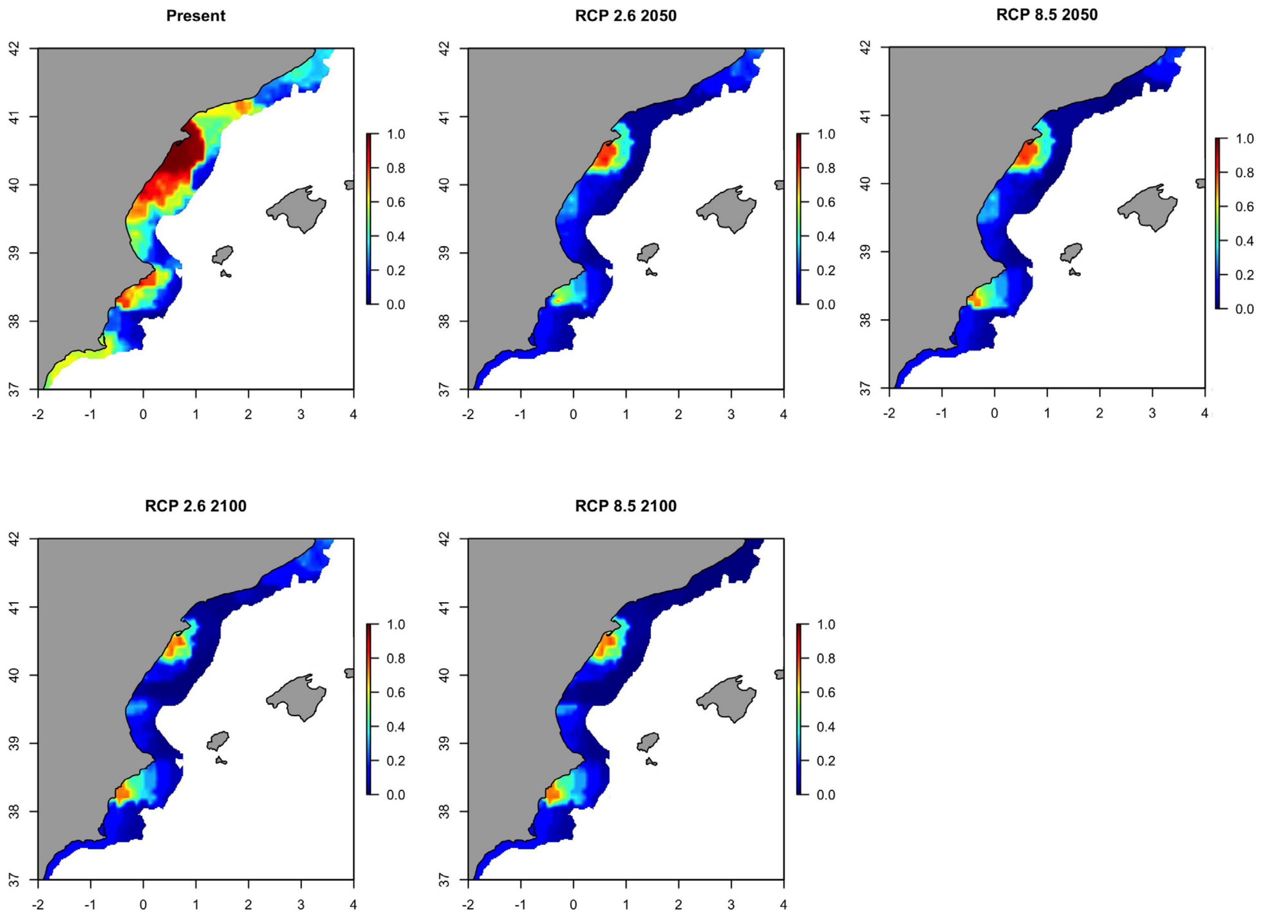


FIGURE 8 | Predicted probability of occurrence of the European sardine (*Sardina pilchardus*) in Geographical Sub-Area 06 for the present situation and using IPCC pathway scenarios obtained with RAC-BRT models.

surveys, trawl surveys and landings) we observed that, except for landings in GSA07, anchovy showed increasing trends (**Figures 4**, **5**). These trends were significant for landings, acoustics and trawl surveys in GSA06 (with rho's higher than 0.7). It is also interesting to notice that in several cases time series were correlated. This correlation was highly significant between acoustic surveys and trawl surveys in GSA06 (rho = 0.86), between acoustic surveys and landings in GSA06 (rho = 0.85) and between landings and trawl surveys in GSA06 (rho = 0.81).

Predictors and Lags of Temporal Trends

Summarizing results of temporal modeling with RFs for sardine using biomass, abundance and landings as dependent variables (**Figure 6** and **Supplementary Figures S1–S3**), we observed that NPP showed mainly a negative effect in GSA06 and mixed effects in GSA07. With the exception of the PELMED abundance for which the relationship found with NPP corresponded to the month of the survey, all the relevant relationships found with NPP were with temporal lags of 9–11 months. SST showed a negative impact in GSA07 and mixed effects in GSA06, while SSS showed mainly a negative effect in GSA06 and GSA07.

Summarizing results of the temporal modeling with RF for anchovy using biomass, abundance and landings as dependent variables (**Figure 7** and **Supplementary Figures S1–S3**), we observed that NPP showed mainly a negative relationship in GSA07, while in GSA06 was less relevant, showing mixed effects. SST showed a positive effect in GSA06 and GSA07, while SSS showed mainly a positive effect in GSA06 and a negative effect in GSA07, especially for landings. In general, results highlighted that time lags were important to explain the relationships between dependent variables for anchovy and sardine, and environmental factors (**Figures 6**, **7** and **Supplementary Figures S1–S3**).

Historical Spatial-Temporal Trends of Anchovy and Sardine Occurrence (2003–2016)

For sardine, RAC-BRTs total deviance explained ranged from 51 to 74% in the GSA07 and from 52 to 78% in GSA06 depending of the year (**Supplementary Table S1**). Similarly, for anchovy the total deviance explained ranged from 33 to 75% in the GSA07 and from 48 to 78% in GSA06 (**Supplementary Table S2**).

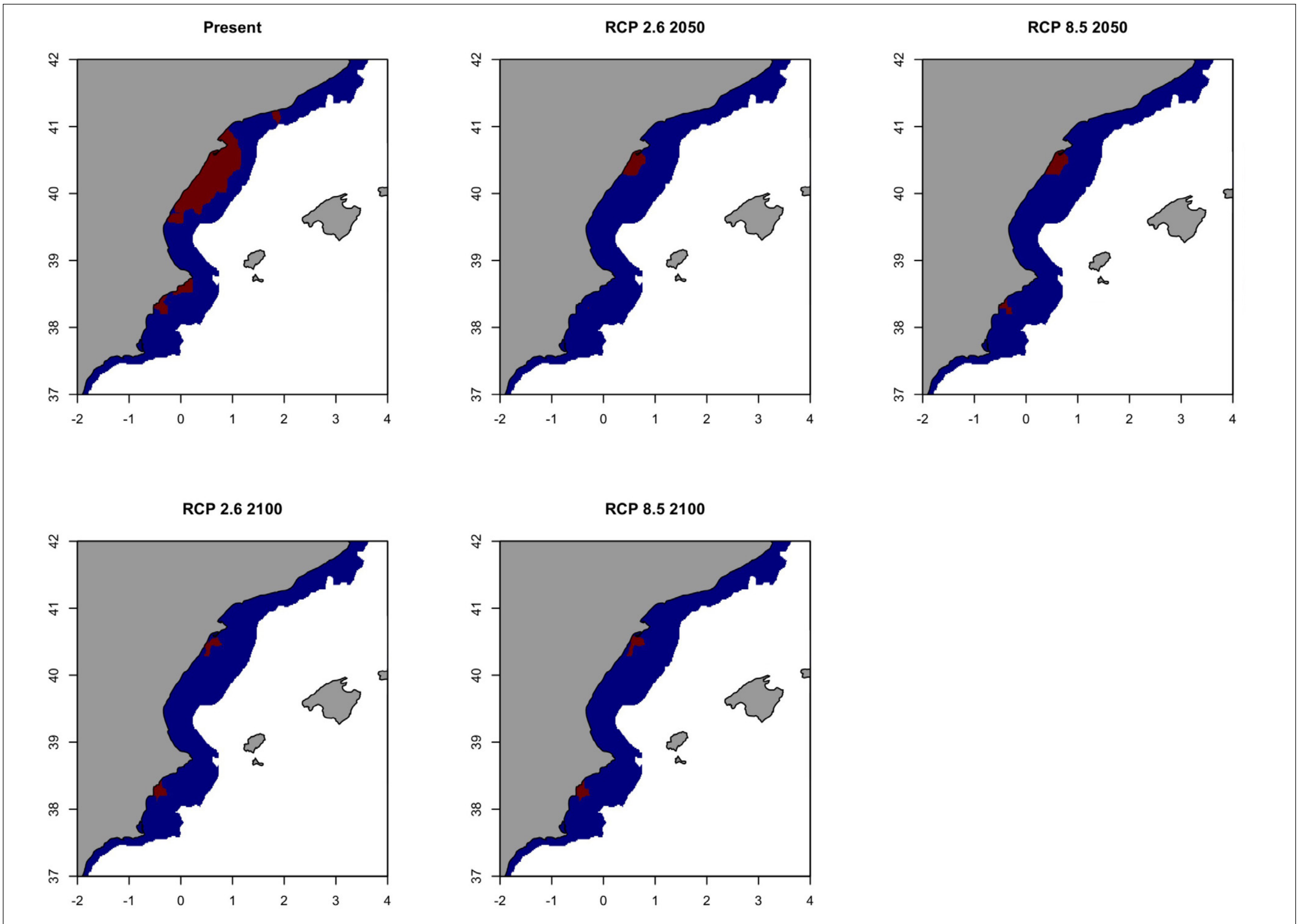


FIGURE 9 | Climate refuges, hot-spots of the probability of occurrence (>0.7) of the European sardine (*Sardina pilchardus*) in Geographical Sub-Area 06 for the present situation and using IPCC pathway scenarios obtained with RAC-BRT models. Red color indicates probability of occurrence >0.7, while blue <0.7.

An absence of spatial autocorrelation was detected in all models (**Supplementary Tables S1, S2**), highlighting that it was accurately handled by the RAC method.

For model validation, reasonably high values for Pearson's rho were obtained for both species and areas (**Supplementary Tables S1, S2**). In particular, from RAC-BRTs for sardine in GSA07, rho values between 0.64 and 0.82 were obtained in the cross-validation (**Supplementary Table S1**). In GSA06 rho values were higher ranging from 0.69 and 0.93. For anchovy in GSA07, rho values ranged from 0.66 to 0.90, while in GSA06 from 0.74 to 0.93 (**Supplementary Table S2**).

Spatial maps of the occurrence in GSA07 highlighted the preference of sardine for the coastal area and changes with time, with compression of the occurrence niche in 2006, 2012, and 2015 (**Supplementary Figure S4**). The inter-annual deviation of sardine occurrence from 2003 to 2016 evidenced the large observed changes during the time period, at times more evident in coastal areas or on the shelf and upper slope (**Supplementary Figure S5**).

In GSA06, spatial maps of the occurrence highlighted a concentration of sardine around the Delta Ebro area, with some years (e.g., 2009, 2013) where the occurrence was especially restricted (**Supplementary Figure S6**), followed by a range expansion in particular towards the south. The inter-annual deviation of sardine occurrence from 2003 to 2016 also evidenced large changes in the whole study area (**Supplementary Figure S7**).

For anchovy, RAC-BRTs spatial maps showed that occurrences were mainly located in the coastal and continental shelf area in GSA07 (**Supplementary Figure S8**). During years 2005, 2006, 2008, 2012, and 2013 the occurrence was closest to the eastern side. Inter-annual variability was also high during the time series (**Supplementary Figure S9**). In GSA06, spatial maps of the occurrence highlighted an extension of both species' distribution ranges from 2011 to the present (**Supplementary Figure S10**). The inter-annual deviation of anchovy occurrence from 2003 to 2016 revealed the expansion of the species in all the study area (**Supplementary Figure S11**).

Future Spatial-Temporal Scenarios

For sardine in GSA06, projection maps (**Figure 8**) highlighted a contraction of distribution ranges with only two remaining hot-spots by 2050. These two hot-spots were located (1) north of the Delta Ebro, and (2) south of Cabo de la Nao, in the Gulf

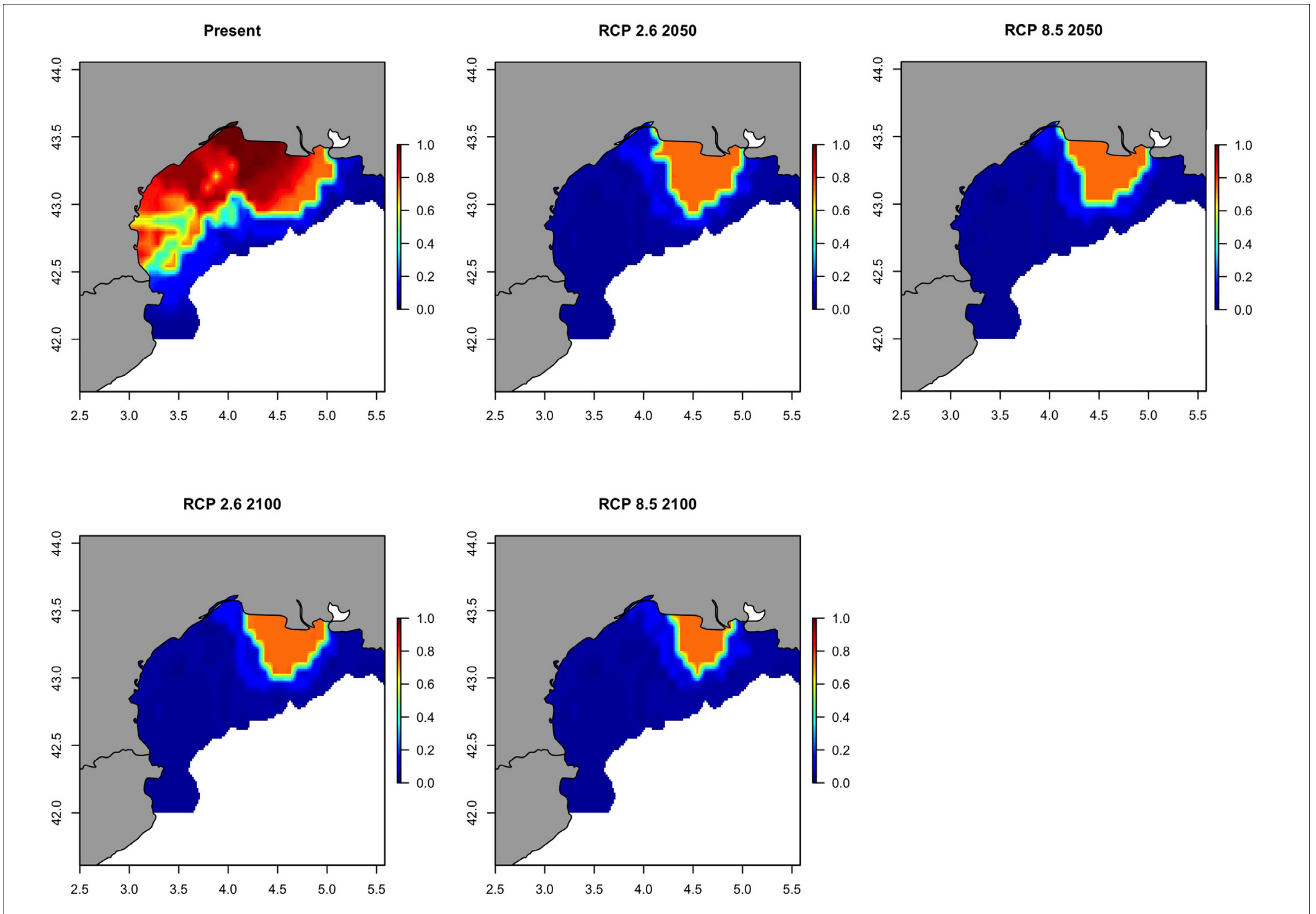


FIGURE 10 | Predicted probability of occurrence of the European sardine (*Sardina pilchardus*) in Geographical Sub-Area 07 for the present situation and using IPCC pathway scenarios obtained with RAC-BRT models.

of Alicante. These hot-spots emerged for both the optimistic and the pessimistic IPCC pathway scenarios. The hot-spot areas were projected to contract even further in 2100 compared to 2050 predictions. In addition, the map of the variability from the present distribution (**Supplementary Figure S12**) highlighted that this decrement of the sardine distribution will be gradual from 2050 to 2100 and will occur across GSA06 except for these two hot-spots.

When areas with a probability of occurrence higher than 0.70 were identified for each scenario, the waters located in the southern area of the Delta Ebro influence resulted as the only zone in which the species may persist in the future (**Figure 9**). It is worth mentioning that this area will suffer a contraction of the distribution of sardine in the southern part of the Delta Ebro from now to 2100 (**Figure 9**). This result is very similar when considering the optimistic or the pessimistic IPCC scenario.

Future projection maps for sardine in GSA07 showed that its spatial distribution and biomass will undergo a gradual decrease from the present to 2100 (**Figure 10**), with the exception of remaining biomass concentrations in the waters off the Rhone River (**Figure 10**). The map of the variability from the present distribution to the future scenarios highlighted that this decrease of sardine distribution and biomass will be constant (**Supplementary Figure S13**).

When the areas with a probability of occurrence higher than 0.70 where computed in each future scenario, sardine will only persist in the zone around the Rhone River by 2100 (**Figure 11**). As for sardine in GSA06, the identified area with higher probability of occurrence is very similar in 2050 and 2100, but with a reduction in size in 2100. Results are similar when considering the optimistic or the pessimistic IPCC scenario.

Anchovy distribution in GSA06 will undergo a decrease in its spatial distribution from the present to 2100. As for sardine, distribution ranges will gradually contract to a minimum area in 2100 (**Figure 12** and **Supplementary Figure S14**). For this species, too, the two main hot-spots that will keep the bulk of biomass will be the area around the Delta Ebro and the Gulf of Alicante. Differently from sardine, these two areas were both identified as hot-spots with a probability of occurrence higher than 0.70 and will persistent into the year 2100 (**Figure 13**). Results were similar when considering the optimistic and the pessimistic pathway scenarios.

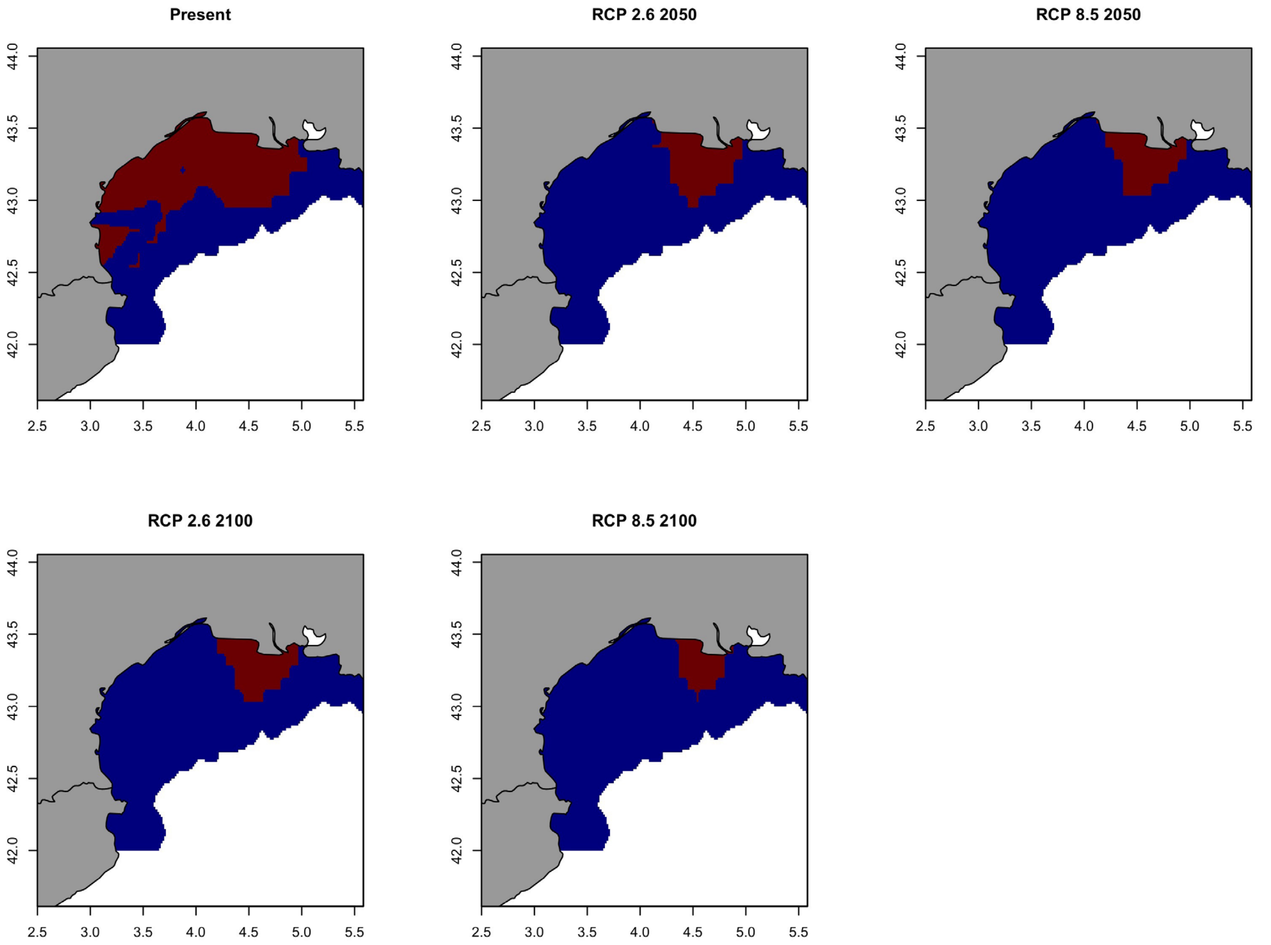


FIGURE 11 | Climate refuges, hot-spots of the probability of occurrence (>0.7) of the European sardine (*Sardina pilchardus*) in Geographical Sub-Area 07 for the present situation and using IPCC pathway scenarios obtained with RAC-BRT models. Red color indicates probability of occurrence >0.7, while blue <0.7.

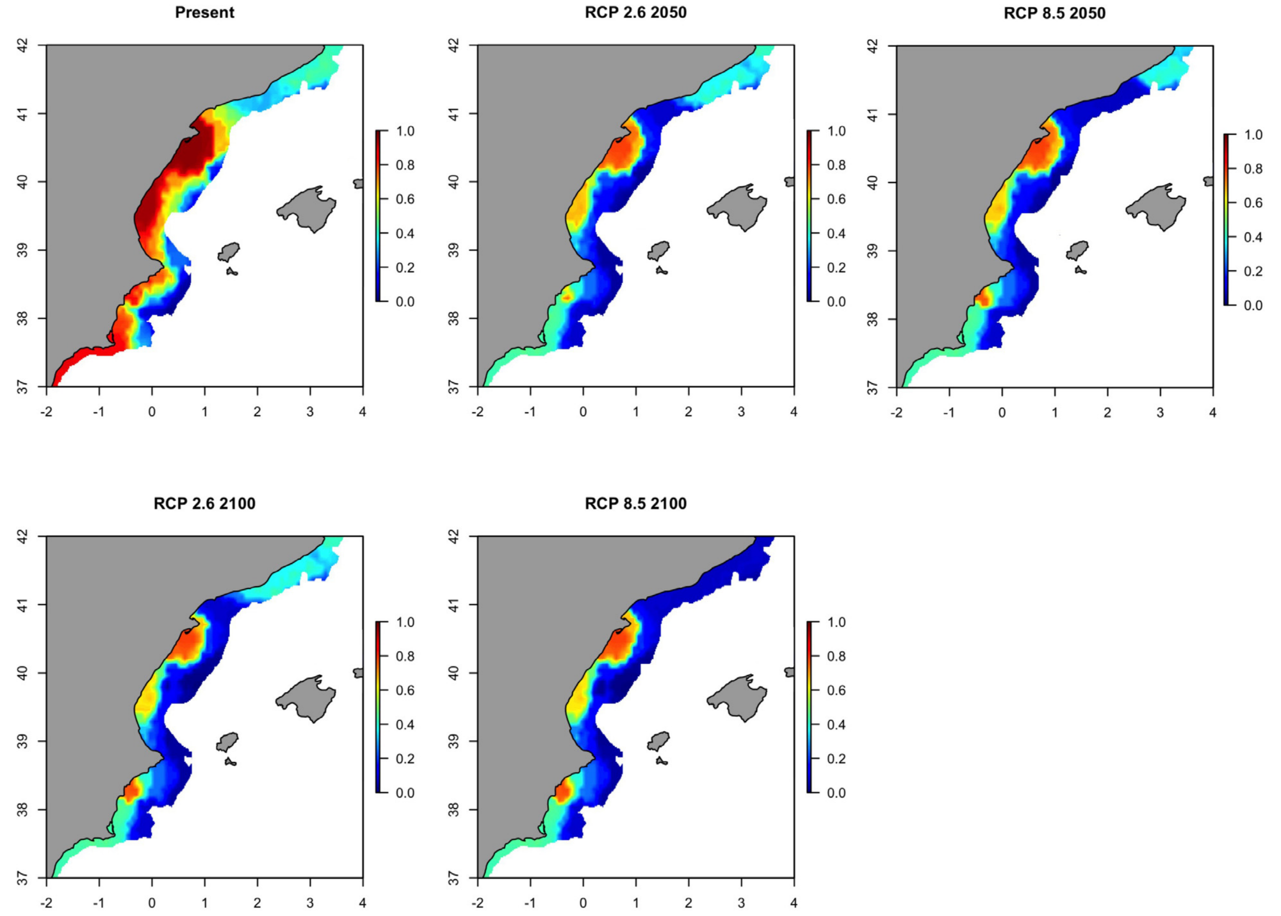


FIGURE 12 | Predicted probability of occurrence of the European anchovy (*Engraulis encrasicolus*) in Geographical Sub-Area 06 for the present situation and using IPCC scenarios obtained with RAC-BRT models.

Future prediction maps of anchovy in the GSA07 showed very similar results to sardine in the same area probably due to the fact the main changes will be happen all in 2050. For pathway scenarios, prediction and variation maps indicate a restriction in spatial distributions (**Figure 14** and **Supplementary Figure S15**), where the bulk of biomass will only be retained near the mouth of the Rhone River. The area with a probability of occurrence higher than 0.70 will be close to the Rhone river plume and will persist in 2100 although strongly reduced (**Figure 15**).

DISCUSSION

In this study, we present main results of a multi-modeling approach to investigate the main effects of environmental factors on anchovy and sardine biomass, abundance, occurrence and landings. To our knowledge, this is one of the most comprehensive studies about the topic in the Mediterranean Sea.

Regarding changes in sardine abundance and biomass, our results demonstrate a general decreasing temporal trend of biomass of sardine in both GSA06 and GSA07, which coincides with a significant decline in landings in both areas, likely reinforced by the depletion of the commercial stock (Quattrocchi et al., 2016; Coll and Bellido, 2018; Coll et al., 2019).The abundance and biomass of anchovy showed a general increase over time in both GSA06 and GSA07, which coincides with a significant increase of catches in GSA06. On the contrary, we observe a decline in landings in GSA07, which can be motivated by changes in the fishing strategy that shifted from pelagic to demersal target species (Van Beveren et al., 2016), and also due to the fact that most of the pelagic vessels targeting sardine stopped their activity at the end of 2009 due to the stock decline (Fisheries in the Gulf of Lions, UNEP-MAP-RAC/SPA, 2013).

Correlations between trends in acoustic surveys, trawl surveys and landings suggest that these data can be complementary. Overall, correlations between datasets are higher for anchovy than for sardine. These correlations coincide with results from the attempt to compare MEDITS temporal estimates with commercial catches of sardine and anchovy in GSA09 (Ligurian Sea and Northern Tyrrhenian Sea) (Sbrana et al., 2010). For instance, Sbrana et al. (2010) showed that MEDITS survey could be a promising descriptor of anchovy abundance in GSA09 as it is the main targeted species of the fisheries sector in the area. However, it is worth to be mentioned that bottom-trawling is

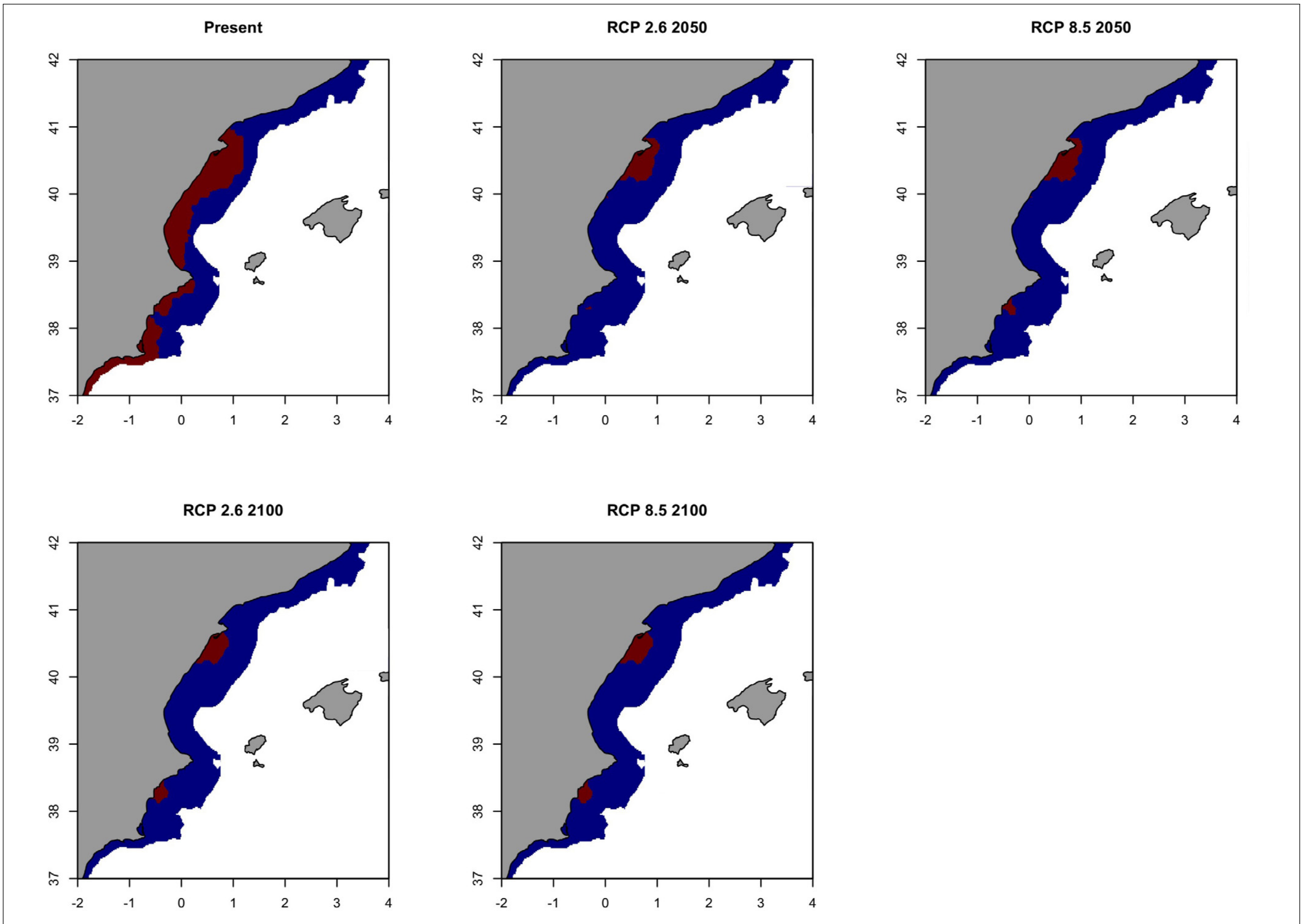


FIGURE 13 | Climate refuges, hot-spots of the probability of occurrence (>0.7) of the European anchovy (*Engraulis encrasicolus*) in Geographical Sub-Area 06 for the present situation and using IPCC pathway scenarios obtained with RAC-BRT models. Red color indicates probability of occurrence >0.7, while blue <0.7.

not the best to sampling collector for pelagic species and thus, although similarities were found, results should be taken into account carefully.

Results from the temporal modeling showed mixed effect between variables for anchovy and sardine and primary productivity, especially in GSA06. In the same area, Bellido et al. (2008) found a relatively weak but positive relationship between primary productivity indicators (i.e., Chl-a) and small pelagic species occurrence, suggesting that fish were not directly related to this environmental factor, but that areas with higher primary productivity were more favorable for both sardine and anchovy. However, other studies pointed out that sardine juveniles prefer areas with moderate primary productivity values (Giannoulaki et al., 2011; Tugores et al., 2011) and negative relationships were also found between anchovy adults and primary productivity in other Mediterranean areas (Giannoulaki et al., 2008, 2013; Martín et al., 2008; Quattrocchi et al., 2016). Recent studies point out that primary productivity concentration is negatively correlated with anchovy individuals of age −1 (Bacha et al., 2010; Basilone et al., 2017). Overall, areas with high primary productivity concentration could affect water transparency, increasing the difficulty of finding prey (Fernández-Corredor, 2018). Also, these mixed effects could be due to the different behavior of life stages of the studied species (i.e., juveniles and adults) (Fernández-Corredor, 2018) and could be explained by the high plasticity of their feeding behavior, switching between the selective prey feeding and the non selective filter-feeding mode (Palomera et al., 2007; Zarrad et al., 2008; Ganias, 2009; Costalago et al., 2015). In addition, another possible explication of these mixed temporal effects could due to the fact that the population structure of these spcies has been changing with time. Indeed, in 2006 there were more age classes than in 2016 (Albo-Puigserver et al., 2018).

In GSA06, mixed effects were found among temporal patterns of sardine indexes and temperature, while in GSA07 the relationship was mainly negative. These results are in accordance with literature in which the effect of temperature on sardine indexes was found mainly negative throughout the Mediterranean basin (Bellido et al., 2008; Martín et al., 2008; Katara et al., 2011; Tugores et al., 2011; Martín et al., 2012; Giannoulaki et al., 2013; Brosset et al., 2015; Bonanno et al., 2016; Quattrocchi et al., 2016). Cooler temperature can be indicative of nutrient enrichment processes such as wind mixing, upwelling

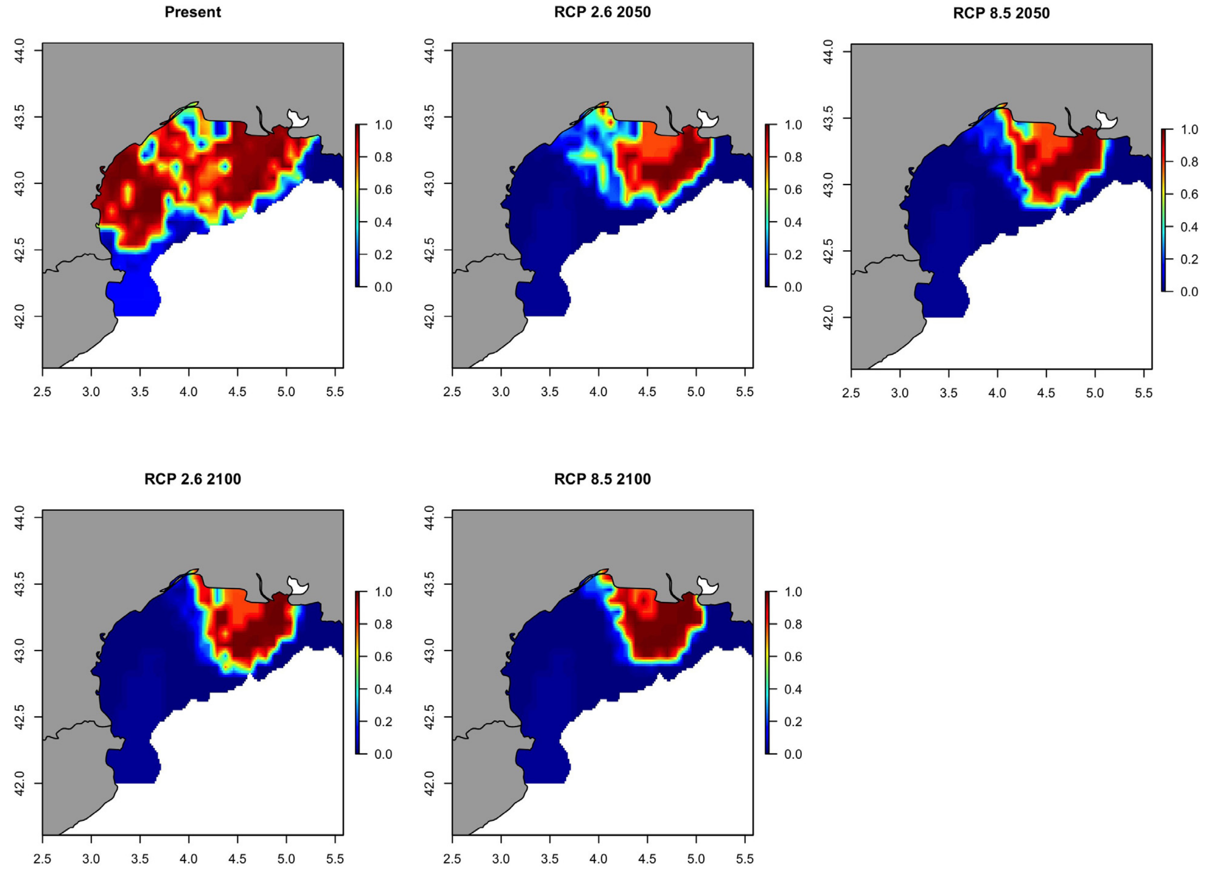


FIGURE 14 | Predicted probability of occurrence of the European anchovy (*Engraulis encrasicolus*) in Geographical Sub-Area 07 for the present situation and using IPCC pathway scenarios obtained with RAC-BRT models.

and river run-off, associated with favorable conditions for fish reproduction and recruitment (Sabatés et al., 2007; Fernández-Corredor, 2018).

On the contrary, for anchovy the relationship with temperature was positive in both areas. This result is consistent with a comprehensive literature review (Fernández-Corredor, 2018). Temperature seems to affect the size of anchovy at the end of the first year of life, and was found positive related with anchovy at age-1 (Bacha et al., 2010; Basilone et al., 2017), and with anchovy body condition factors (Basilone et al., 2006).

Salinity showed overall a negative relationship for both species and areas, with exception for anchovy in GSA06 for which a positive relationship was found with several indexes and temporal lags, as well as with landings. This result is in line with Carpi et al. (2015), which found that marked salinity gradients could have a positive effect on anchovy catches in the Adriatic Sea, while Palomera et al. (2007) show that anchovy is the only small pelagic fish in the NW Mediterranean Sea that spawns in a wide salinity range. On the contrary, landings of sardine in both areas, and for anchovy in GSA07, presented a consistent negative relationship with salinity. Sardine aggregations tend to be higher in shallower areas characterized by lower salinitythat probably are less favorable for this species (Quattrocchi and Maynou, 2017). The negative relationship between salinity and anchovy seems to be correlated to the spawning success (Zorica et al., 2013), lower salinity values endorse the euryhaline condition of anchovies, indicating a connection between salinity fluctuations and their spawning.

Results from the species distribution modeling showed contrasting results between anchovy and sardine and between GSA06 and 07, historically. Anchovy mainly showed an expansion of the population with time in GSA06, especially evident from 2009 onwards, while in GSA07 results illustrate changes between coastal and shelf areas, with some lower than average years in 2005–2008.

Interestingly, in both GSAs for anchovy there was a contraction in the distribution in 2005–2006, coinciding with the years preceding the collapse observed in abundance, landings, growth and body conditions (Van Beveren et al., 2014; Brosset et al., 2015). Also, in both GSAs, in 2013 there was a high retraction of the distribution, coinciding with the year before the second peak of the decline in the species body condition observed 2014 (Albo-Puigserver et al., 2018).

Sardine showed a decrease of occurrence in GSA06 with time, with a slight expansion to the south in the recent years, while in GSA07 a general decline is also observed with a

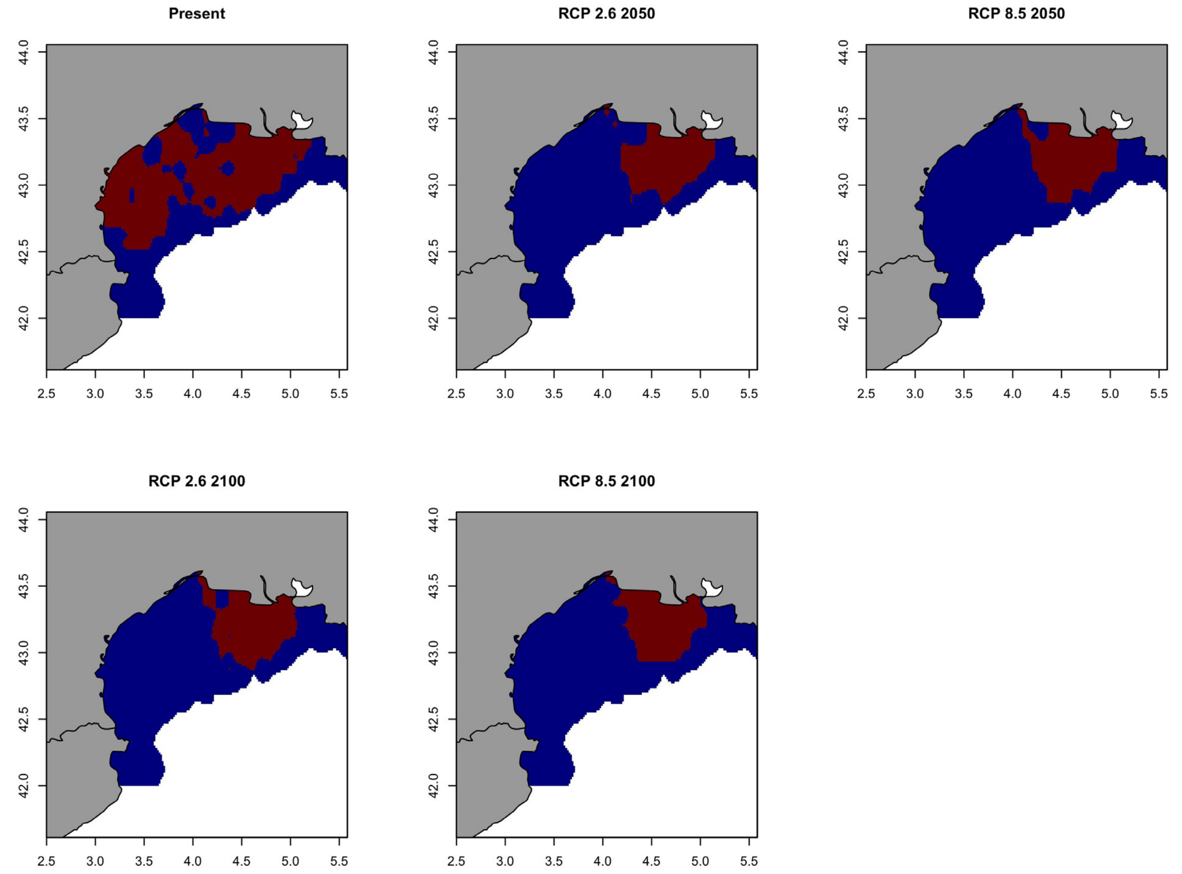


FIGURE 15 | Climate refuges, hot-spots of the probability of occurrence (>0.7) of the European anchovy (*Engraulis encrasicolus*) in Geographical Sub-Area 07 for the present situation and using IPCC pathway scenarios obtained with RAC-BRT models. Red color indicates probability of occurrence >0.7, while blue <0.7.

change in concentration of the species from coastal to deeper waters. The last years of historical time series showed a more profound decline. Overall, range contractions during periods of decline in biomass have been observed in a number of different species in the northwest Atlantic including yellowtail flounder (Simpson and Walsh, 2004) and Atlantic cod (Atkinson et al., 1997). The range contraction and expansion are consistent with McCall's basin hypothesis (MacCall, 1990), where during periods of low biomass, species concentrated in preferred habitats as density-dependent effects declined, and would be in line with recent studies in the Cantabrian Sea (Cabrero et al., 2019). Interestingly, spatially modeled acoustic biomass surveys data for both species in GSA07 obtained similar results (Saraux et al., 2014). This is an indicator that occurrence data from MEDITS could be a complementary descriptor for the distribution of these species.

Also, as for the case of the anchovy, the contraction in the distribution observed in 2013 in both GSAs, coincided with the year before the minimum values of body condition for sardine 2014 (Brosset et al., 2017).

In general, the geographical distribution of the studied species was highly variable from year-to-year, which was expected as these species have a highly mobile behavior and are affected mostly by dynamic environmental factors, which change from year to year. In this sense, averaged environmental functional responses obtained with RAC-BRTs for the entire time series coincide to identify a negative relationship between depth for both anchovy and sardine. These results were in line with several studies that linked anchovy and sardines' indexes to shallower waters (Giannoulaki et al., 2008; Carpi et al., 2015; Bonanno et al., 2016), showing preferences for areas shallower than 100 m (Bellido et al., 2008). Tugores et al. (2011) found a higher probability of occurrence for sardine in waters less than 65 m depth during summer in GSA06. In GSA07, Saraux et al. (2014) identified preferential areas close to the coast for anchovies (isobaths of ˜70 to 100 m) and near the coast and in the Western part of the Gulf of Lions for sardines. RAC-BRTs also captured a mainly positive relationship with primary productivity, while the relationships with temperature and salinity were not linear and showed some thresholds in agreement to what has been found in the literature (Palomera et al., 2007; Fernandez et al., submitted).

Interestingly, and despite the different historical trajectories of anchovy and sardine in the study area, future pathway projection for these two species highlighted that both anchovy and sardine will undergo a reduction in their spatial distributions in both GSA06 and GSA07 due to future climate conditions. Due to the mid trophic level position of sardines and anchovies and their key roles in the ecosystem of the western Mediterranean Sea (Coll et al., 2008, 2019), a reduction on their populations could impact the ecosystem dynamics across entire marine food web, from species that mainly prey on these forage fish to the dynamics of plankton (Tudela and Palomera, 1999; Navarro et al., 2017; Coll et al., 2019). For both species, optimal environmental values (SST and SSS) will be exceeded, first for sardine but eventually for anchovy, too, in combination with a reduction of eggs and larvae of anchovy in the last decades in GSA06 (Maynou et al., 2020) since the reproduction success of sardine and anchovy are highly influenced by SST and SSS condition (Palomera et al., 2007). The areas that will keep a probability of occurrence higher than 0.70 are around the Rhone River in the GSA07 and around the Ebro river in the GSA06 for both sardine and anchovy, and waters around the Gulf of Alicante for anchovy. This coastal area close to the river delta, might be preferred areas in the future, due to the river runoff that could compensate the changes expected from an increase of SST, with increasing stratification of the water column affecting the plankton dynamics to a lower biomass or changes in composition (Calvo et al., 2011). Optimistic and pessimistic IPCC pathway scenarios result in very similar future outcomes for both species and this is probably due to the fact that the most drastic changes will already occur in 2050 for these species and will continue until 2100.

Nowadays pathway scenarios did not include how the river waters itself will change in the future. Future studies should assess whether and how river waters and land use will affect species distribution predictions. However, the identified areas could be seen as "*future climate refuges*" for these species. Identifying areas that are most likely to persist under adverse climate change conditions in the future is important for anticipating the complex impacts that climate change will have on ecosystems and societies (Monsarrat et al., 2019). The socio-ecological implications of some species that recolonize part of their historical niche or occupy new areas should be carefully considered, in particular for species with a high socio-ecological interest such as small pelagic fishes.

These results are especially relevant to elaborate spatially explicit management plan (e.g., Marine Spatial Planning, MPA, etc.) for small pelagic species. Indeed, they show that despite the high mobility of small pelagic fish and high interannual variability, some areas consistently offer favorable habitats and should be prioritize for conservation measures and marine spatial planning.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: The dataset was received from an European Data Call for the development of SPELMED project and we are not authorized to share it. Requests to access these datasets should be directed to "European Data Call" or MC, mcoll@icm.csic.es, and JB, josem.bellido@ieo.es.

AUTHOR CONTRIBUTIONS

MP and MC designed the research. MP, EF-C, and MC performed the research. MP, EF-C, and JS analyzed the data. All authors wrote the manuscript.

FUNDING

This study was carried out within the Spanish Research project PELWEB (CTM2017-88939-R) funded by the Spanish Ministry of Science, Innovation and Universities, the European Research Contract SPELMED (EASME/EMFF/2016/032) funded by the ECEASME and the Catalonian Government PELCAT projects (CAT 152CAT00013 and TAIS ARP059/19/00005). The information and views set out in this publication are those of the author(s) and do not necessarily reflect the official opinion of the Executive Agency for Small- and Medium-sized Enterprises (EASME) or of the European Commission. Neither EASME, nor the Commission can guarantee the accuracy of the data included in this publication. Neither EASME, nor the Commission or any person acting on the EASME's or on the Commission's behalf may be held responsible for the use which may be made of the information contained therein.

ACKNOWLEDGMENTS

Thanks are due to the General Secretariat of Fisheries of the Spanish Ministry of Agriculture, Food and Environment (MAPAMA) for providing fishery landings data from GSA06. Thanks are also due to European institutions to provide GSA07 fishery landings data and survey data throughout a European Data Call for the development of SPELMED project.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00622/full#supplementary-material

REFERENCES

Albo-Puigserver, M., Navarro, J., Coll, M., Layman, C. A., and Palomera, I. (2016). Trophic structure of pelagic species in the northwestern Mediterranean Sea. *J. Sea Res.* 117, 27–35. doi: 10.1016/j.seares.2016.09.003

Albo-Puigserver, M., Giráldez, A., Hidalgo, M., Ramírez, J. G., Torres, P., Massaro, A., et al. (2018). *Report on Historical Reproductive Pattern (Size and Age at First Maturity and Reproductive Period).* Evaluation of the population status and specific management alternatives for the small pelagic fish stocks in the Northwestern Mediterranean

Sea (SPELMED) - SC NR. 02 - TENDEREASME/EMFF/2016/32 D1.3.2.2, 29.

Anonymous (2008). *Adoption of a Common Protocol for MEDiterranean Acoustic Surveys (MEDIAS) in the Framework of European Data Collection Regulation. Athens, 25-26 February 2008. Sterring Committee Report*. Available at http://www.medias-project.eu/medias/website/meetingrep.html.

Atkinson, D. B., Rose, G. A., Murphy, E. F., and Bishop, C. A. (1997). Distribution changes and abundance of northern cod (*Gadus morhua*), 1981 1993. *Can. J. Fish. Aquat. Sci.* 54, 132–138. doi: 10.1139/cjfas-54-s1-132

Bacha, M., Moali, A., Benmansour, N. E., Brylinski, J. M., Mahe, K., and Amara, R. (2010). Relationships between age, growth, diet and environmental parameters for anchovy (*Engraulis encrasicolus* L.) in the Bay of Bénisaf (SW Mediterranean, west Algerian coast). *Cybium* 34, 47–57.

Bakun, A. (2006). Wasp-waist populations and marine ecosystem dynamics: navigating the "predator pit" topographies. *Prog. Oceanogr.* 68, 271–288. doi: 10.1016/j.pocean.2006.02.004

Barcala, E., Bellido, J. M., Bellodi, A., Carbonara, P., Carlucci, R., Casciaro, L., et al. (2020). Spatio-temporal variability in the distribution pattern of anglerfish species in the Mediterranean Sea. *Sci. Mar.* 83, 129–139.

Basilone, G., Guisande, C., Patti, B., Mazzola, S., Cuttitta, A., Bonanno, A., et al. (2006). Effect of habitat conditions on reproduction of the European anchovy (*Engraulis encrasicolus*) in the Strait of Sicily. *Fish. Oceanogr.* 15, 271–280. doi: 10.1111/j.1365-2419.2005.00391.x

Basilone, G., Mangano, S., Pulizzi, M., Fontana, I., Giacalone, G., Ferreri, R., et al. (2017). European anchovy (*Engraulis encrasicolus*) age structure and growth rate in two contrasted areas of the Mediterranean Sea: the paradox of faster growth in oligotrophic seas. *Mediterr. Mar. Sci.* 18, 504–516.

Bellido, J. M., Brown, A. M., Valavanis, V. D., Giráldez, A., Pierce, G. J., Iglesias, M., et al. (2008). Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. *Hydrobiologiain* 612, 171–184. doi: 10.1007/978-1-4020-9141-4_13

Bennett, K. D., and Provan, J. (2008). What do we mean by 'refugia'? *Q. Sci. Rev.* 27, 2449–2455. doi: 10.1016/j.quascirev.2008.08.019

Bertrand, J. A., De Sola, L. G., Papaconstantinou, C., Relini, G., and Souplet, A. (2002). The general specifications of the MEDITS surveys. *Sci. Mar.* 66, 9–17.

Bivand, R., Altman, M., Anselin, L., Assunção, R., Berke, O., Bernat, A., et al. (2015). *Package 'spdep'*. Available online at: ftp://garr. tucows. com/mirrors/CRAN/web/packages/spdep/spdep. pdf (accessed 9 December 2015).

Bonanno, A., Barra, M., Basilone, G., Genovese, S., Rumolo, P., Goncharov, S., et al. (2016). Environmental processes driving anchovy and sardine distribution in a highly variable environment: the role of the coastal structure and riverine input. *Fish. Oceanogr.* 25, 471–490. doi: 10.1111/fog.12166

Bosc, E., Bricaud, A., and Antoine, D. (2004). Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. *Glob. Biogeochem. Cycles* 18:GB1005. doi: 10.1029/2003GB002034

Breiman, L. (2001). Random forests. *Mach. Learn.* 45, 5–32.

Brosset, P., Fromentin, J. M., Van Beveren, E., Lloret, J., Marques, V., Basilone, G., et al. (2017). Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. *Prog. Oceanogr.* 151, 149–162. doi: 10.1016/j.pocean.2016.12.002

Brosset, P., Ménard, F., Fromentin, J., Bonhommeau, S., Bigot, J., Bourdeix, J., et al. (2015). Influence of environmental variability and age on the body condition of small pelagic fish in the Gulf of Lions. *Mar. Ecol. Prog. Ser.* 529, 219–231. doi: 10.3354/meps11275

Cabrero, Á., González-Nuevo, G., Gago, J., and Cabanas, J. M. (2019). Study of sardine (*Sardina pilchardus*) regime shifts in the Iberian Atlantic shelf waters. *Fish. Oceanogr.* 28, 305–316. doi: 10.1111/fog.12410

Calvo, E., Simó, R., Coma, R., Ribes, M., Pascual, J., Sabatés, A., et al. (2011). Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. *Clim. Res.* 50, 1–29. doi: 10.3354/cr01040

Carpi, P., Martinelli, M., Belardinelli, A., Russo, A., Arneri, E., Coluccelli, A., et al. (2015). Coupling an oceanographic model to a Fishery Observing System through mixed models: the importance of fronts for anchovy in the Adriatic Sea. *Fish. Oceanogr.* 24, 521–532. doi: 10.1111/fog.12126

Checkley, D. M., Alheit, J., Oozeki, Y., and Roy, C. (2009). *Climate Change and Small Pelagic Fish*. Cambridge: Cambridge University Press.

Coll, M., Albo-Puigserver, M., Navarro, J., Palomera, I., and Dambacher, J. M. (2019). Who is to blame? Plausible pressures on small pelagic fish population changes in the northwestern Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 617, 277–294. doi: 10.3354/meps12591

Coll, M., and Bellido, J. M. (2018). Evaluation of the population status and Specific Management Alternatives for the Small Pelagic Fish Stocks in the Northwestern Mediterranean Sea (SPELMED) - Final Report SC NR 02 - TENDER EASME/EMFF/2016/32 – SPELMED.

Coll, M., Palomera, I., Tudela, S., and Dowd, M. (2008). Food-web dynamics in the South Catalan Sea ecosystem (NW Mediterranean) for 1978–2003. *Ecol. Modell.* 217, 95–116. doi: 10.1016/j.ecolmodel.2008.06.013

Costalago, D., Garrido, S., and Palomera, I. (2015). Comparison of the feeding apparatus and diet of European sardines *Sardina pilchardus* of Atlantic and Mediterranean waters: ecological implications. *J. Fish Biol.* 86, 1348–1362. doi: 10.1111/jfb.12645

Crase, B., Liedloff, A. C., and Wintle, B. A. (2012). A new method for dealing with residual spatial autocorrelation in species distribution models. *Ecography* 35, 879–888. doi: 10.1111/j.1600-0587.2011.07138.x

Cury, P., Bakun, A., Crawford, R. J., Jarre, A., Quinones, R. A., Shannon, L. J., et al. (2000). Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES J. Mar. Sci.* 57, 603–618. doi: 10.1006/jmsc.2000.0712

Cury, P., and Roy, C. (1989). Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.* 46, 670–680. doi: 10.1139/f89-086

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., et al. (2011). Global seabird response to forage fish depletion—one-third for the birds. *Science* 334, 1703–1706. doi: 10.1126/science.1212928

Doray, M., Masse, J., and Petitgas, P. (2010). *Pelagic Fish Stock Assessment by Acoustic Methods at Ifremer, Internal report*. Available online at: epic.awi.de/33739/1/ifremer-acoustic-methods.pdf

Elith, J., Leathwick, J. R., and Hastie, T. (2008). A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813. doi: 10.1111/j.1365-2656.2008.01390.x

Escalle, L., Pennino, M. G., Gaertner, D., Chavance, P., Delgado, de Molina, A., et al. (2016). Environmental factors and megafauna spatio-temporal co-occurrence with purse-seine fisheries. *Fish. Oceanogr.* 25, 433–447. doi: 10.1111/fog.12163

Estrada, M. (1996). Primary production in the northwestern Mediterranean. *Sci. Mar.* 60, 55–64.

FAO (2018). *The State of Mediterranean and Black Sea fisheries 2018. General Fisheries Commission for the Mediterranean*. Rome: FAO.

Fauchald, P., Skov, H., Skern-Mauritzen, M., Johns, D., and Tveraa, T. (2011). Wasp-waist interactions in the North Sea ecosystem. *PLoS One* 6:e22729. doi: 10.1371/journal.pone.0022729

Fernández Corredor, E. (2018). *Review on the Influence of Environmental Variables in European Anchovy (Engraulis encrasicolus) and European Sardine (Sardina pilchardus) Ecology in the Mediterranean Sea, Environmental Biology*. Barcelona: Autonomous University of Barcelona, 41.

Fielding, A. H., and Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49. doi: 10.1017/s0376892997000088

Foote, K. G. (1987). Fish target strengths for use in echo integrator surveys. *J. Acoust. Soc. Am.* 82, 981–987. doi: 10.1121/1.395298

Ganias, K. (2009). Linking sardine spawning dynamics to environmental variability. *Estuar. Coast. Shelf Sci.* 84, 402–408. doi: 10.1016/j.ecss.2009.07.004

Giannoulaki, M., Iglesias, M., Tugores, M. P., Bonanno, A., Patti, B., De Felice, A., et al. (2013). Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages. *Fish. Oceanogr.* 22, 69–89. doi: 10.1111/fog.12005

Giannoulaki, M., Pyrounaki, M. M., Liorzou, B., Leonori, I., Valavanis, V. D., Tsagarakis, K., et al. (2011). Habitat suitability modelling for sardine juveniles (*Sardina pilchardus*) in the Mediterranean Sea. *Fish. Oceanogr.* 20, 367–382. doi: 10.1111/j.1365-2419.2011.00590.x

Giannoulaki, M., Valavanis, V. D., Palialexis, A., Tsagarakis, K., Machias, A., Somarakis, S., et al. (2008). Modelling the presence of anchovy Engraulis encrasicolus in the Aegean Sea during early summer, based on satellite environmental data. *Hydrobiologia* 612, 225–240. doi: 10.1007/s10750-008-9498-6

Gómez-Campos, E., Borrell, A., Cardona, L., Forcada, J., and Aguilar, A. (2011). Overfishing of small pelagic fishes increases trophic overlap between immature and mature striped dolphins in the Mediterranean Sea. *PLoS One* 6:e24554. doi: 10.1371/journal.pone.0024554

Hijmans, R. J., Phillips, S., Leathwick, J., Elith, J., and Hijmans, M. R. J. (2017). Package 'dismo'. *Circles* 9, 1–68.

Katara, I., Pierce, G. J., Illian, J., and Scott, B. E. (2011). Environmental drivers of the anchovy/sardine complex in the Eastern Mediterranean. *Hydrobiologia* 670, 49–65. doi: 10.1007/s10750-011-0693-5

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., et al. (2012). Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob. Ecol. Biogeogr.* 21, 393–404. doi: 10.1111/j.1466-8238.2011.00686.x

Kuhn, M. (2008). Building predictive models in R using the caret package. *J. Stat. Softw.* 28, 1–26.

MacCall, A. D. (1990). *Dynamic Geography of Marine Fish Populations*. Seattle, WA: Washington Sea Grant Program.

Machias, A., Pyrounaki, M. M., Leonori, I., Basilone, G., Iglesias, M., De Felice, A., et al. (2013). Catch of pelagic hauls in Mediterranean acoustic surveys: Is it the same between day and night? *Sci. Mar.* 77, 69–79. doi: 10.3989/scimar.03656.21d

Martín, P., Bahamon, N., Sabatés, A., Maynou, F., Sánchez, P., and Demestre, M. (2008). "European anchovy (*Engraulis encrasicolus*) landings and environmental conditions on the Catalan Coast (NW Mediterranean) during 2000–2005," in *Essential Fish Habitat Mapping in the Mediterranean*, ed. V. D. Valavanis (Dordrecht: Springer), 185–199. doi: 10.1007/978-1-4020-9141-4_14

Martín, P., Sabatés, A., Lloret, J., and Martin-Vide, J. (2012). Climate modulation of fish populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) production in the north-western Mediterranean. *Clim. Change* 110, 925–939. doi: 10.1007/s10584-011-0091-z

Martínez-Minaya, J., Cameletti, M., Conesa, D., and Pennino, M. G. (2018). Species distribution modeling: a statistical review with focus in spatio-temporal issues. *Stoch. Environ. Res. Risk Assess.* 32, 3227–3244. doi: 10.1007/s00477-018-1548-7

Maynou, F., Sabatés, A., and Raya, V. (2020). Changes in the spawning habitat of two small pelagic fish in the Northwestern Mediterranean. *Fish. Oceanogr.* 29, 201–213. doi: 10.1111/fog.12464

Maynou, F., Sabatés, A., and Salat, J. (2014). Clues from the recent past to assess recruitment of Mediterranean small pelagic fishes under sea warming scenarios. *Clim. Change* 126, 175–188. doi: 10.1007/s10584-014-1194-0

Mellon-Duval, C., Harmelin-Vivien, M., Métral, L., Loizeau, V., Mortreux, S., Roos, D., et al. (2017). Trophic ecology of the European hake in the Gulf of Lions, northwestern Mediterranean Sea. *Sci. Mar.* 81, 7–18.

Monsarrat, S., Jarvie, S., and Svenning, J. C. (2019). Anthropocene refugia: integrating history and predictive modelling to assess the space available for biodiversity in a human-dominated world. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 374:20190219. doi: 10.1098/rstb.2019.0219

Navarro, J., Louzao, M., Igual, J. M., Oro, D., Delgado, A., Arcos, J. M., et al. (2009). Seasonal changes in the diet of a critically endangered seabird and the importance of trawling discards. *Mar. Biol.* 156, 2571–2578. doi: 10.1007/s00227-009-1281-3

Navarro, J., Sáez-Liante, R., Albo-Puigserver, M., Coll, M., and Palomera, I. (2017). Feeding strategies and ecological roles of three predatory pelagic fish in the western Mediterranean Sea. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 140, 9–17. doi: 10.1016/j.dsr2.2016.06.009

Olivar, M. P., Salat, J., and Palomera, I. (2001). Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 217, 111–120. doi: 10.3354/meps217111

Ospina-Álvarez, A., Bernal, M., Catalan, I. A., Roos, D., Bigot, J. L., and Palomera, I. (2013). Modeling fish egg production and spatial distribution from acoustic data: a step forward into the analysis of recruitment. *PLoS One* 8:e73687. doi: 10.1371/journal.pone.0073687

Palomera, I., Olivar, M. P., Salat, J., Sabatés, A., Coll, M., García, A., et al. (2007). Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Prog. Oceanogr.* 74, 377–396. doi: 10.1016/j.pocean.2007.04.012

Piroddi, C., Coll, M., Liquete, C., Macias, D., Greer, K., Buszowski, J., et al. (2017). Historical changes of the Mediterranean Sea ecosystem: modelling the role and impact of primary productivity and fisheries changes over time. *Sci. Rep.* 7:44491.

Quattrocchi, F., Mamouridis, V., and Maynou, F. (2016). Occurrence of adult anchovy in Catalonia (NW Mediterranean) in relation to sea surface conditions. *Sci. Mar.* 80, 457–466.

Quattrocchi, F., and Maynou, F. (2017). Environmental drivers of sardine (*Sardina pilchardus*) in the Catalan Sea (NW Mediterranean Sea). *Mar. Biol. Res.* 13, 1003–1014. doi: 10.1080/17451000.2017.1331039

Ramirez, J. G., Giráldez, A., Bellido, J. M., Coll, M., and Maynou, F. (2018). *Report on Stock Status and reference points. SC NR* 02 - TENDER EASME/EMFF/2016/32 – SPELMED: Evaluation of the population status and specific management alternatives for the small pelagic fish stocks in the Northwestern Mediterranean Sea. 119.

R Core Team (2019). *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna.

Recasens, L., Lombarte, A., Morales-Nin, B., and Tores, G. J. (1998). Spatiotemporal variation in the population structure of the European hake in the NW Mediterranean. *J. Fish Biol.* 53, 387–401. doi: 10.1111/j.1095-8649.1998.tb00988.x

Sabatés, A., Olivar, M. P., Salat, J., Palomera, I., and Alemany, F. (2007). Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Prog. Oceanogr.* 74, 355–376. doi: 10.1016/j.pocean.2007.04.017

Sabatés, A. N. A., Martín, P., Lloret, J., and Raya, V. (2006). Sea warming and fish distribution: the case of the small pelagic fish, *Sardinella aurita*, in the western Mediterranean. *Glob. Change Biol.* 12, 2209–2219. doi: 10.1111/j.1365-2486.2006.01246.x

Saraux, C., Fromentin, J. M., Bigot, J. L., Bourdeix, J. H., Morfin, M., Roos, D., et al. (2014). Spatial structure and distribution of small pelagic fish in the northwestern Mediterranean Sea. *PLoS One* 9:e111211. doi: 10.1371/journal.pone.0111211

Saraux, C., Van Beveren, E., Brosset, P., Queiros, Q., Bourdeix, J. H., Dutto, G., et al. (2019). Small pelagic fish dynamics: a review of mechanisms in the Gulf of Lions. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 159, 52–61. doi: 10.1016/j.dsr2.2018.02.010

Sbrana, M., De Ranieri, S., Ligas, A., Reale, B., Rossetti, I., and Sartor, P. (2010). *Comparison of Trawl Survey and Commercial Data on Small Pelagics from the FAO Geographic Sub-Area 9 (Western Mediterranean)*. Available online at: http://www.ciesm.org/online/archives/abstracts/pdf/39/PG_0658.pdf

Scientific Technical and Economic Committee for Fisheries [STECF] (2016). *The 2016 Annual Economic Report on the EU Fishing Fleet (STECF*. Brussels: European Union.

Simpson, M. R., and Walsh, S. J. (2004). Changes in the spatial structure of Grand Bank yellowtail flounder: testing MacCall's basin hypothesis. *J. Sea Res.* 51, 199–210. doi: 10.1016/j.seares.2003.08.007

Strobl, C., Malley, J., and Tutz, G. (2009). An introduction to recursive partitioning: rationale, application, and characteristics of classification and regression trees, bagging, and random forests. *Psychol. Methods* 14, 323–348. doi: 10.1037/a0016973

Tudela, S., and Palomera, I. (1999). Potential effect of an anchovy-mediated pump on the vertical availability of nitrogen for primary production in the Catalan Sea (northwest Mediterranean). *J. Sea Res.* 42, 83–92. doi: 10.1016/s1385-1101(99)00018-0

Tugores, M. P., Giannoulaki, M., Iglesias, M., Bonanno, A., Tièina, V., Leonori, I., et al. (2011). Habitat suitability modelling for sardine *Sardina pilchardus* in a highly diverse ecosystem: the Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 443, 181–205. doi: 10.3354/meps09366

UNEP-MAP-RAC/SPA (2013). *Fisheries in the Gulf of Lions*, ed. H. Farrugio (Tunis: RAC/SPA), 79.

Van Beveren, E., Bonhommeau, S., Fromentin, J. M., Bigot, J. L., Bourdeix, J. H., Brosset, P., et al. (2014). Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean. *Mar. Biol.* 161, 1809–1822. doi: 10.1007/s00227-014-2463-1

Van Beveren, E., Fromentin, J. M., Rouyer, T., Bonhommeau, S., Brosset, P., and Saraux, C. (2016). The fisheries history of small pelagics in the Northern Mediterranean. *ICES J. Mar. Sci.* 73, 1474–1484. doi: 10.1093/icesjms/fsw023

Vilela, R., and Bellido, J. M. (2015). Fishing suitability maps: helping fishermen reduce discards. *Can. J. Fish. Aquat. Sci.* 72, 1191–1201. doi: 10.1139/cjfas-2013-0522

Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., and Zemla, J. (2017). Package 'corrplot'. *Statistician* 56, 316–324.

Wickham, H. (2011). ggplot2. *Wiley Interdiscip. Rev. Comput. Stat.* 3, 180–185. doi: 10.1002/wics.147

Zarrad, R., Missaoui, H., Alemany, F., Hamza, A., Romdhane, M. S., García, A., et al. (2008). Distribution and abundance of early life stages of *Sardina pilchardus* in the Gulf of Tunis (Central Mediterranean Sea) in relation to environmental and biological factors. *Sci. Mar.* 72, 299–309.

Zorica, B., Vilibiæ, I., Keè, V. È, and Šepiæ, J. (2013). Environmental conditions conducive to anchovy (*Engraulis encrasicolus*) spawning in the Adriatic Sea. *Fish. Oceanogr.* 22, 32–40. doi: 10.1111/fog.12002

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 31 July 2020
doi: 10.3389/fmars.2020.00604

Impact of Climate Change on Wintering Ground of Japanese Anchovy (*Engraulis japonicus*) Using Marine Geospatial Statistics

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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: 23 March 2020
Accepted: 30 June 2020
Published: 31 July 2020

Citation:
Liu S, Liu Y, Alabia ID, Tian Y, Ye Z, Yu H, Li J and Cheng J (2020) Impact of Climate Change on Wintering Ground of Japanese Anchovy (Engraulis japonicus) Using Marine Geospatial Statistics. Front. Mar. Sci. 7:604. doi: 10.3389/fmars.2020.00604

The distribution and fluctuations in abundance of small pelagic species such as anchovy are largely affected by climate change. We hypothesized that the future projected rise in temperature will result to a northward shift of Japanese anchovy (*Engraulis japonicus*) habitat and a subsequent increase in relative abundance. To test this hypothesis, we explored the link between Japanese anchovy abundance and environmental conditions using machine-learning and statistical models. The models were fitted with catch per unit effort (CPUE) as the response variable and remotely sensed data of sea surface temperature (SST), sea surface chlorophyll-a (Chl-a), assimilated information of sea surface salinity (SSS), meridional and zonal ocean currents, and depth as environmental covariates. Our results showed that the abundance of *E. japonicus* was significantly influenced by environmental factors. In particular, salinity front and SST highlight strong relationships with winter CPUE distribution. Based on these models, the results reinforced our hypothesis and showed that the warming ocean will drive a substantial shift in Japanese anchovy habitat in the China seas. SST and CPUE showed negative correlations with the El Niño Southern Oscillation (ENSO) index. These findings underpin ramifications of the climate-driven habitat shift of small pelagic fish species on the regional marine ecosystem in the China seas.

Keywords: Japanese anchovy, habitat characterization, salinity front, abundance distribution models, climate change

INTRODUCTION

Climate change is considered as one of the major drivers of the fluctuations in abundance and distributions of small pelagic fish resources such as anchovy (Lecomte et al., 2004). For instance, European anchovy in the northern British waters is expected to shift northward in response to climate change (Pinnegar et al., 2017). In the China seas, Japanese anchovy is also highly susceptible to climate change (Ma et al., 2019a). One of the climate phenomena that impacts fish resources is the El Niño Southern Oscillation (ENSO), which is a coupled atmosphere-ocean variability in the tropical Pacific Ocean. This event is also defined by indices such as the Niño1 + 2, which better captures the ENSO signal in winter (Trenberth and Stepaniak, 2001; Hanley et al., 2003; Gen et al., 2010; Yan et al., 2017). During an El Niño, the surface temperature changes in the Yellow Sea (Wei et al., 2010), and the increase in precipitation enhances the riverine discharge from the Yangtze River, thus leading to salinity changes (Park et al., 2015). Many studies have found that fishery resource variations are closely linked to ENSO events. For instance, ENSO is shown to affect the hotspots and distributions of chub mackerel in the East China Sea (Yasuda et al., 2014) and also causes regional changes in the density of young Bluefin tuna in the East China Sea (Kitagawa et al., 2006). Fluctuation in abundance between the sardine and anchovy is influenced by ENSO (Brierley and Kingsford, 2009). Few studies to date have explored the relationship between climate change and the distribution of Japanese anchovy, specifically in the climate-sensitive waters of the China seas where ENSO was shown to affect its early life history (Tian et al., 2004; Kim et al., 2005). Thus, the impact of present and future marine environmental changes to fish resources deserves our attention. We proposed a hypothesis that a climate-driven temperature rise will result in the northward shift of anchovy habitat and increase of anchovy relative abundance. We tested this hypothesis using the climate projections from the IPCC (Intergovernmental Panel on Climate Change)–RCP (Representative Concentration Pathway) scenarios. The IPCC forecasts future climate change and discusses the impacts of climate change, future risks, and adaptation strategies. The R of the IPCC project global mean surface temperatures describe four scenarios (RCP 2.6, RCP4.5, RCP6.0, and RCP8.5) based on different greenhouse gas emissions (Nurdin et al., 2017; Silva et al., 2019). By the end of the 21st century (2081–2100), the IPCC-RCP scenarios projected that the global surface temperature would rise between 1.0°C and 3.7°C compared to the 1986–2005 baseline (IPCC, 2014b). Thus, this raises the urgent need to study the impacts of future climate change on fisheries. Using the Japanese anchovy as a model species to study this topic is likely to disclose processes and mechanisms similar to other small pelagic fisheries across the globe.

Japanese anchovy (*Engraulis japonicus*) is a widely distributed species and is particularly abundant in the northwestern Pacific region. It is a small pelagic fish that undergoes diurnal vertical migration and is considered a key species linking lower and upper trophic components of the food web (Zhao et al., 2008). Japanese anchovy is a forage fish that moves between its spawning, feeding, and wintering grounds (**Figure 1**). The separate stocks of Japanese anchovy do not exist in the Yellow Sea and East China Sea (Zheng et al., 2015). During the onset of its spawning migration in late March, Japanese anchovy migrates north and northwest of the basin and spawns from June to August. After spawning, *E. japonicus* commences its feeding migration and shifts south from November toward its wintering grounds in the Yellow Sea and the East China Sea, where it has the most concentrated and stable stock in winter (December to March) (Zhao, 2006). Therefore, our analyses are focused on the wintering ground of Japanese anchovy in these waters, and it exists in the eastern and southern regions of the Yellow Sea. It is also concentrated in the northern East China Sea and around Jeju Island, with the most considerable wintering ground in the central waters of the southern Yellow Sea (Kwon et al., 2012; Huang et al., 2014; Niu et al., 2014). We delineated the regions of the eastern and southern Yellow Sea and northern East China Sea as the winter fishing grounds (WFG). The monthly averaged CPUE within the winter fishing ground was calculated as the WFG CPUE index (ton h^{-1}). Chinese industrial trawl vessels catch Japanese anchovy, and the government implemented the summer fishing moratorium for protecting fishery resources (Jiang et al., 2009). Since the 1990s, the stock biomass of Japanese anchovy in the Yellow Sea has significantly declined from 4.12 million tons in 1993 to 1.75 million tons in 2000 based on acoustic surveys (Zhao et al., 2003). The fishing yield of Japanese anchovy declined from 1.26 million tons in 2001 to 0.52 million tons in 2009, which then increased to 0.95 million tons in 2015; the Japanese anchovy catch accounts for 10.56% concerning the total fish catches in China (Yuan and Zhao, 2016).

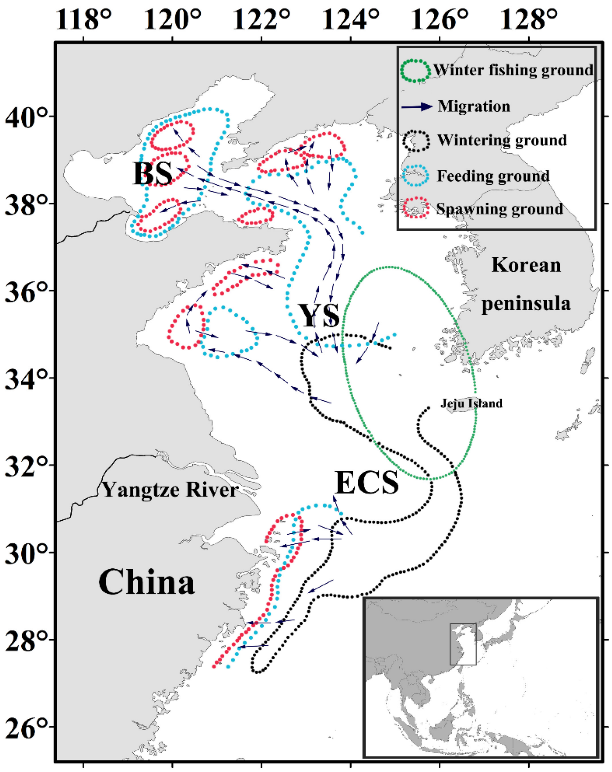

FIGURE 1 | Map showing the Japanese anchovy migration route modified from Zhu (1990) and Zhao (2006). The different regions comprising the China seas are indicated on the map, and overlain are the migration route (purple arrows), spawning (red), feeding (blue), wintering (black), and winter fishing (green) grounds.

In order to effectively monitor and manage the fishery for making sustainable utilization of marine resources, a number of geospatial statistical methods have been used to explore the relationships between environmental factors and species distributions. Among these statistical tools are machine learning methods such as random forest (RF) (Smoliñski and Radtke, 2017), generalized linear models (GLM) (Zhang et al., 2017), and generalized additive models (GAM) (Murase et al., 2009). As the applicability of models is dependent on the target species and regional differences, we constructed all three models to identify the best suited model for projecting the abundance and distribution of wintering Japanese anchovy in the northwestern Pacific region. Remote sensing technology could provide environmental information of suitable temporal and spatial resolution (Klemas, 2012). Moreover, Geographic Information Systems (GIS) technology provides analytical tools to extract environmental ranges from the spatial surveys and map the essential species habitats (Valavanis et al., 2008). Likewise, Simple Ocean Data Assimilation provides numerical model-derived data for comprehensive and accurate oceanographic information continuously corrected through the assimilation of observational data (Carton and Giese, 2008). It can be used complementary to remote sensing data for species-environment studies. Thus, the combination of GIS, remote sensing technology, and statistical models can provide scientific information for marine resource management (Mugo et al., 2011) and the design of appropriate policies to protect fishery resources.

The objectives of this study are (1) to elucidate wintering ground distributions of Japanese anchovy using multiple models; (2) to analyze the impacts of various environmental factors on Japanese anchovy, and (3) to investigate the effect of projected climate scenarios on its spatial and temporal distributions.

MATERIALS AND METHODS

Study Area and Target Species

The China seas consist of the waters of the Bohai Sea (BS), Yellow Sea (YS), East China Sea (ECS), and the South China Sea, and this study was conducted in regions of the Yellow Sea and East China Sea (26–42°N and 118–128°E) (**Figure 1**). The YS is a semi-enclosed shelf between China and the Korean Peninsula while the East China Sea is located south of the Yellow Sea (Dong et al., 2011) and links Chinese, Korean, and Japanese waters. The Yellow Sea and the East China Sea are affected by the tides and monsoon winds and influenced by the intrusion of the Kuroshio current (Xing et al., 2020). The China seas are also among the most productive fishery areas in the word (Ma et al., 2019b), which represent 66.10% of the total catch of the Japanese anchovy in the northern Pacific (FAO, 2017).

Fishery Data

Daily catch data of Japanese anchovy in China seas based on the double trawl surveys were provided by the East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences. These data were digitized and compiled into a monthly database from 2009 to 2015 (**Table 1**), which comprised the daily fishing locations (latitude and longitude), fishing dates, and catch per unit effort (CPUE), expressed in terms of tons/hour-boat day (ton/fishing boat-hours). We preprocessed the fishery data and averaged the CPUE when fishing activities were operated in the same location for many consecutive days within a month. An abnormally high CPUE or an abnormally low CPUE during a short fishing interval at the same fishing location were considered to be outliers. We then matched the fishery information with the environmental data at each specific date to obtain the database for fishing location and environmental data.

Environmental Variables

Remotely sensed Level 3 sea surface temperature (SST) and sea surface chlorophyll-a (Chl-a) were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data from 2009 to 2015[1] (**Table 2**). However, the numerical model-derived sea surface salinity (SSS), meridional (V) and zonal (U) current velocities from Simple Ocean Data Assimilation (SODA) v3.3.1 were downloaded from the APDRC data repository[2]. From the SSS data, salinity fronts were identified based on Cayula and Cornillon single-image edge detection algorithm (Cayula and Cornillon, 1992). Bathymetric data were also downloaded from the online database[3]. All data were resampled into a 0.01° spatial resolution.

Future Projections and Climate Index

The projection was based on different IPCC-RCP scenarios with temperature increases at 1.0°C, 1.8°C, 2.2°C, 3.7°C, for RCPs 2.6, 4.5, 6.0, and 8.5, respectively, at the end of the 21st century. The CPUE distributions of Japanese anchovy were predicted based on the temperature increases for different scenarios at the end of the 21st century. The anomalies were calculated as the difference between predicted CPUE based on different scenarios and the predicted CPUE in 2015. The index of Niño1 + 2 was

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[1] https://oceancolor.gsfc.nasa.gov/

[2] http://apdrc.soest.hawaii.edu/data/data.php

[3] https://www.ngdc.noaa.gov/mgg/global/

TABLE 1 | Summary information on the fishery data used for the analyses between January and December 2009–2015.

	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sep	Oct	Nov	Dec	Station No.
2009			■	■	■				■	■	■	■	90
2010	■	■			■				■	■	■	■	90
2011	■	■	■	■	■				■	■	■	■	77
2012	■	■	■	■	■				■	■	■	■	84
2013	■		■	■	■				■	■	■	■	38
2014	■								■	■	■		23
2015	■	■	■	■					■	■	■	■	35

Periods with and without available fishery information are presented in gray and white, respectively.

TABLE 2 | Summary of environmental data used for model construction and subsequent analyses.

Data sources	Variable (unit)	Spatial resolution	Temporal resolution
SODA	Salinity	0.5° × 0.5°	5 days
SODA	U (m s^{-1})	0.5° × 0.5°	5 days
SODA	V (m s^{-1})	0.5° × 0.5°	5 days
Etopo1 Global Relief Model	Depth (m)	1/60°	
MODIS	SST (°C)	4 km	8 days
MODIS	Chl-a (mg m^{-3})	4 km	8 days

The data sources and original spatial and temporal data resolutions are noted.

used to represent the ENSO events (Hanley et al., 2003) and was downloaded from the online data repository[4]. The wintering fishing ground CPUE index was used to analyze the relationship with mean SST in China seas and the Niño1 + 2 index.

Model Construct

We constructed a total of 63 GLMs, 31 GAMs, and 6 RF models using the stepwise add variable approach, and the intermediate results were shown in **Supplementary Material**. Here, environmental data (SSS, Depth, Chl-a, SST, U, and V) were used as the predictor variables in all models to predict the CPUE distribution of the Japanese anchovy. Marine Geospatial Ecology Tool (MGET) of ArcGIS 10.5, an add-in program for applying advanced analytical methods (Roberts et al., 2010), was used to detect the frontal features.

Generalized linear models generalizes the traditional linear models, which is an expansion of the maximum likelihood estimation in probit analysis that combines both systematic and random components in the model (Nelder and Wedderburn, 1972). GAM is a semi-parametric extension of a GLM and assumes that the functions are additive and the components are smooth. GAMs can deal with highly non-linear and non-monotonic relationships between the response and predictor variables (Guisan et al., 2002). Here, GAM is constructed using the "mgcv" package (Wood, 2006). The collinearity of all predictor variables was examined using the variable inflation factor (VIF) (**Supplementary Material 1**), where factors without collinearity have VIF values less than 5 (Cornic and Rooker, 2018). As all predictor variables have VIF below the cut-off, they were all used for constructing the models. In the construction of GAMs, the smoothing function used was the thin plate regression spline with "shrinkage" to get poorly performing predictor variables. Due to the low model contribution of V, this factor was disregarded to improve the model's predictive performance (Roberts et al., 2010). The CPUE follows a continuous distribution, logarithmic transformation was used to normalize the asymmetrical distribution, and a factor of 0.1 is commonly used in CPUE standardizations (**Supplementary Material 2.1**). GAM is modeled using the Gaussian distribution family (Solanki et al., 2017). The GAM Equation (1) and the GLM Equation (2) implemented were presented as follows:

$$g(Y) = a + \sum_{i=1}^{n} f_i(X_i) + \varepsilon \tag{1}$$

$$g(Y) = a + \sum_{i=1}^{n} \beta(X_i) + \varepsilon \tag{2}$$

Where g is the link function, Y is the response variable (CPUE), X_i is the predictor variables (SSC, Depth, Chl-a, SST, U, V), f_i is a spline smoothing function for each model predictor X_i, a, and β are model constants, and ε is a random error (Wood, 2006).

Finally, RF model is a classification method that uses multiple decision trees, which are used as statistical classifiers composed of tree predictors. RF generates decision trees based on predictor variables from the original database, and decision trees provide classification by a majority vote from trees (Breiman, 2001). The RF model is constructed using the "Random Forest" package (Liaw and Wiener, 2002).

Model Selection Method

Pearson's correlation coefficient was used to test the linear relationship between two variables by using a t-test; the tests of statistical significance levels used were 0.05 and 0.01 (Liu et al., 2014, 2018). In GLM and GAM, the addition of different predictor variables leads to changes in the deviance explained and Akaike's Information Criterion (AIC). Model selection was based on the contribution of the predictor variable, the highest values of deviance explained, and the lowest values of AIC (Johnson and Omland, 2004). For the RF models, the chi-square test and AIC results were not computed. Instead, the model selection was only based on the increases in deviance explained. Finally, the databases were used to construct RF, GLM, and GAM for the period between 2009 and 2014, and the best models of RF, GLM, and GAM were used to predict CPUE using monthly raster composites of environmental predictors in 2015. Model performance was evaluated by comparing the predicted and actual fishing CPUE in 2015.

RESULTS

Comparison of RF, GLM, and GAM

The final selected models for GLM, GAM, and RF (model, predictor variable, AIC, p-value, and deviance explained) are shown in **Table 3**. In GAM, the best-performing model has five predictor variables (SSS, Depth, Chl-a, SST, U) that were highly significant ($p < 0.01$) with the lowest AIC (217.53) and the highest deviance explained (36.7%). For GLM, the final selected model with three significant predictors (SSS, Chl-a, V; $p < 0.01$) had the lowest AIC (303.84) and a high explained variance (9.30%). In RF, the addition of predictor variables resulted in an increased deviance explained; hence, the model with six variables (SSS, Depth, Chl-a, SST, U, and V) was the selected model.

The predicted CPUE ranged from 0 to 2 tons per hour (ton h^{-1}) using the selected models for RF, GLM, and

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[4] https://www.ncdc.noaa.gov/teleconnections/enso/indicators/sst/

GAM. A histogram of residuals and normal quantile-quantile plots indicated that the distribution of residuals of GAM adequately conformed to the application of Gaussian distribution (**Supplementary Material 2.2**). **Figure 2** shows GAM was the best model by comparing the relationships between the predicted and actual CPUEs for each of the selected models. The GAM-based model showed the highest correlation ($R^2 = 0.72, p < 0.01$), which was greater than those from RF ($R^2 = 0.19, p < 0.01$) and GLM ($R^2 = 0.15, p < 0.05$).

Preferred Oceanographic Conditions for Japanese Anchovy

Generalized additive models analysis indicated that five variables such as SSS, Depth, Chl-a, SST, and U significantly influenced CPUE of Japanese anchovy ($p < 0.01$). The importance of each variable was ranked based on the deviance explained and AIC (**Table 4**).

The non-linear relationship between environment variables and CPUE is shown in **Figure 3**. GAM plots can be interpreted as the effect of each environmental variable on the CPUE. A narrow confidence interval represents high relevance. The positive effect of SSS on the CPUE was observed between 28 and 33. From 18.5 to 28 and 33 to 34.5 (**Figure 3A**), there were negative effects on the fish CPUE and the density of the data points within the former was lower with a wider confidence interval relative to the latter. A positive effect of depth on CPUE was observed between −50 and −110 m, while negative effects were noted from −30 to −50 m (**Figure 3B**). For Chl-a (**Figure 3C**), a positive effect on the CPUE is evident from 0.71 to 1.25 mg m^{-3}, and a negative effect was observed between 1.25 and 3.16 mg m^{-3}. The plot highlighted a positive effect on CPUE beyond 3.16 mg m^{-3}, but with a wide confidence interval. Considering the confidence interval and the fitted curve, a positive SST effect on CPUE was observed for ranges between 8–14°C and 19–22.5°C (**Figure 3D**).

TABLE 3 | List of the final selected models for GLM, GAM, and RF, with their predictor variables, AIC, *p*-value, and deviance explained (RF did not provide chi-square test and AIC results).

Model	Predictor variable	AIC	*p*-value	Deviance explained
GAM	SSS	217.53	7.7×10^{-14} **	36.7%
	Depth		0.000197 **	
	Lg(Chl-a)		0.006866 **	
	SST		0.000302 **	
	U		0.000800 **	
GLM	SSS	303.84	1.5×10^{-7} **	9.3%
	Chl-a		0.008404 **	
	V		0.000247 **	
RF	SSS			32.5%
	Depth			
	Chl-a			
	SST			
	U			
	V			

$^{**}p < 0.01$.

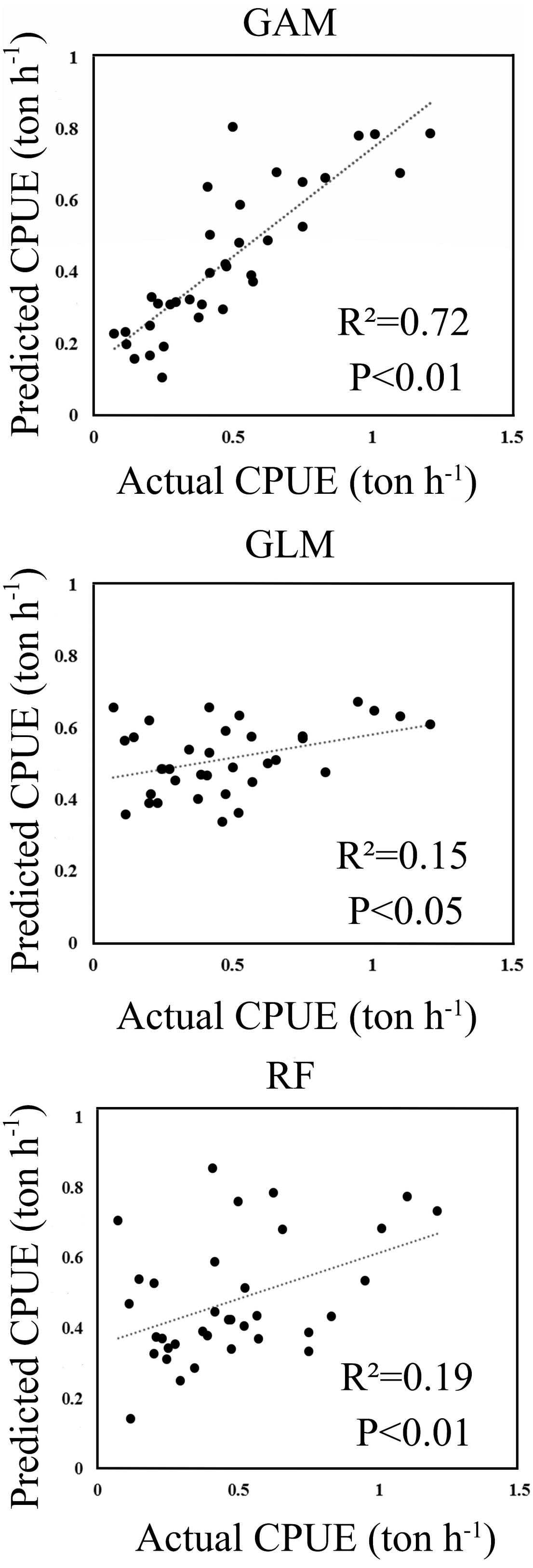

FIGURE 2 | The scatter plots of actual versus predicted CPUE computed within the wintering grounds in 2015.

TABLE 4 | GAM single parameter models.

Predictor variable	AIC	*p*-Value	Deviance explained
SSS	276.77	1.94×10^{-14} **	15.90%
Depth	314.08	7.57×10^{-6} **	9.03%
Lg(Chl-a)	321.98	0.00023 **	7.35%
SST	325.63	0.00152 **	5.36%
U	329.54	0.00867 **	4.94%

$^{**}p < 0.01$.

The positive effects of U on CPUE were captured between −0.09 and −0.02 m s^{-1}, between 0.01 and 0.04 m s^{-1} (**Figure 3E**).

The Distribution of Japanese Anchovy Prediction Wintering Ground CPUE

The distribution of monthly CPUE (ton h^{-1}) of Japanese anchovy predicted during the wintering period (2009–2015) using the GAM model is shown in **Figure 4**. Japanese anchovy was distributed in the eastern and southern parts of the Yellow Sea and the northern waters of the East China Sea. Its distribution also extended near the Yangtze River estuary and the Jeju Island. The black dots correspond to the actual fishing CPUE; the size of the symbol increases as the actual CPUE increases. The actual fishing locations coincided with regions of high predicted CPUE. The values of CPUE were predominantly highest in December and lowest in March. Generally, the CPUEs decreased in the Yellow Sea and increased in the East China Sea from December to March.

The Effect of Climate Change on the CPUE of Japanese Anchovy Stock in Winter

As shown in **Figures 5a–d**, the changes in CPUE are significantly different from under the four climate scenarios. We found that CPUE increased by 0.02, 0.03, 0.05, and 0.11 in the Yellow Sea for RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5 scenarios, respectively, but decreased by 0.01 for RCP 8.5 and a slight change in other scenarios in the East China Sea. The center of gravity of predicted CPUE moved northward (**Supplementary Material 2.3**) with a corresponding northward movement of winter habitat under increasing SST.

Correlation Between SST and the WFG CPUE Index

The SST showed that it decreased to 9.2°C in January 2011 and then increased to 10.5°C in February 2011 (**Figure 6**), but generally increased in China seas. The WFG CPUE index also tended to have an increasing trend from 2009 to 2015. In December, the WFG CPUE index was highest and declined as SST decreased. SST and WFG CPUE index showed a significant positive relationship ($R^2 = 0.69$, $p < 0.01$) (**Figure 7A**).

DISCUSSION

Impact of Environmental Variables on the CPUE of Japanese Anchovy

Our work proposed multiple marine statistical models to elucidate wintering ground distribution of Japanese anchovy, based on remotely sensed data and assimilated information. In the marine environment, the statistical model has been extensively used to predict species richness, diversity, and geographical abundance distributions (Smoliňski and Radtke, 2017). By comparing the predicted CPUE and the actual CPUE and the predicted and actual fishing ground locations, a multiple-models approach could generate the robust wintering ground predictions for Japanese anchovy. The spatial distribution of Japanese anchovy cannot be adequately monitored due to technical constraints and economic reasons, and the marine geospatial statistics model as an accurate and cost-effective technology could predict the inevitable gaps and species distribution in the unsurveyed area (Murase et al., 2009). The statistical models show the distribution of anchovy CPUE and infer the wintering ground of anchovy location. The model disclosed the impact of climate change on small pelagic fish by using Japanese anchovy as a model species; the result held the hypothesis that the rising temperature caused by climate change resulted in the shift of anchovy habitat northwardly and the increase of anchovy relative abundance. We could quantitatively evaluate the predictive ability of the marine statistical model through the comparison of different models for fishery resource protection and management application.

Freshwater discharge from the Yangtze River affects the salinity of the East China Sea (Delcroix and Murtugudde, 2002). The wide range of salinity preference of Japanese anchovy (**Figure 3A**) suggests that it can take advantage of nutrient-rich estuarine waters for foraging. The Changjiang Diluted Water makes the Yangtze River estuary and the adjacent East China Sea increasingly eutrophicated (Chai et al., 2006) and provides excellent feeding opportunities for the Japanese anchovy during their spawning and feeding migration. The concentration of winter fishing locations close to salinity fronts also supports these findings (**Figure 8**). The wintering migration of the Japanese anchovy is driven by temperature and salinity. A strong salinity front forms west of the Jeju Island in winter (Lie, 1985), where the wintering grounds for Japanese anchovy in the Yellow Sea coincides with the front near the Jeju Island (Huang et al., 2010). The Japanese anchovy catch in the south sea of the Korean peninsula accounted for 25% of the total catch in the adjacent waters (Kim and Kang, 2000). The salinity front created a good feeding environment for Japanese anchovy due to the accumulation of microalgae and zooplankton in the frontal region (Bertrand et al., 2002).

The salinity front is strongest in winter and is associated with topography (Chen, 2009). Depth is also relatively important for the CPUE distribution of the Japanese anchovy, where shallow waters (depth <50 m) generally exerted a negative effect on its CPUE. In the western margin of the North Pacific, depth indirectly plays an important role in the distribution of Japanese anchovy.

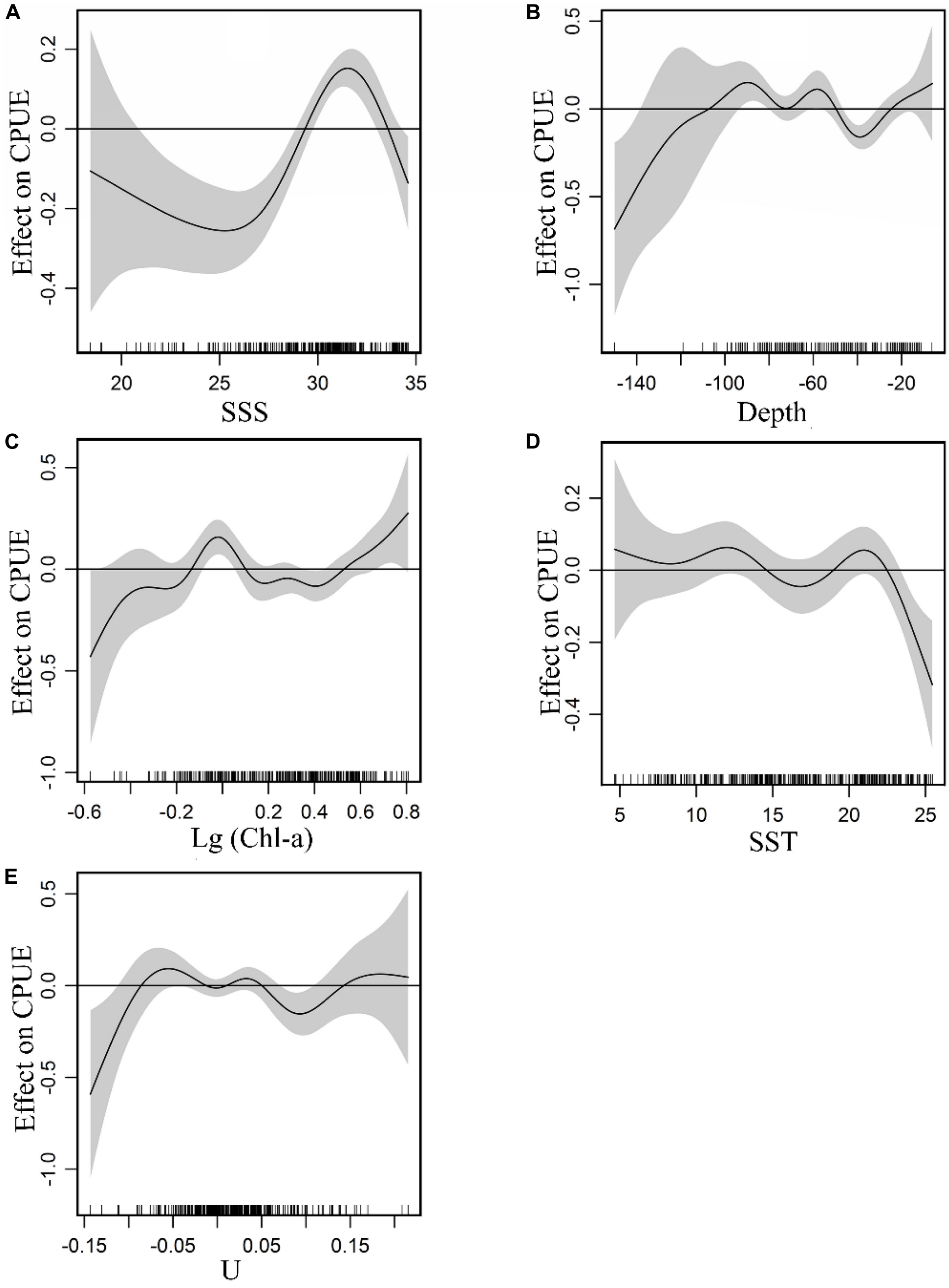

FIGURE 3 | Effect of environmental variables on CPUE: **(A)** SSS, **(B)** Depth, **(C)** Chl-a, **(D)** SST, **(E)** U. Gray-shaded areas representing 95% confidence intervals with rug plot on the *x*-axis representing actual fishing data points, and the solid curve shows fitted GAM functions that describe the effect of environmental variables on response variables (CPUE). GAM indicates that the environmental variable had a positive effect on CPUE when the fitted solid curve of the GAM function was above the zero axis.

Japanese anchovy feeds on zooplankton rather than the phytoplankton (Niu et al., 2014). The earlier study has reported that the catch of Japanese anchovy is related to Chl-a concentration (Ihsan et al., 2018). Chl-a and zooplankton were also shown to be positively correlated with the catch of Japanese anchovy (Kim and Kang, 2000). Micro-zooplankton provides food sources for Japanese anchovy during their spawning and feeding migration, and Chl-a plays an indirect role in the distribution of Japanese anchovy. However, there may be a time-delayed relationship between pelagic fish and primary productivity (Yen and Lu, 2016), and Japanese anchovy feed rarely during their winter migration (Zhu, 1990). This may account for low deviance explained obtained for Chl-a.

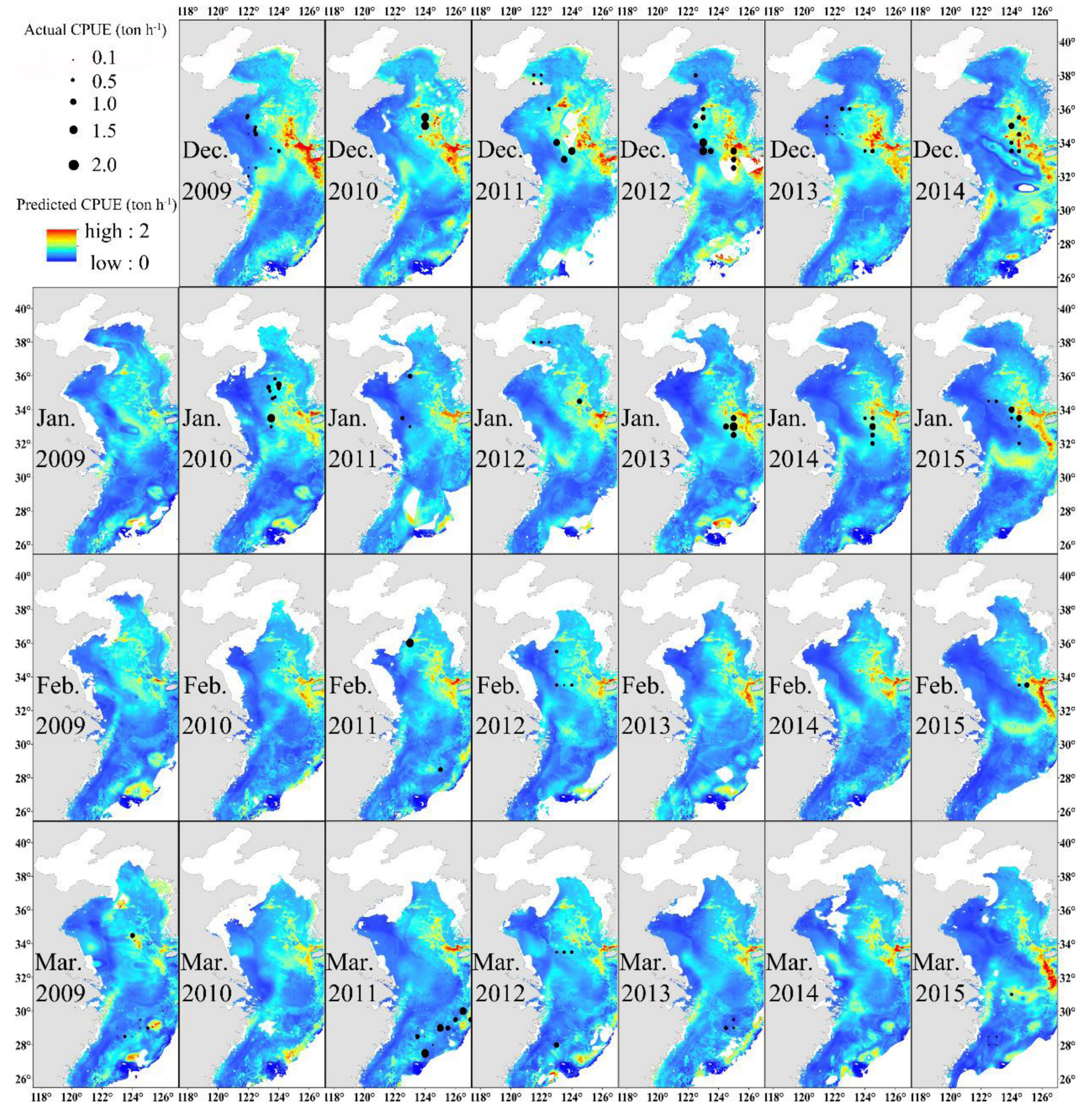

FIGURE 4 | Predicted Japanese anchovy CPUE (ton h^{-1}) overlaid with actual fishing CPUE (black dots) from December to March in 2009–2015.

Temperature plays a vital role in Japanese anchovy distribution (Hayashi et al., 2016). The SST range of positive effects on spawning and feeding migration is 19–22.5°C, and our results show that SST significantly influenced Japanese anchovy CPUE. The range between 8°C and 15°C was suitable for wintering Japanese anchovy, and it is concentrated between 11 and 13°C (Ma, 1989; Li et al., 2007). SST has a positive effect on the abundance of anchovy between 5°C and 9.5°C in winter (Niu et al., 2014). Our results were also consistent with the previous researches. The Japanese anchovy migrated vertically in the water layer (Zhao et al., 2008). The temperature experienced by the fish in different depth layers is the variable, and vertical change of temperature may be more influential to the distribution of Japanese anchovy and may explain the low deviance explained by SST.

The salinity front is related to the ocean current in the China seas (Chen, 2009). The current plays an indirect role in the distribution of the CPUE. In the sub-mesoscale physical process, plankton is concentrated as patches, and these patches were related to the spatial distribution of

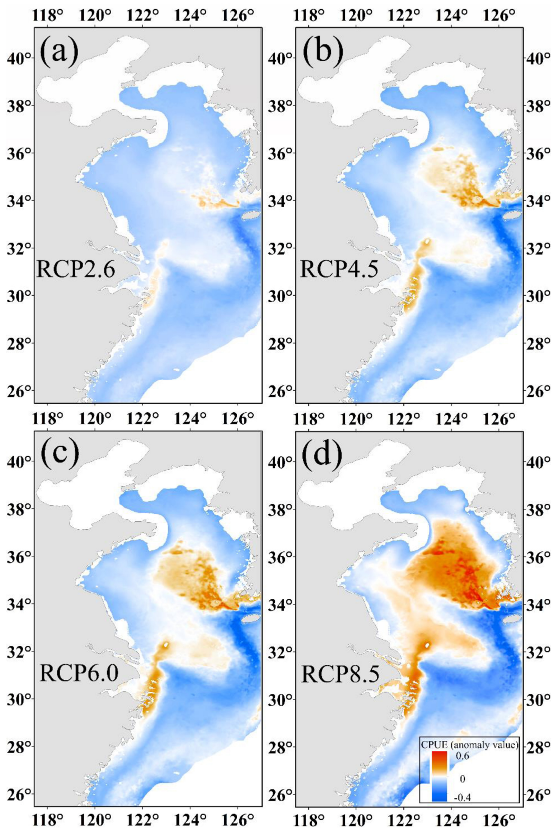

FIGURE 5 | The predicted CPUE (ton h^{-1}) anomaly value of Japanese anchovy based on projected increases of SST at **(a)** 1°C, **(b)** 1.8°C, **(c)** 2.2°C, and **(d)** 3.7°C at the end of the 21st century.

anchovy (Bertrand et al., 2008). Upwelling, that brings nutrient-rich waters to the sub-surface, also promotes primary productivity and copepod production, thus, facilitating the feeding and growth of Japanese anchovy larvae (Nakata et al., 2000).

Impact of Climate Change on Japanese Anchovy CPUE in Winter

Sea surface temperature was associated with biomass of wintering Japanese anchovy (Niu and Wang, 2017), and its catch positively correlates with SST in December (Kim and Kang, 2000). This is also consistent with our findings of an overall increasing SST trend in the China seas corresponding to an increase in WFG CPUE from 2009 to 2015 (**Figures 6**, **7A**). The wintering ground formed in December, and as the SST decreases, Japanese anchovy in the Yellow Sea migrated southward and partially entered the East China Sea (Zhao, 2006). This migration pattern was also captured from our study and was apparent from the respective CPUE decrease and increase in the Yellow Sea and the East China Sea from December to March (**Figure 4**).

The suitable SST promoted Japanese anchovy migration to northern regions under warm periods over a long-term time scale (Zhou et al., 2015). Our results likewise supported our hypothesis of potential northward habitat shift and CPUE increase for Japanese anchovy under future projected warming (**Figure 5**). During actual fishing activities, the fishermen carry out fishing operations in areas with high fish density for several consecutive days to ensure a high catch rate (measured by CPUE). If fishing activities cannot maintain a high level of catch rate, then fishermen tend to move to other areas (Li et al., 2014). Thus, the catch rate (CPUE) could be used as an index of abundance (Maunder and Punt, 2004) and is assumed to provide a better indication of abundance than the catch and fishing effort (Lehodey et al., 1998; Chang et al., 2012). It is also effective to use the catch rate (CPUE) to explore the effects of climate change on fish (Syamsuddin et al., 2016). The maximum catch potential in the central and eastern parts of the Yellow Sea is also increasing during 2051–2060 compared to 2001–2010 (IPCC, 2014a). This suggests that the catch potential of Japanese anchovy

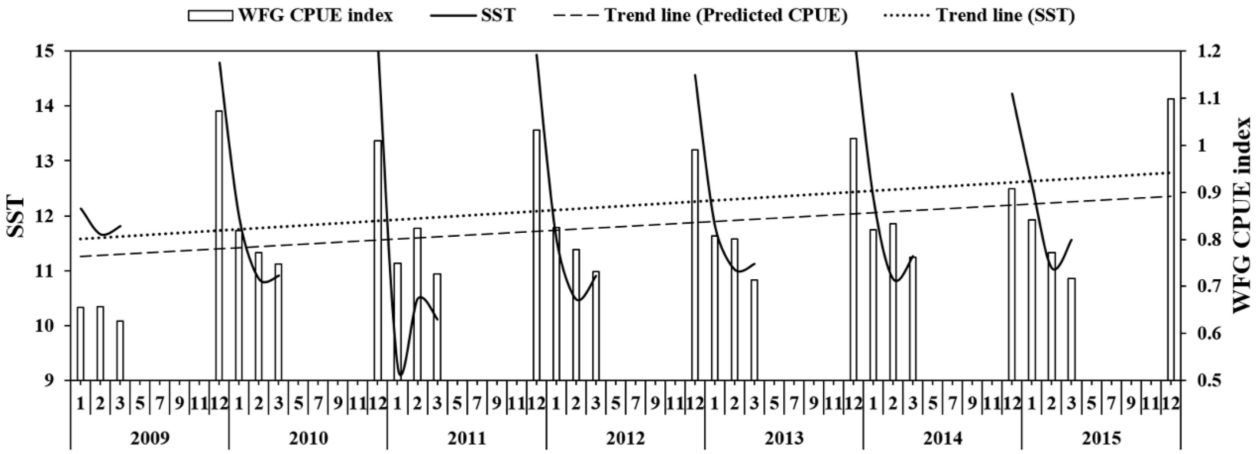

FIGURE 6 | The relationship between predicted CPUE (ton h^{-1}) of winter fishing ground (WFG) and SST (°C), the dotted line is the trend line of SST and predicted CPUE.

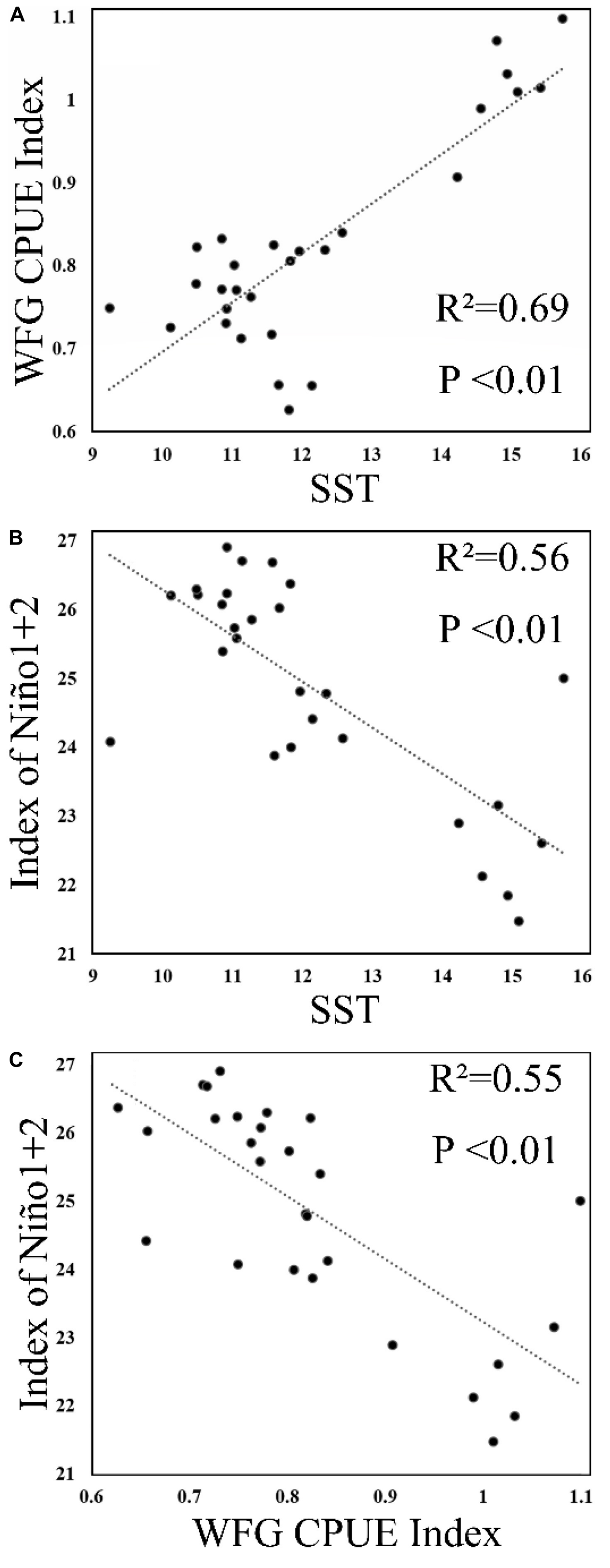

FIGURE 7 | Scatterplot of **(A)** SST and winter fishing ground (WFG) CPUE index, **(B)** Niño1 + 2 and SST, and **(C)** Niño1 + 2 and WFG CPUE index.

could increase in response to the rising temperatures. Our results showed that CPUE would increase in response to future climate-driven warming, which is also consistent with our hypothesis.

As a small pelagic fish, Japanese anchovy exerts a top-down control on zooplankton and bottom-up control on pelagic predators, and hence occupy a central role in the marine food web (Rice, 1995). It is imperative that we pay attention to the migration of small pelagic as it can induce the redistribution of pelagic predators under climate change. The climate impacts on various marine species are increasingly prominent and require robust forecasts of species distribution for conservation and management of fishery resources. Global climate change effects on small pelagics (e.g., anchovies, sardines) are summarized in **Table 5**. For instance, European anchovy could better adapt to environmental variability. The IPCC-based model predictions for the European anchovy and Atlantic horse mackerel showed potential increase and northward habitat movement (Lenoir et al., 2011; Petitgas et al., 2013; Raybaud et al., 2017). However, the European anchovy stock was expected to decline in southern Europe due to climatic and eutrophication impacts (Macías et al., 2014; George, 2019). California anchovy was also projected to shift northward and likely become a dominant species (Cheung et al., 2015). These earlier results are also consistent with our findings. Moreover, two-thirds of the 36 reported warming-related species shifts in the North Sea highlighted northward habitat movement (Perry et al., 2005). The horse mackerel and anchovy showed a northward expansion of suitable habitats and an increased occurrence probability in the northern British waters by the 2090s (Pinnegar et al., 2017). The copepod abundance and composition will most likely lead to an increase in anchovy abundance under global warming (Stenevik and Sundby, 2007). In the Southern Hemisphere, the habitat distribution of Peruvian anchovy also showed climate-driven poleward shifts (except summer), with decreases in the potential relative in the north and central-south areas (Silva et al., 2016, 2019). Similarly, anchovy and sardine exhibited a large-scale phenomenon of alternation in abundance, associated with climate-associated temperature changes. In particular, the anchovy and sardine abundance showed respective positive and negative correlations against SST, with a stronger correlation between SST and anchovy abundance (Chavez et al., 2003; Checkley et al., 2009; Nakayama et al., 2018). The CPUE and landings of common sardine in the coastal areas off Chile were also projected to decrease in response to climate change (Silva et al., 2015; Yáñez et al., 2016). The biomass and expected profits of the European sardine will obviously decrease with increasing surface temperatures in Iberian-Atlantic (Garza-Gil et al., 2011). However, it would increase in the Bay of Biscay, which is north of the Iberian-Atlantic (Shchepetkin and McWilliams, 2005). The Japanese and Pacific sardines were also expected to expand northward with warming and the latter's suitable habitat was expected to decrease by 50% in the Gulf of California and Mexican Northwest (Okunishi et al., 2012; Cheung et al., 2015; Petatán-Ramírez et al., 2019).

Our result also showed that anchovy CPUE has a significant positive correlation with SST, albeit the Niño1 + 2 showed a significant negative correlation with SST and WFG CPUE index

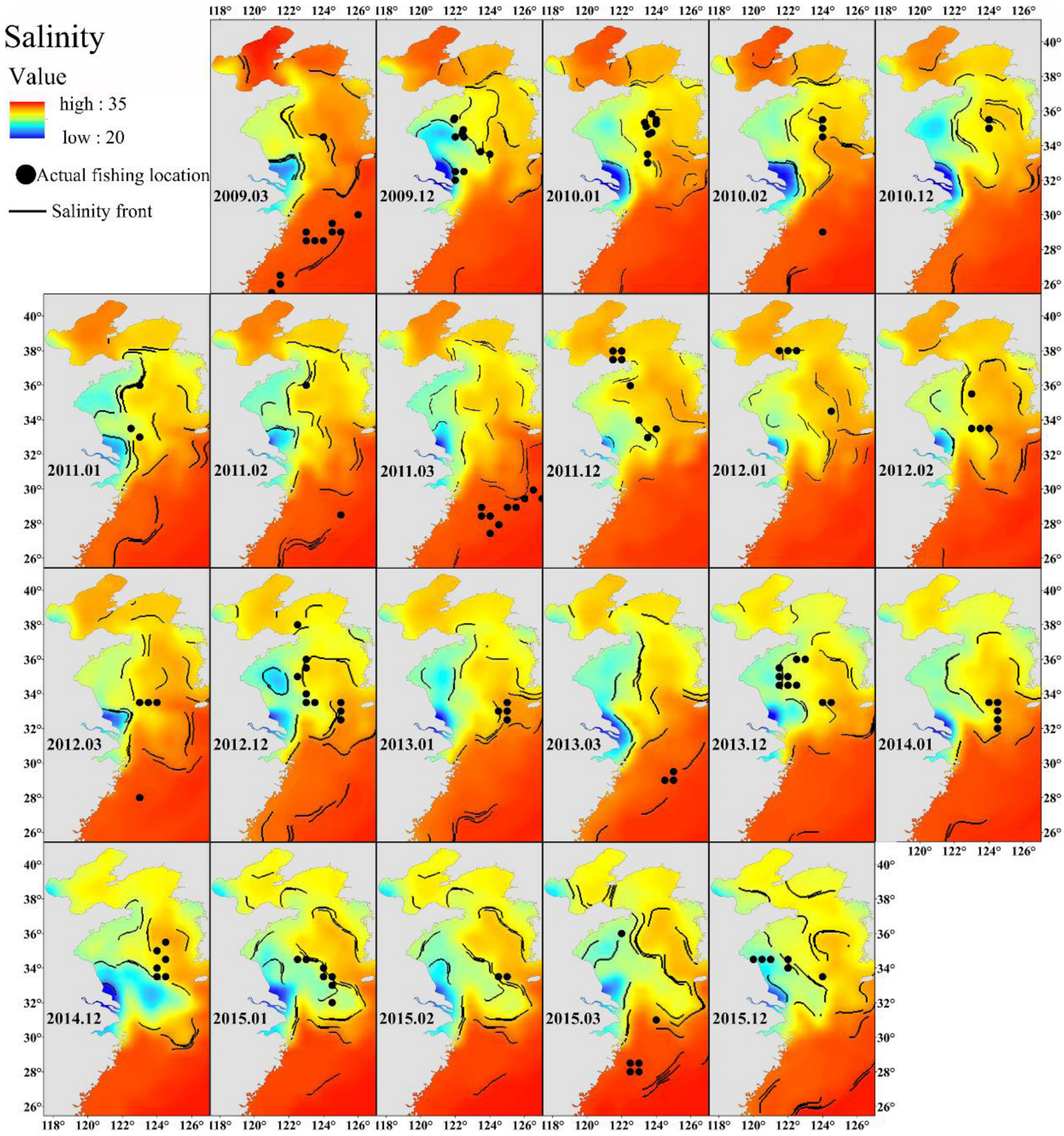

FIGURE 8 | The relationship between winter Japanese anchovy fishing location (solid dots) and the salinity front (contours) in the China seas.

(**Figures 7B,C**). During an El Niño (positive Niño 1 + 2), the SST in the China seas was lower than during La Niña (negative Niño 1 + 2) (Jia and Sun, 2002; Wang et al., 2012). One possible mechanism to explain the impact of ENSO on the Japanese anchovy habitat could be provided by looking into the ENSO-related phenomena: ENSO affects the precipitation and subsequent discharge of the Yangtze River that influences temperature and salinity in the China seas. The variability in marine environments affects the wintering grounds and the life history of the Japanese anchovy. For pelagic fish, ENSO is also known to impact the environmental features of their spawning and feeding grounds (Yu et al., 2019). Here, the extent of its impact is likewise evident in the Japanese anchovy wintering ground, when it has the highest annual concentration.

TABLE 5 | Summary of recent studies on the climate change impacts on small pelagic fish (anchovies, sardines) across the different regions of the world.

Species	Methodologies	Predictor variables	Forecast year	Region	Main findings	References
European anchovy (*Engraulis encrasicolus*)	Ecological niche model	SST, SSS, bathymetry	2099	North Atlantic (80°W–70.5°E and 25–85°N).	Northward shift and increase in potential habitat.	Lenoir et al., 2011
	Ecological niche model	SST, SSS, Chl-a	2099	30°W–60°E and 43°S–70°N.	Poleward habitat movement and decrease in occurrence probability in areas under 48°N and increase in northern areas.	Raybaud et al., 2017
	Coupled hydrological-biogeochemical model	Horizontal current, Chl-a	2100	Alboran Sea (0–8°W and 34–38°N)	Decrease in catch and stock size.	Macías et al., 2014
	POM (Princeton ocean model)-ERSEM (European regional seas ecosystem model) Lower Trophic Level	Chl-a, SST, SSS, mesozooplankton, net primary production, mixed layer depth	2100	North Aegean Sea (22–27°W and 39–41°N)	Stock size reduction due to the decline in plankton productivity.	George, 2019
	Review		2090s	Northern British waters.	Northward habitat shift	Pinnegar et al., 2017
California anchovy (*Engraulis mordax*)	Dynamic bioclimate envelope model	SST, SSS, distance from sea ice, habitat types	2050	Northeast Pacific shelf seas (100°–180° and 10–70°N)	Poleward shift with dominance of warmer water species.	Cheung et al., 2015
Peruvian anchovy (*Engraulis ringens*)	Habitat suitability index model	Distance to coast, SST, Chl-a	2055	Chilean coasts (75–70°W and 18–41°S).	Habitat suitability declines in the north and central-south areas; increase in southern areas (except summer)	Silva et al., 2016
	Maxent model	SST, Chl-a, upwelling index	2050	Central–northern Chile (73–70°W and 25–31°S).	Decrease in habitat suitability in north areas of Chile.	Silva et al., 2019
Common sardine (*Strangomera bentincki*)	GAM GLM	SST, Month, Latitude, Longitude	2065	The coastal areas off Chile (70–90°W and 18–42°S).	Negative relationship between CPUE and SST, climate-driven decrease in CPUE (potential relative abundance).	Silva et al., 2015
	Artificial neural networks	SST	2065	Central-southern Chile (70–78°W and 32–42°S)	Decreasing trends in future sardine landings.	Yáñez et al., 2016
Japanese sardine (*Sardinops melanostictus*)	Multi-trophic level ecosystem model	SST	2086	Western North Pacific (130°E–180° and 30–50°N)	Northward shift of juvenile sardines	Okunishi et al., 2012
European sardine (*Sardina pilchardus*)	Applied bio-economic model	SST	2030	Iberian-Atlantic (36–43°N)	Reduction in biomass and expected profits of sardine	Garza-Gil et al., 2011
	ROMS-$N_2P_2Z_2D_2$-OSMOSE model	SST, phytoplankton, zooplankton biomass	2099	Bay of Biscay in Europe (0–10°W and 43–48°N)	Increase in sardine biomass by 15%	Shchepetkin and McWilliams, 2005
Pacific sardine (*Sardinops sagax*)	Habitat suitability index model	SST, SSS, bathymetry, net primary productivity	2100	Northwestern Mexico (103–116°W and 16–34°N)	Northward shift and reduction of the suitable habitat in the Gulf of California and Mexican Northwest	Petatán-Ramírez et al., 2019
	Dynamic bioclimate envelope model	SST, SSS, distance from sea ice, habitat types	2050	Northeast Pacific shelf seas (100°–180° and 10–70°N)	Poleward shift with dominance of warmer water species.	Cheung et al., 2015

CONCLUSION

The marine geospatial statistical model using environmental predictors provided important information on the wintering ground of Japanese anchovy. A comparison of the three models showed that GAM is the most suitable prediction model for wintering Japanese anchovy. Its distribution was not only affected by SST but also closely related to the salinity front, feeding opportunity, and ocean currents. From SSS images, the salinity front was detected as the main surface feature associated with its wintering ground, highlighting the importance of SSS to the distribution of anchovy. The impact of ENSO on the Japanese anchovy distribution is captured through its influence on the SST on the wintering fishing ground, where CPUE and Niño1 + 2 indices showed a significant negative correlation. We also proposed a hypothesis and explored the influence of future warming on its winter habitat based on four IPCC climate scenarios. Our research reinforced our hypothesis, where temperature increases resulted in a northward habitat shift and CPUE enhancement by the end of the century. This information would be useful in formulating protection policies and promoting sustainable development of fishery resources in the region.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

All authors listed have made a direct and substantial contribution to this work. SL performed the data analyses and wrote the manuscript. YL conceived the idea for the study and analyses and edited the manuscript. IA edited and proofread the earlier versions of the manuscript. YT collected the data and edited the manuscript. ZY, HY, and JL edited the manuscript. JC provided the fishery data.

FUNDING

This study was supported by the National Key R&D Program of China (No. 2018YFD0900902), Shandong Key R&D Program (No. 2019GHY112014), National Natural Science Foundation of China (Nos. 41876177 and 41976210), and the Fundamental Research Funds for the Central Universities (Nos. 201822027 and 201762015).

ACKNOWLEDGMENTS

We are grateful to Dr. Suam Kim (Pukyong National University), Dr. Yoshiro Watanabe (The University of Tokyo), and Dr. Mikko Petteri Heino (University of Bergen) for valuable discussions, comments, and advice on the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00604/full#supplementary-material

REFERENCES

Bertrand, A., Gerlotto, F., Bertrand, S., Gutiérrez, M., Alza, L., Chipollini, A., et al. (2008). Schooling behaviour and environmental forcing in relation to anchoveta distribution: an analysis across multiple spatial scales. *Prog. Oceanogr.* 79, 264–277. doi: 10.1016/j.pocean.2008.10.018

Bertrand, A., Josse, E., Bach, P., Gros, P., and Dagorn, L. (2002). Hydrological and trophic characteristics of tuna habitat: consequences on tuna distribution and longline catchability. *Can. J. Fish. Aquat. Sci.* 59, 1002–1013. doi: 10.1139/f02-073

Breiman, L. (2001). Random forests. *Mach. Learn.* 45, 5–32. doi: 10.3390/rs10060911

Brierley, A. S., and Kingsford, M. J. (2009). Impacts of climate change on marine organisms and ecosystems. *Curr. Biol.* 19, R602–R614. doi: 10.1016/j.cub.2009.05.046

Carton, J. A., and Giese, B. S. (2008). A reanalysis of ocean climate using Simple Ocean Data Assimilation (SODA). *Mon. Weather Rev.* 136, 2999–3017. doi: 10.1175/2007MWR1978.1

Cayula, J. F., and Cornillon, P. (1992). Edge detection algorithm for SST images. *J. Atmos. Ocean. Technol.* 9, 67–80. doi: 10.1175/1520-0426(1992)009<0067:edafsi>2.0.co;2

Chai, C., Yu, Z., Song, X., and Cao, X. (2006). The status and characteristics of eutrophication in the Yangtze River (Changjiang) estuary and the adjacent East China Sea, China. *Hydrobiologia* 563, 313–328. doi: 10.1007/s10750-006-0021-7

Chang, Y. J., Sun, C. L., Chen, Y., Yeh, S. Z., and Dinardo, G. (2012). Habitat suitability analysis and identification of potential fishing grounds for swordfish, *Xiphias gladius*, in the South Atlantic Ocean. *Int. J. Remote Sens.* 33, 7523–7541. doi: 10.1080/01431161.2012.685980

Chavez, F. P., Ryan, J., Lluch-Cota, S. E., and Ñiquen, C. M. (2003). Climate: from anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299, 217–221. doi: 10.1126/science.1075880

Checkley, D. M., Alheit, J., Oozeki, Y., and Roy, C. (2009). *Climate Change and Small Pelagic Fish*. Cambridge: Cambridge University Press.

Chen, C. T. A. (2009). Chemical and physical fronts in the Bohai, Yellow and East China seas. *J. Mar. Syst.* 78, 394–410. doi: 10.1016/j.jmarsys.2008.11.016

Cheung, W. W. L., Brodeur, R. D., Okey, T. A., and Pauly, D. (2015). Projecting future changes in distributions of pelagic fish species of Northeast Pacific shelf seas. *Prog. Oceanogr.* 130, 19–31. doi: 10.1016/j.pocean.2014.09.003

Cornic, M., and Rooker, J. R. (2018). Influence of oceanographic conditions on the distribution and abundance of blackfin tuna (*Thunnus atlanticus*) larvae in the Gulf of Mexico. *Fish. Res.* 201, 1–10. doi: 10.1016/j.fishres.2017.12.015

Delcroix, T., and Murtugudde, R. (2002). Sea surface salinity changes in the East China Sea during 1997-2001: influence of the Yangtze River. *J. Geophys. Res. Ocean.* 107, 1–11. doi: 10.1029/2001jc000893

Dong, L. X., Guan, W. B., Chen, Q., Li, X. H., Liu, X. H., and Zeng, X. M. (2011). Sediment transport in the Yellow Sea and East China Sea. *Estuar. Coast. Shelf Sci.* 93, 248–258. doi: 10.1016/j.ecss.2011.04.003

FAO, (2017). *Fishery and Aquaculture Statistics*. Rome: FAO. doi: 10.1109/BMEI.2010.5639447

Garza-Gil, M. D., Torralba-Cano, J., and Varela-Lafuente, M. M. (2011). Evaluating the economic effects of climate change on the European sardine fishery. *Reg. Environ. Change* 11, 87–95. doi: 10.1007/s10113-010-0121-9

Gen, L., Baohua, R., Chengyun, Y., and Jianqiu, Z. (2010). Indices of El Niño and El Niño Modoki: an improved El Niño Modoki index. *Adv. Atmos. Sci.* 27, 1210–1220. doi: 10.1007/s00376-010-9173-5.1.Introduction

George, T. (2019). Climatic and eutrophication effects on the North Aegean Sea productivity and anchovy (*Engraulis encrasicolus*) stock. *Oceanogr. Fish. Open Access J.* 8, 1–11. doi: 10.19080/ofoaj.2018.08.555749

Guisan, A., Edwards, T. C., and Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol. Modell.* 157, 89–100. doi: 10.1016/s0304-3800(02)00204-1

Hanley, D. E., Bourassa, M. A., O'Brien, J. J., Smith, S. R., and Spade, E. R. (2003). A quantitative evaluation of ENSO indices. *J. Clim.* 16, 1249–1258. doi: 10.1175/1520-0442(2003)16<1249:aqeoei>2.0.co;2

Hayashi, A., Zhang, K., Saruwatari, T., Kawamura, T., and Watanabe, Y. (2016). Distribution of eggs and larvae of Japanese anchovy *Engraulis japonicus* in the Pacific waters off northern Japan in summer. *Fish. Sci.* 82, 311–319. doi: 10.1007/s12562-015-0966-4

Huang, D., Zhang, T., and Zhou, F. (2010). Sea-surface temperature fronts in the Yellow and East China Seas from TRMM microwave imager data. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 57, 1017–1024. doi: 10.1016/j.dsr2.2010.02.003

Huang, J., Sun, Y., Jia, H., Yang, Q., and Tang, Q. (2014). Spatial distribution and reconstruction potential of Japanese anchovy (*Engraulis japonicus*) based on scale deposition records in recent anaerobic sediment of the Yellow Sea and East China Sea. *Acta Oceanol. Sin.* 33, 138–144. doi: 10.1007/s13131-014-0573-8

Ihsan, E. N., Enita, S. Y., Kunarso, and Wirasatriya, A. (2018). Oceanographic factors in fishing ground location of anchovy at Teluk Cenderawasih National Park, West Papua : are these factors have an effect of whale sharks appearance frequencies? *IOP Conf. Ser. Earth Environ. Sci.* 116:012017. doi: 10.1088/1755-1315/116/1/012017

IPCC, (2014a). *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Summaries, Frequently Asked Questions, and Cross-Chapter Boxes. A Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, eds C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, and M. D. Mastrandrea Geneva, (Geneva: World Meteorological Organization).

IPCC, (2014b). *Climate Change 2014 Synthesis Report Summary Chapter for Policymakers*. Geneva: IPCC. doi: 10.1017/CBO9781107415324

Jia, R. L., and Sun, L. (2002). Distribution features of the Yellow and Bohai Seas temperature in winter and summer. *Mar. Sci. Bull.* 21, 1–8.

Jiang, Y. Z., Cheng, J. H., and Li, S. F. (2009). Temporal changes in the fish community resulting from a summer fishing moratorium in the northern East China Sea. *Mar. Ecol. Prog. Ser.* 387, 265–273. doi: 10.3354/meps08078

Johnson, J. B., and Omland, K. S. (2004). Model selection in ecology and evolution. *Trends Ecol. Evol.* 19, 101–108. doi: 10.1016/j.tree.2003.10.013

Kim, J. Y., Kang, Y. S., Oh, H. J., Suh, Y. S., and Hwang, J. D. (2005). Spatial distribution of early life stages of anchovy (*Engraulis japonicus*) and hairtail (*Trichiurus lepturus*) and their relationship with oceanographic features of the East China Sea during the 1997-1998 El Niño Event. *Estuar. Coast. Shelf Sci.* 63, 13–21. doi: 10.1016/j.ecss.2004.10.002

Kim, S., and Kang, S. (2000). Ecological variations and El Niño effects off the southern coast of the Korean Peninsula during the last three decades. *Fish. Oceanogr.* 9, 239–247. doi: 10.1046/j.1365-2419.2000.00142.x

Kitagawa, T., Sartimbul, A., Nakata, H., Kimura, S., Yamada, H., and Nitta, A. (2006). The effect of water temperature on habitat use of young Pacific bluefin tuna *Thunnus orientalis* in the East China Sea. *Fish. Sci.* 72, 1166–1176. doi: 10.1111/j.1444-2906.2006.01273.x

Klemas, V. (2012). Remote sensing of environmental indicators of potential fish aggregation: an overview. *Baltica* 25, 99–112. doi: 10.5200/baltica.2012.25.10

Kwon, D. H., Hwang, S. D., and Lim, D. (2012). Catch predictions for pacific anchovy *Engraulis japonicus* larvae in the Yellow Sea. *Fish. Aquat. Sci.* 15, 345–352. doi: 10.5657/fas.2012.0345

Lecomte, F., Grant, W. S., Dodson, J. J., Rodríguez-Sánchez, R., and Bowen, B. W. (2004). Living with uncertainty: genetic imprints of climate shifts in East Pacific anchovy (*Engraulis mordax*) and sardine (*Sardinops sagax*). *Mol. Ecol.* 13, 2169–2182. doi: 10.1111/j.1365-294X.2004.02229.x

Lehodey, P., Bertignac, M., Christophe, A. S., Memery, M. L., and Grima, N. (1998). Predicting skipjack tuna forage distributions. *Fish. Oceanogr.* 7, 317–325. doi: 10.1046/j.1365-2419.1998.00063.x

Lenoir, S., Beaugrand, G., and Lecuyer, É. (2011). Modelled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. *Glob. Change Biol.* 17, 115–129. doi: 10.1111/j.1365-2486.2010.02229.x

Li, G., Chen, X., Lei, L., and Guan, W. (2014). Distribution of hotspots of chub mackerel based on remote-sensing data in coastal waters of China. *Int. J. Remote Sens.* 35, 4399–4421. doi: 10.1080/01431161.2014.916057

Li, Y., Zhao, X. Y., Zhang, T., Li, X. S., and Wei, H. (2007). Wintering migration and distribution of anchovy in the Yellow Sea and its relation to physical environment. *Mar. Fish. Res.* 28, 104–112.

Liaw, A., and Wiener, M. (2002). Classification and regression by randomForest. *R News* 2, 18–22.

Lie, H. J. (1985). Wintertime temperature-salinity characteristics in the southeastern Hwanghae (Yellow Sea). *J. Oceanogr. Soc. Jpn.* 41, 291–298. doi: 10.1007/BF02109236

Liu, Y., Saitoh, S., Maekawa, K., Mochizuki, K. I., and Tian, Y. (2018). Impact of short-term climate effects and sea ice coverage variation on Japanese scallop aquaculture in Saroma Lake, Japan. *Aquac. Res.* 49, 1752–1767. doi: 10.1111/are.13630

Liu, Y., Saitoh, S. I., Igarashi, H., and Hirawake, T. (2014). The regional impacts of climate change on coastal environments and the aquaculture of Japanese scallops in northeast Asia: case studies from Dalian, China, and Funka Bay, Japan. *Int. J. Remote Sens.* 35, 4422–4440. doi: 10.1080/01431161.2014.916435

Ma, S., Cheng, J., Li, J., Liu, Y., Wan, R., and Tian, Y. (2019a). Interannual to decadal variability in the catches of small pelagic fishes from China Seas and its responses to climatic regime shifts. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 159, 112–129. doi: 10.1016/j.dsr2.2018.10.005

Ma, S., Liu, Y., Li, J., Fu, C., Ye, Z., Sun, P., et al. (2019b). Climate-induced long-term variations in ecosystem structure and atmosphere-ocean-ecosystem processes in the Yellow Sea and East China Sea. *Prog. Oceanogr.* 175, 183–197. doi: 10.1016/j.pocean.2019.04.008

Ma, S. S. (1989). Relationship between distribution and hydrological conditions of the wintering anchovy in Yellow Sea and East China Sea. *J. Fish. China* 13, 201–206.

Macías, D., Castilla-Espino, D., García-del-Hoyo, J. J., Navarro, G., Catalán, I. A., Renault, L., et al. (2014). Consequences of a future climatic scenario for the anchovy fishery in the Alboran Sea (SW Mediterranean): a modeling study. *J. Mar. Syst.* 135, 150–159. doi: 10.1016/j.jmarsys.2013.04.014

Maunder, M. N., and Punt, A. E. (2004). Standardizing catch and effort data: a review of recent approaches. *Fish. Res.* 70, 141–159. doi: 10.1016/j.fishres.2004.08.002

Mugo, R. M., Saitoh, S.-I., Nihira, A., and Kuroyama, T. (2011). "Application of multi-sensor satellite and fishery data, statistical models and marine-GIS to detect habitat preferences of skipjack tuna," in *Handbook of Satellite Remote Sensing Image Interpretation: Applications for Marine Living Resources Conservation and Management*, eds S. S. Jesus Morales, V. Stuart, and T. Platt, (Dartmouth: EU PRESPO & IOCCG), 169–185.

Murase, H., Nagashima, H., Yonezaki, S., Matsukura, R., and Kitakado, T. (2009). Application of a generalized additive model (GAM) to reveal relationships between environmental factors and distributions of pelagic fish and krill : a case study in Sendai Bay, Japan. *ICES J. Mar. Sci.* 6, 1417–1424. doi: 10.1093/icesjms/fsp105

Nakata, H., Kimura, S., Okazaki, Y., and Kasai, A. (2000). Implications of meso-scale eddies caused by frontal disturbances of the Kuroshio current for anchovy recruitment. *ICES J. Mar. Sci.* 57, 143–151. doi: 10.1006/jmsc.1999.0565

Nakayama, S. I., Takasuka, A., Ichinokawa, M., and Okamura, H. (2018). Climate change and interspecific interactions drive species alternations between anchovy and sardine in the western North Pacific: detection of causality by convergent cross mapping. *Fish. Oceanogr.* 27, 312–322. doi: 10.1111/fog.12254

Nelder, J. A., and Wedderburn, R. W. M. (1972). Generalized linear models. *Stat. Models S* 135, 195–247. doi: 10.1201/9780203738535

Niu, M., Jin, X., Li, X., and Wang, J. (2014). Effects of spatio-temporal and environmental factors on distribution and abundance of wintering anchovy *Engraulis japonicus* in central and southern Yellow Sea. *Chin. J. Oceanol. Limnol.* 32, 565–575. doi: 10.1007/s00343-014-3166-7

Niu, M., and Wang, J. (2017). Variation in the distribution of wintering anchovy *Engraulis japonicus* and its relationship with water temperature in the central and southern Yellow Sea. *Chin. J. Oceanol. Limnol.* 35, 1134–1143. doi: 10.1007/s00343-017-6134-1

Nurdin, S., Mustapha, M. A., Lihan, T., and Zainuddin, M. (2017). Applicability of remote sensing oceanographic data in the detection of potential fishing grounds of *Rastrelliger kanagurta* in the archipelagic waters of Spermonde, Indonesia. *Fish. Res.* 196, 1–12. doi: 10.1016/j.fishres.2017.07.029

Okunishi, T., Shin-ichi, I., Hashioka, T., Sakamoto, T. T., Yoshie, N., Sumata, H., et al. (2012). Impacts of climate change on growth, migration and recruitment success of Japanese sardine (*Sardinops melanostictus*) in the western North Pacific. *Clim. Change* 115, 485–503. doi: 10.1007/s10584-012-0484-7

Park, T., Jang, C. J., Kwon, M., Na, H., and Kim, K. Y. (2015). An effect of ENSO on summer surface salinity in the Yellow and East China Seas. *J. Mar. Syst.* 141, 122–127. doi: 10.1016/j.jmarsys.2014.03.017

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. (2005). Ecology: climate change and distribution shifts in marine fishes. *Science* 308, 1912–1915. doi: 10.1126/science.1111322

Petatán-Ramírez, D., Ojeda-Ruiz, M. Á., Sánchez-Velasco, L., Rivas, D., Reyes-Bonilla, H., Cruz-Piñón, G., et al. (2019). Potential changes in the distribution of suitable habitat for Pacific sardine (*Sardinops sagax*) under climate change scenarios. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 169–170:104632. doi: 10.1016/j.dsr2.2019.07.020

Petitgas, P., Rijnsdorp, A. D., Dickey-Collas, M., Engelhard, G. H., Peck, M. A., Pinnegar, J. K., et al. (2013). Impacts of climate change on the complex life cycles of fish. *Fish. Oceanogr.* 22, 121–139. doi: 10.1111/fog.12010

Pinnegar, J. K., Cheung, W. W. L., Jones, M., Merino, G., Turrell, B., and Reid, D. (2017). Impact of climate change on fisheries. *Mar. Clim. Change Impacts Partnersh. Sci. Rev.* 9, 257–280. doi: 10.1016/B978-0-12-812160-3.00009-X

Raybaud, V., Bacha, M., Amara, R., and Beaugrand, G. (2017). Forecasting climate-driven changes in the geographical range of the European anchovy (*Engraulis encrasicolus*). *ICES J. Mar. Sci.* 74, 1288–1299. doi: 10.1093/icesjms/fsx003

Rice, J. (1995). "Food web theory, marine food webs, and what climate changes may do to northern marine fish populations," in *Climate Change and Northern Fish Populations*, ed. R. J. Beamish, (Ottawa: NRC Research Press).

Roberts, J. J., Best, B. D., Dunn, D. C., Treml, E. A., and Halpin, P. N. (2010). Marine geospatial ecology tools: an integrated framework for ecological geoprocessing with ArcGIS, python, R, MATLAB, and C++. *Environ. Model. Softw.* 25, 1197–1207. doi: 10.1016/j.envsoft.2010.03.029

Shchepetkin, A. F., and McWilliams, J. C. (2005). The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Model.* 9, 347–404. doi: 10.1016/j.ocemod.2004.08.002

Silva, C., Andrade, I., Yáñez, E., Hormazabal, S., Barbieri, M. Á., Aranis, A., et al. (2016). Predicting habitat suitability and geographic distribution of anchovy (*Engraulis ringens*) due to climate change in the coastal areas off Chile. *Prog. Oceanogr.* 146, 159–174. doi: 10.1016/j.pocean.2016.06.006

Silva, C., Leiva, F., and Lastra, J. (2019). Predicting the current and future suitable habitat distributions of the anchovy (*Engraulis ringens*) using the Maxent model in the coastal areas off central-northern Chile. *Fish. Oceanogr.* 28, 171–182. doi: 10.1111/fog.12400

Silva, C., Yáñez, E., Barbieri, M. A., Bernal, C., and Aranis, A. (2015). Forecasts of swordfish (*Xiphias gladius*) and common sardine (*Strangomera bentincki*) off Chile under the A2 IPCC climate change scenario. *Prog. Oceanogr.* 134, 343–355. doi: 10.1016/j.pocean.2015.03.004

Smoliñski, S., and Radtke, K. (2017). Spatial prediction of demersal fish diversity in the Baltic Sea: comparison of machine learning and regression-based techniques. *ICES J. Mar. Sci.* 74, 102–111. doi: 10.1093/icesjms/fsw136

Solanki, H. U., Bhatpuria, D., and Chauhan, P. (2017). Applications of generalized additive model (GAM) to satellite-derived variables and fishery data for prediction of fishery resources distributions in the Arabian Sea. *Geocarto Int.* 32, 30–43. doi: 10.1080/10106049.2015.1120357

Stenevik, E. K., and Sundby, S. (2007). Impacts of climate change on commercial fish stocks in Norwegian waters. *Mar. Policy* 31, 19–31. doi: 10.1016/j.marpol.2006.05.001

Syamsuddin, M., Saitoh, S., Hirawake, T., and Syamsudin, F. (2016). Interannual variation of Bigeye tuna (*Thunnus obesus*) hotspots in the eastern Indian Ocean off Java. *Int. J. Remote Sens.* 37, 2087–2100. doi: 10.1080/01431161.2015.1136451

Tian, Y., Akamine, T., and Suda, M. (2004). Modeling the influence of oceanic-climatic changes on the dynamics of Pacific saury in the northwestern Pacific using a life cycle model. *Fish. Oceanogr.* 13, 125–137. doi: 10.1111/j.1365-2419.2004.00314.x

Trenberth, K. E., and Stepaniak, D. P. (2001). Indices of El Niño evolution. *J. Clim.* 14, 1697–1701.

Valavanis, V. D., Pierce, G. J., Zuur, A. F., Palialexis, A., Saveliev, A., Katara, I., et al. (2008). Modelling of essential fish habitat based on remote sensing, spatial analysis and GIS. *Hydrobiologia* 612, 5–20. doi: 10.1007/s10750-008-9493-y

Wang, Z., Zuo, J., Chen, M., Xu, Q., and Yang, Y. (2012). Relationship between El Niño and sea surface temperature variation in coastal region of Yellow Sea and East China Sea. *J. Hohai Univ. Nat. Sci.* 40, 461–468.

Wei, H., Shi, J., Lu, Y., and Peng, Y. (2010). Interannual and long-term hydrographic changes in the Yellow Sea during 1977-1998. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 57, 1025–1034. doi: 10.1016/j.dsr2.2010.02.004

Wood, S. N. (2006). *Generalized Additive Models: an Introduction with R*. Boca Raton, FL: Chapman and Hall.

Xing, Q., Yu, H., Yu, H., Sun, P., Liu, Y., Ye, Z., et al. (2020). A comprehensive model-based index for identification of larval retention areas: a case study for Japanese anchovy *Engraulis japonicus* in the Yellow Sea. *Ecol. Indic.* 116:106479. doi: 10.1016/j.ecolind.2020.106479

Yan, H., Liu, C., Zhang, W., Li, M., Zheng, X., Wei, G., et al. (2017). ENSO variability around 2000 years ago recorded by *Tridacna gigas* δ18O from the South China Sea. *Quat. Int.* 452, 148–154. doi: 10.1016/j.quaint.2016.05.011

Yáñez, E., Plaza, F., Silva, C., Sánchez, F., Barbieri, M. Á., and Aranis, A. (2016). Pelagic resources landings in central-southern Chile under the A2 climate change scenarios. *Ocean Dyn.* 66, 1333–1351. doi: 10.1007/s10236-016-0984-5

Yasuda, T., Yukami, R., and Ohshimo, S. (2014). Fishing ground hotspots reveal long-term variation in chub mackerel *Scomber japonicus* habitat in the East China Sea. *Mar. Ecol. Prog. Ser.* 501, 239–250. doi: 10.3354/meps10679

Yen, K. W., and Lu, H. J. (2016). Spatial–temporal variations in primary productivity and population dynamics of skipjack tuna *Katsuwonus pelamis* in the western and central Pacific Ocean. *Fish. Sci.* 82, 563–571. doi: 10.1007/s12562-016-0992-x

Yu, W., Chen, X., Zhang, Y., and Yi, Q. (2019). Habitat suitability modelling revealing environmental-driven abundance variability and geographical distribution shift of winter–spring cohort of neon flying squid *Ommastrephes bartramii* in the northwest Pacific Ocean. *ICES J. Mar. Sci.* 76, 1722–1735. doi: 10.1093/icesjms/fsz051

Yuan, X. C., and Zhao, W. W. (2016). *China Fishery Statistics Yearbook 2016.* Beijing: China Agriculture Press.

Zhang, X., Saitoh, S. I., and Hirawake, T. (2017). Predicting potential fishing zones of Japanese common squid (*Todarodes pacificus*) using remotely sensed images in coastal waters of south-western Hokkaido, Japan. *Int. J. Remote Sens.* 38, 6129–6146. doi: 10.1080/01431161.2016.1266114

Zhao, X., Hamre, J., Li, F., Jin, X., and Tang, Q. (2003). Recruitment, sustainable yield and possible ecological consequences of the sharp decline of the anchovy (*Engraulis japonicus*) stock in the Yellow Sea in the 1990s. *Fish. Oceanogr.* 12, 495–501. doi: 10.1046/j.1365-2419.2003.00262.x

Zhao, X., Wang, Y., and Dai, F. (2008). Depth-dependent target strength of anchovy (*Engraulis japonicus*) measured in situ. *ICES J. Mar. Sci.* 65, 882–888. doi: 10.1093/icesjms/fsn055

Zhao, X. Y. (2006). *Population Dynamic Characteristics and Sustainable Utilization of the Anchovy Stock in the Yellow Sea*. Shandong: Ocean University of China.

Zheng, W., Zou, L., and Han, Z. (2015). Genetic analysis of the populations of Japanese anchovy *Engraulis japonicus* from the Yellow Sea and East China Sea based on mitochondrial cytochrome b sequence. *Biochem. Syst. Ecol.* 58, 169–177. doi: 10.1016/j.bse.2014.12.007

Zhou, X., Sun, Y., Huang, W., Smol, J. P., Tang, Q., and Sun, L. (2015). The Pacific decadal oscillation and changes in anchovy populations in the Northwest Pacific. *J. Asian Earth Sci.* 114, 504–511. doi: 10.1016/j.jseaes.2015.06.027

Zhu, D. (1990). Anchovy and other fish resources in the Yellow Sea and East China Sea. *Mar. Fish. Res. China* 11:143.

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.

frontiers
in Marine Science

ORIGINAL RESEARCH
published: 31 July 2020
doi: 10.3389/fmars.2020.00540

Exploring Temporal Variability in the Southern Benguela Ecosystem Over the Past Four Decades Using a Time-Dynamic Ecosystem Model

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This paper presents a new, updated, temporally dynamic *Ecosim* model for the Southern Benguela (1978–2015) by capturing recent advancements in our understanding of the dynamics and newly available data series from an additional decade of research in the region. The paper documents the model development and the thinking behind incorporating a newly available upwelling index, and observed fishing effort as important drivers of modeled ecosystem dynamics. The most sensitive predator-prey interactions were identified and vulnerabilities (of prey to predators) were estimated to improve model fit to field observations under each scenario. Sardine interactions with prey and predators were consistently found to be sensitive interactions in model fitting, accounting for at least 40% of the most sensitive trophic interactions in the southern Benguela modeled food web. Model fits to data were improved by a total of 85% reduction in sum of squares when upwelling effects on large phytoplankton availability to zooplankton and small pelagic fish was incorporated, geographic shifts in sardine distribution were captured by means of altered availability of sardine to predators, corresponding vulnerabilities of prey to predators were estimated, and an additional, small, hypothetical forcing function was fitted to small phytoplankton production. African penguin and Cape gannet fits to data series were improved by incorporating a recently published bird Food Availability Index, although model fits of several fish groups then deteriorated, emphasizing the need for additional empirical species-specific functional response studies. Attempts at fitting the full area model to either west coast or south coast time series did not improve overall model fits, highlighting limitations of the current non-spatialized model in describing coast-specific dynamics. This study shows promise in unraveling the observed dynamics of the Benguela upwelling ecosystem, and points to the importance of exploring spatially disaggregated approaches, in

OPEN ACCESS

Edited by:
Manuel J. Zetina-Rejón,
National Polytechnic Institute
of Mexico (IPN), Mexico

Reviewed by:
Sean Lucey,
Northeast Fisheries Science Center
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Specialty section:
This article was submitted to
Marine Fisheries, Aquaculture
and Living Resources,
a section of the journal
Frontiers in Marine Science

Received: 13 March 2020
Accepted: 15 June 2020
Published: 31 July 2020

Citation:
Shannon LJ, Ortega-Cisneros K,
Lamont T, Winker H, Crawford R,
Jarre A and Coll M (2020) Exploring
Temporal Variability in the Southern
Benguela Ecosystem Over the Past
Four Decades Using a Time-Dynamic
Ecosystem Model.
Front. Mar. Sci. 7:540.
doi: 10.3389/fmars.2020.00540

particular the new foraging habitat capacity of the Ecospace approach, to improve our understanding of processes whereby variability in upwelling influences dynamics of the Southern Benguela ecosystem. This is important in reconciling knowledge needed to manage fisheries and to protect marine biodiversity by means of ecosystem-based management in South Africa, and to advance management advice under future scenarios of climate change.

Keywords: Ecosim, southern Benguela, temporal variability, forcing functions, upwelling index

INTRODUCTION

The Benguela upwelling system is one of four major eastern boundary current systems in the world. The southern Benguela is a well-studied upwelling ecosystem bounded by the warm Agulhas current to the south and east, and the northern Benguela upwelling area off Namibia to the north. It is influenced by strong, wind-driven upwelling, which results in high biological productivity and supports several important commercial fisheries including the small pelagics, hake and squid fisheries but also an important small-scale sector.

Variability in the southern Benguela is high on a monthly, interannual and decadal scale, and populations of many species in the system reflect the high variability of the system (Cochrane et al., 2009) and thus predictions on the dynamics of the system and its populations can be challenging (e.g., Shannon et al., 2006; Travers and Shin, 2010). In the last two decades, substantial changes in environmental variables have been observed in this system, including changes in sea surface temperature, upwelling intensity, incidence of harmful algal blooms and extreme events (Rouault et al., 2010; van der Lingen et al., 2016; Lamont et al., 2018) among others. For example, the Agulhas Current has warmed by 0.2–0.4°C throughout the year over the period 1982–2009 (Rouault et al., 2010). The total cumulative upwelling (TCU) and the number of upwelling days in the Agulhas Bank significantly increased between 1979 and 2014, while a linear, albeit non-significant trend in the TCU has been identified for the southern Benguela (Lamont et al., 2018).

In the southern Benguela, changes in the distribution and abundance of several species of ecological and commercial importance have been recorded, and have been related to fishing and environmental changes (Blamey et al., 2015). Eastward shifts have been observed in the distribution of sardine, anchovy, West Coast rock lobster and kelp (e.g., Roy et al., 2007; Cockcroft et al., 2008; Bolton et al., 2012; Watermeyer et al., 2016). Anchovy *Engraulis encrasicolus* showed an eastward shift in distribution in 1996, and more than 50% of its biomass is now located east of Cape Agulhas (Coetzee et al., 2018). This distributional change is believed to be environmentally driven, attributed to a decrease in sea surface temperature in the inner shelf of the Agulhas Bank to the east of Cape Agulhas (Roy et al., 2007). The eastward distributional shift of West Coast rock lobster *Jasus lalandii* resulted in severe impacts on the fishery and local communities (Cockcroft et al., 2008). The distributional shift coincided with a decrease in the somatic growth of West Coast Rock lobster and an increase in the occurrence of lobster walk-outs, suggesting that these changes were environmentally driven (Cockcroft et al., 2008).

Zooplankton abundance has shown considerable variability in the southern Benguela and has been related to changes in the abundance of their predators. Copepod abundance increased from 1950 to the late 1990s in the southern Benguela (Verheye et al., 1998, 2016; Hutchings et al., 2012). This trend was attributed to the decrease in small pelagics fish after the start of the fishery and to increased productivity. Similarly, a decline in copepod biomass has been recorded in the Agulhas Bank since 1996 including the biomass of the dominant large copepod in the Agulhas Bank *Calanus agulhensis* (Huggett et al., 2019). It is likely that the eastward shift in the distribution of small pelagics increased predation pressure on copepods and resulted in decreased copepod abundance in the area. Higher proportions of *Calanus agulhensis* over the past 3 years, indicating a possible reversal of the previously noted trend, was synonymous with below average biomass of both anchovy and sardine east of Cape Agulhas (Huggett et al., 2019).

Ecosystem models are being widely applied to quantify food web dynamics and ecosystem responses to multiple drivers (e.g., Travers-Trolet et al., 2014; Corrales et al., 2018; Ortega-Cisneros et al., 2018a). Ecopath with Ecosim (EwE, Walters et al., 1999; Christensen and Walters, 2004) models fitted to time series data are proving to be useful tools for providing the ecosystem context for ecosystem-based fisheries management (EBFM; Heymans et al., 2016) in their ability to capture food web responses to environmental and fisheries drivers, both past (e.g., Shannon et al., 2004a, 2009; Watermeyer et al., 2008) and future (Serpetti et al., 2017; Corrales et al., 2018).

The aim of this study was to revise, update and re-fit the existing EwE models of the Southern Benguela (Shannon et al., 2004a, 2008; Smith et al., 2011) based on advancements in our understanding of dynamics and new available data sources emerging from an additional decade of research in the region. This paper documents the model and the thinking behind this modeling process involved in the development of the new time-dynamic trophic model of the Southern Benguela. The model was designed to facilitate future model testing of alternative management scenarios under scenarios of climate change, to assist developing future spatial-temporal modeling efforts and to provide a tool for use in further unpacking

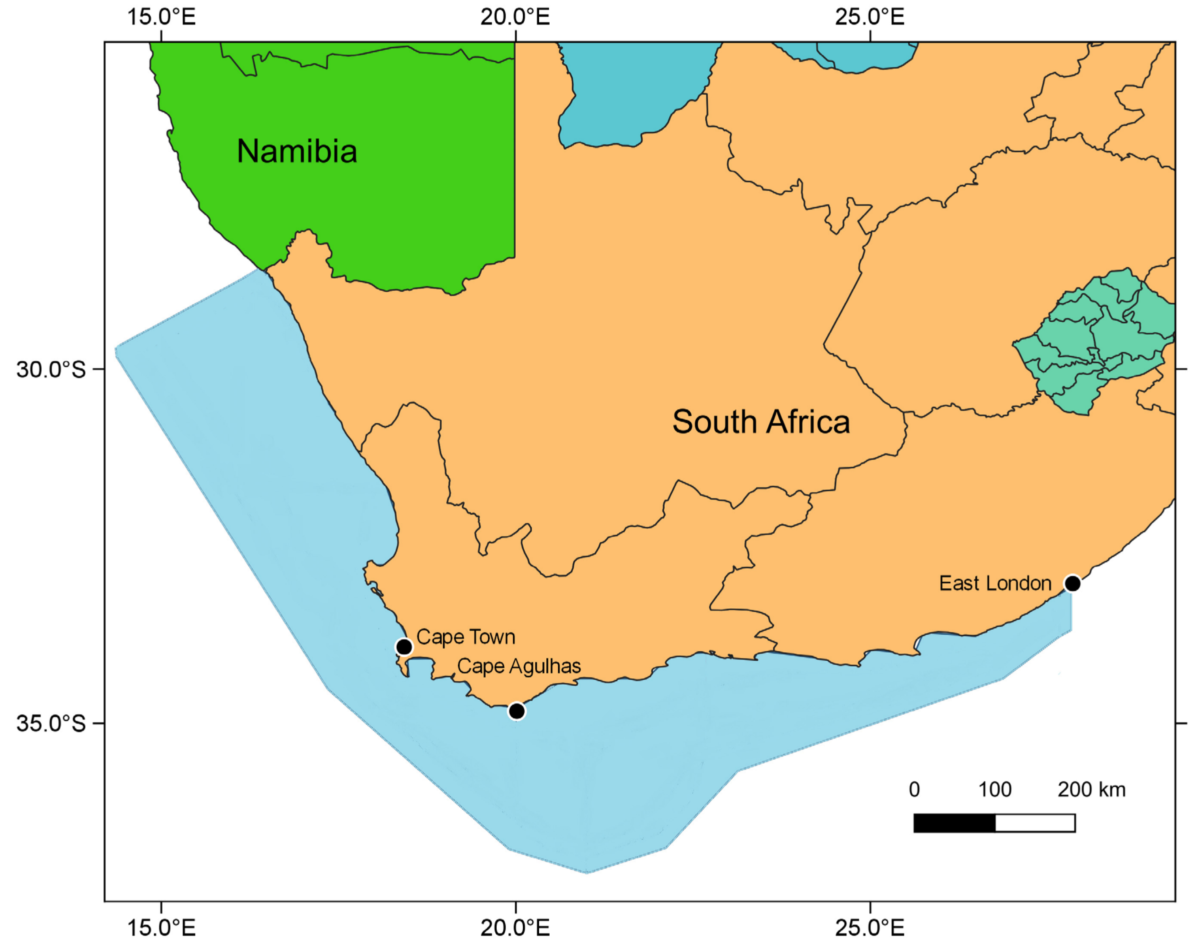


FIGURE 1 | Map showing modeled area (blue shaded) and Cape Agulhas, determining the boundary between the west coast vs. the south coast subsystems of the Southern Benguela ecosystem (Hutchings et al., 2009; Watermeyer et al., 2016).

key trophic interactions currently under closer inspection by colleagues in the region.

MATERIALS AND METHODS

Model Construction and Functional Groups

The Ecopath with Ecosim (Walters et al., 2000) modeling approach was used to construct an improved and updated food web model of the Southern Benguela ecosystem, following guidelines of best practice as outlined in Heymans et al. (2016). The existing models of the Southern Benguela extend from the Orange River mouth in the north west (29°S) to 28°E (East London) in the south east (Shannon et al., 2004a), spanning an area of 220,000 km^2 (**Figure 1**) and the years 1978–2003 (Shannon et al., 2008). These were expanded and updated to 2015, from 31 to 48 living model groups, comprising 26 fish groups and 7 top predators (see **Table 1**). The single phytoplankton model group previously used (Shannon et al., 2004a, 2008) was subdivided into two groups: small phytoplankton (Phytoplankton 1) $< 10\ \mu m$ and larger phytoplankton (Phytoplankton 2) $> 10\ \mu m$, based on Probyn (1992). This disaggregation was performed to incorporate bottom-up environmental processes as a key driver in upwelling systems such as the Benguela.

Pelagic fish are pivotal in the functioning of upwelling ecosystems, regulating the flow of energy up and down the food web (Cury et al., 2000). Multi-stanza groups (**Supplementary Table S1**) were added for anchovy and sardine in the revised model presented herein, to facilitate future fisheries management simulations to explore the extent to which fisheries and predators compete for small pelagics. For both anchovy and sardine, two stanzas were modeled: (i) recruits (under 1 year old) and (ii) adults (1 year and older). In the case of sardine, the adult stanza includes several year classes as sardine are longer lived. Mesopelagic fish were disaggregated in the revised model since relative abundances of lanternfish (*Lampanyctodes hectoris*) and lightfish (*Maurolicus muelleri*) have been changing over the past decade (DAFF, unpublished data; Janet Coetzee, personal Communication), and since there is a move to target lanternfish using midwater trawling on the West Coast (ANON, 2016).

TABLE 1 | Revised species and fishing fleet aggregation: (a) species groups and (b) fishing fleets modeled.

	(a) Modeled groups/species	Corresponding aggregated group used in earlier EwE models
1	**Small phytoplankton (<10 μ m)**	Phytoplankton
2	**Larger phytoplankton (≥10 μ m)**	Phytoplankton
3	Microzooplankton (2–200 μm equivalent spherical diameter)	
4	Mesozooplankton (200–2000 μm)	
5	Macrozooplankton (2–20 mm)	
6	Gelatinous zooplankton	
7	**Anchovy recruits (<1 year) *Engraulis encrasicolus***	Anchovy
8	**Anchovy adults (≥1 year) *E. encrasicolus***	Anchovy
9	**Sardine recruits (<1 year) *Sardinops sagax***	Sardine
10	**Sardine adults (≥1 year) *S. sagax***	Sardine
11	Redeye round herring *Etrumeus whiteheadii*	
12	Other small pelagic fish	
13	Horse mackerel juveniles (<2 years) *Trachurus trachurus capensis*	
14	Horse mackerel adults (≥2 years) *T. trachurus capensis*	
15	Chub mackerel *Scomber japonicus*	
16	**Lanternfish *Lampanyctodes hectoris***	Mesopelagics
17	**Lightfish *Maurolicus muelleri***	Mesopelagics
18	Shallow-water Cape Hake small (<3 years) *Merluccius capensis*	
19	Shallow-water Cape hake large (≥3 years) *M. capensis*	
20	Deep-water Cape hake small (<3 years) *M. paradoxus*	
21	Deep-water Cape hake large (≥3 years) *M. paradoxus*	
22	Snoek *Thyrsites atun*	
23	**Tuna (*Thunnus* spp.) and Atlantic bonito (*Sarda sarda*), commonly called kartonkel**	Other large pelagics
24	**Sciaenids**	Other large pelagics
25	**Medium Sparidae**	Other large pelagics
26	**Large Sparidae**	Other large pelagics
27	**Yellowtail *Seriola lalandii***	Other large pelagics
28	**Other linefish**	Other large pelagics
29	**Mullet *Liza richardsonii,* commonly called haarder**	New group
30	Pelagic-feeding demersal fish	
31	Benthic-feeding demersal fish	
32	**Agulhas Sole *Austroglossus pectoralis***	Benthic-feeding demersal fish
33	Benthic-feeding Chondrichthyans	
34	Pelagic-feeding Chondrichthyans	
35	Apex Chondricthyans	
36	**Chokka Squid *Loligo reynaudii***	Cephalopods
37	Other cephalopods	
38	Seals *Arctocephalus pusillus pusillus*	
39	Cetaceans	
40	**African Penguin *Spheniscus demersus***	Seabirds
41	**Cape Gannet *Morus capensis***	Seabirds
42	**Cape Cormorant *Phalacrocorax capensis***	Seabirds
43	Other seabirds	
44	Benthic Producers	
45	Meiobenthos	
46	Macrobenthos	
47	**West Coast Rock Lobster *Jasus lalandii***	Macrobenthos
48	**South Coast Rock Lobster *Panulirus homarus***	Macrobenthos

(Continued)

TABLE 1 | Continued

	(b) Modeled fishing fleets
1	Purse seine
2	Demersal trawl
3	Hake inshore trawl - south coast
4	Hake longline
5	Hake handline
6	Offshore trawl for shallow-water hake *M. capensis* on the west coast (*Cap WC offsh trawl*)
7	Offshore trawl for shallow-water hake on the south coast (*Cap SC offsh trawl*)
8	Offshore trawl for deep-water hake *Merluccius paradoxus* on the west coast (*Par WC offsh trawl*)
9	Offshore trawl for deep-water hake on the south coast (*Par SC offsh trawl*)
10	Line fishery for snoek on the west coast (*Snoek WC line*)
11	Line fishery for tuna and billfish on the west coast (*Tuna and billfish WC line*)
12	Tuna pole
13	Line fishery for sciaenids on the west coast (*Sciaenids WC line*)
14	Line fishery for sciaenids on the south coast (*Sciaenids SC line*)
15	Line fishery for medium sparids on the west coast (*Medium Sparids WC line*)
16	Line fishery for medium sparids on the south coast (*Medium Sparids SC line*)
17	Line fishery for large Sparids on the west coast (*Large Sparids WC line*)
18	Line fishery for large sparids on the south coast (*Large Sparids SC line*)
19	Line fishery for yellowtail on the west coast (*Yellowtail WC line*)
20	Large pelagic longline
21	Line fishery – other fish species
22	Line fishery for chondrichthyans on the south coast (*Chonds SC line*)
23	Line fishery for chondrichthyans on the west coast (*Chonds WC line*)
24	Longline for demersal chondrichthyans (*Dem Shark Longline*)
25	Midwater trawl for horse mackerel (Hmack Midwater trawl)
26	Inshore trawl for sole *Austroglossus pectoralis* (*sole insh trawl*)
27	Squid jig
28	West coast rock lobster fishery (*WCRL*)
29	South Coast rock lobster fishery (*SCRL*)
30	Beach seine and gillnet
31	Non-specified fisheries catching some species (*Other*)

Groups in bold type are those that have been disaggregated in this revised model compared to previous models of the system. Species listings corresponding to aggregated functional groups in previous models of the Southern Benguela (Shannon et al., 2003, 2008) are provided in the second column. Detailed information on species listings in aggregated demersal fish and chondrichthyan groups are provided in ***Supplementary Table S2****. Shortened labels used in parameter and results tables are provided in parentheses. Fleets often catch across multiple species groups; for detailed catches by fleet see* ***Supplementary Table S3*** *(corresponding abbreviations of fishing fleets are provided in italics in parentheses).*

The importance of modeling key predators of small pelagic fish as separate entities to ascertain possible dependencies of predators on forage fish has been well noted by Koehn et al. (2016). To facilitate model versatility for future simulation modeling for management/conservation purposes, the three most abundant breeding seabirds off South Africa, namely African Penguin *Spheniscus demersus*, Cape Gannet *Morus capensis,* and Cape Cormorant *Phalacrocorax capensis*, previously included in a single seabird group, were accommodated as separate model groups. African penguin is categorized as Endangered according to the IUCN classification, Cape Gannet was classified as Endangered but it has been suggested that the species be reclassified as Vulnerable based on recent trends in the northern Benguela (Sherley et al., 2019), and Cape Cormorant is Vulnerable. The "other seabirds" model group comprised breeding (resident) or more common migrant seabirds excluding the afore-mentioned three species (Crawford et al., 1991). Consideration was given to splitting the "Detritus" group into two: "normal detritus" and "discarded fish including offal." However, to preserve the origin of the fish scavenged during fishing operations (e.g., Ryan and Moloney, 1988; Wickens et al., 1992; Watkins et al., 2008) in food web analyses, a single "detritus" group was retained and fish (in particular hake) scavenged from nets by seabirds and seals was considered as "live" consumption despite being mostly offal from "large hake" caught by trawlers (Grémillet et al., 2008). Available cetacean data were too sparse to warrant splitting into resident cetaceans and migratory cetaceans, or even into toothed and baleen whales.

In the case of predatory line fish ("traditional" boat-based, hand-line caught species), species relative abundance and effort time series were disaggregated by region according five functional groups based on objective clustering techniques and standardization procedures described in Winker et al. (2013, 2014) and Blamey et al. (2015) (see **Table 1**). Mullet was modeled as a separate functional group since it occurs inshore and in bays. Demersal fish were modeled as before (Shannon et al., 2004a) with the exception of Agulhas Sole (*Austroglossus pectoralis*), an important commercial species in the inshore trawl fishery on the South Coast, now modeled as a separate group. This decision was taken in anticipation of fisheries management simulation testing in future studies. West coast sole (*Austroglossus microlepis*) was retained in the general "benthic-feeding demersal fish" model group.

Model diets previously used for setting the 1978 model (Shannon et al., 2004a, 2008) were assumed in this study, with updates to account for species disaggregation and revised dietary knowledge, where applicable and as documented in the **Supplementary Material Section 4** and **Supplementary Table S4**.

Best practices guidelines available for EwE models were followed during the model development (Heymans et al., 2016). The "prebal" approach (Link, 2010) was invoked to check for any obvious inconsistencies or peculiarities in the base (1978) model of the Southern Benguela. While "prebal" serves as a useful set of guidelines and warning signals as to potential problems in construction of food web models (Heymans et al., 2016), the various guidelines need to be viewed in the context of the system under consideration, and in light of the objectives of the model under development.

Fitting the Model to Data Time Series

Fitting of the revised Ecosim model of the Southern Benguela food web (1978–2015) was undertaken following previous procedures (Shannon et al., 2004a), but in this study fished groups were driven by 13 time series of fishing effort and two time series of fishing mortality, and model trajectories of biomass and landings outputs for 1978–2015 were compared to over 50 catch, abundance, and mortality time series (**Supplementary Table S5**). These data series were the best available at the start of this study, and the ones for which we were able to secure access to at the time. Before continuing with model fitting, general model structure was checked against guidelines provided by Link (2010) (**Supplementary Material Section 6**). To aid in the model fitting process, an estimate of relative uncertainty associated with the model parameters was also made (**Supplementary Material Section 7**). Model pedigree was estimated using the classification system in Ecopath, which takes into account the likely degree of uncertainty that various parameter sources infer. These scores were used to assist in weighting of time series for model fitting. Subsequently, most of the catch, abundance (mostly biomass), mortality and fishing effort time series assembled (**Supplementary Table S5**) were used in model fitting with the exception of survey-based spawner biomass series for anchovy and sardine [instead, stock assessment (modeled) time series were used as per the "Status of the South Africa Marine Fishery Resources, 2014" report]. In the case of anchovy and sardine, combined west and south coast estimates of biomass and harvest proportion were used.

Using Ecosim (Walters et al., 1997) "Fit to Time Series" routines, the most sensitive predator-prey interactions were identified and vulnerabilities (of prey to predators) were estimated to improve model fit to data series of field observations. The automated stepwise routine to explore EwE model fitting to available time series (Scott et al., 2016) was used as a means of identifying a suitable number and combination of vulnerability and primary production anomaly parameters that would facilitate fitting of the Southern Benguela model.

Initial Sequential Model Fitting Incorporating an Upwelling Anomaly

As mentioned in the introduction, TCU per year (m^{-3} s^{-1} 100 m^{-1}) in the Southern Benguela was higher in mid-1990s and decreased again in the 2000s, but in the latter part of the timeseries, there were more years where upwelling exceeded the long-term mean (from Lamont et al., 2018; **Figure 2**). Annual means were computed, from July of one calendar year to June of the following calendar year, such that the full upwelling cycle was captured in a single annual value. These annual means were then used to drive primary production changes in the model via a forcing function (*Upwell*) on large-celled phytoplankton following Lockerbie and Shannon (2019), and then only was an additional hypothetical environmental anomaly applied to small phytoplankton. The latter was fitted using the routine available in

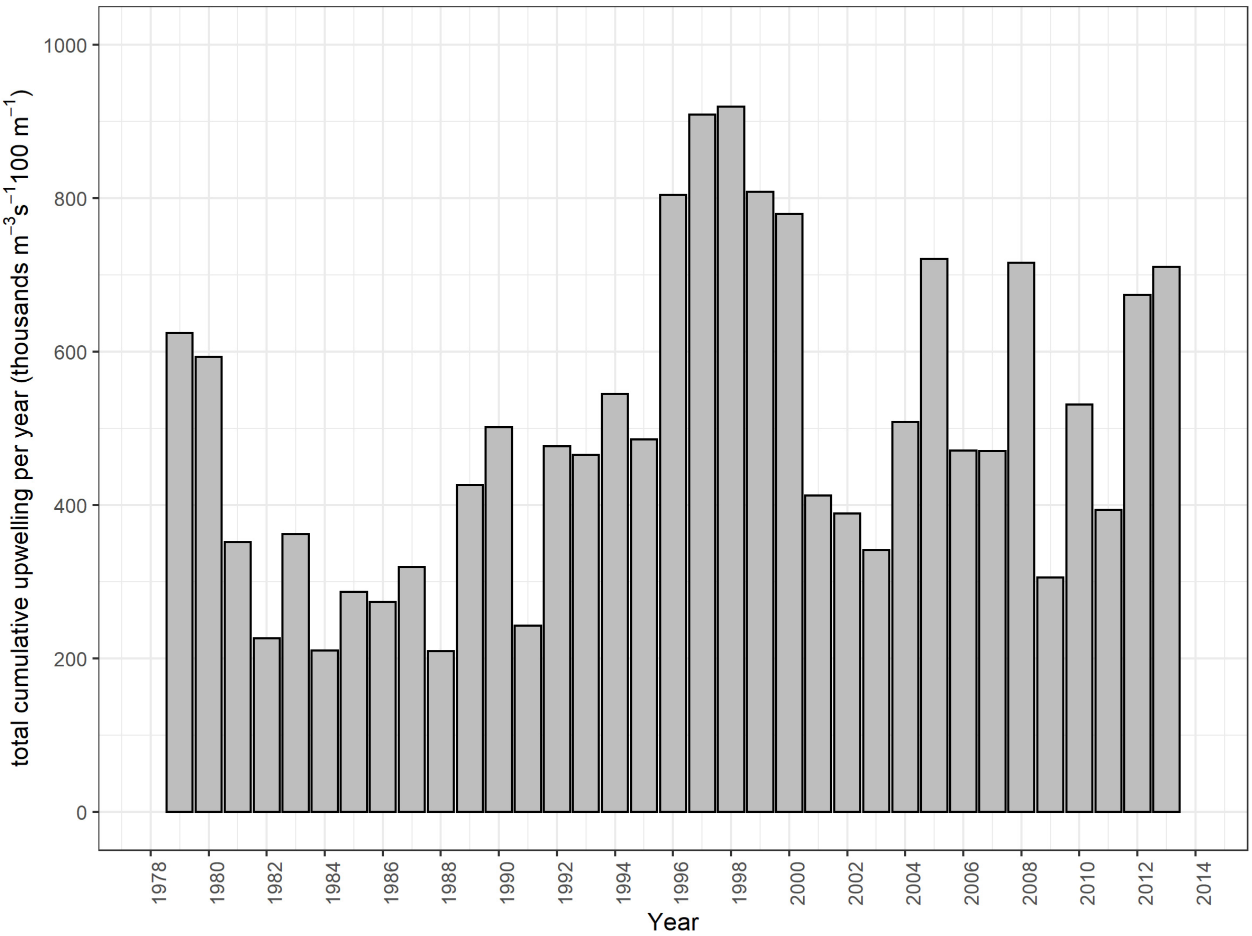


FIGURE 2 | Total cumulative upwelling per year (m^{-3} s^{-1} 100 m^{-1}) in the Southern Benguela (replotted from Lamont et al., 2018).

Ecosim to estimate an environmental forcing function applicable to primary production to improve fit of the model to observed time series data. We applied this routine to estimate additional environmental forcing that modified the dynamics of small-celled phytoplankton production in an attempt to further refine model fitting by emulating additional environmental "noise" in the ecosystem.

Weighting of Time Series Corresponding to Focus Model Groups

An initial weighting of time series was explored in a second fitting process in which sardine, anchovy, penguin, hakes and line fish were all afforded higher weightings (weightings1 in **Supplementary Table S8**) in an attempt to better capture the ecosystem effects of observed small pelagic fish and key predator dynamics.

Refined Fitting Process to Include Sardine and Anchovy Availability on the West Coast

In order to account for the change in availability of small pelagic fish to predators in the 2000s due to the observed southward and eastward shift that was reflected in several fish resources off South Africa (Watermeyer et al., 2016), spatial change in forage fish availability was modeled as follows:

- A forcing function based on TCU (*Upwell*) was applied to large-celled phytoplankton production, and vulnerability parameters for predator-prey interactions were estimated,
- A forcing function based on the modeled relative proportion of sardine spawners west of Cape Agulhas (Carryn de Moor, personal communication; **Figure 3**) was applied to the availability of juvenile and adult sardine to all their predators,
- A forcing function based on relative anchovy biomass surveyed in November west of Cape Agulhas (Coetzee et al., 2016; **Figure 3**) was applied to the availability of anchovy recruits and spawners to all their predators,
- A forcing function based on the Food Availability index of Crawford et al. (2019) was applied to anchovy and sardine availability to their predators and its inverse was applied to affect additional mortality of African penguins,
- Finally, a hypothetical, model-fitted environmental anomaly was incorporated on small phytoplankton to fine-tune model fits, which mainly improved fits of anchovy data

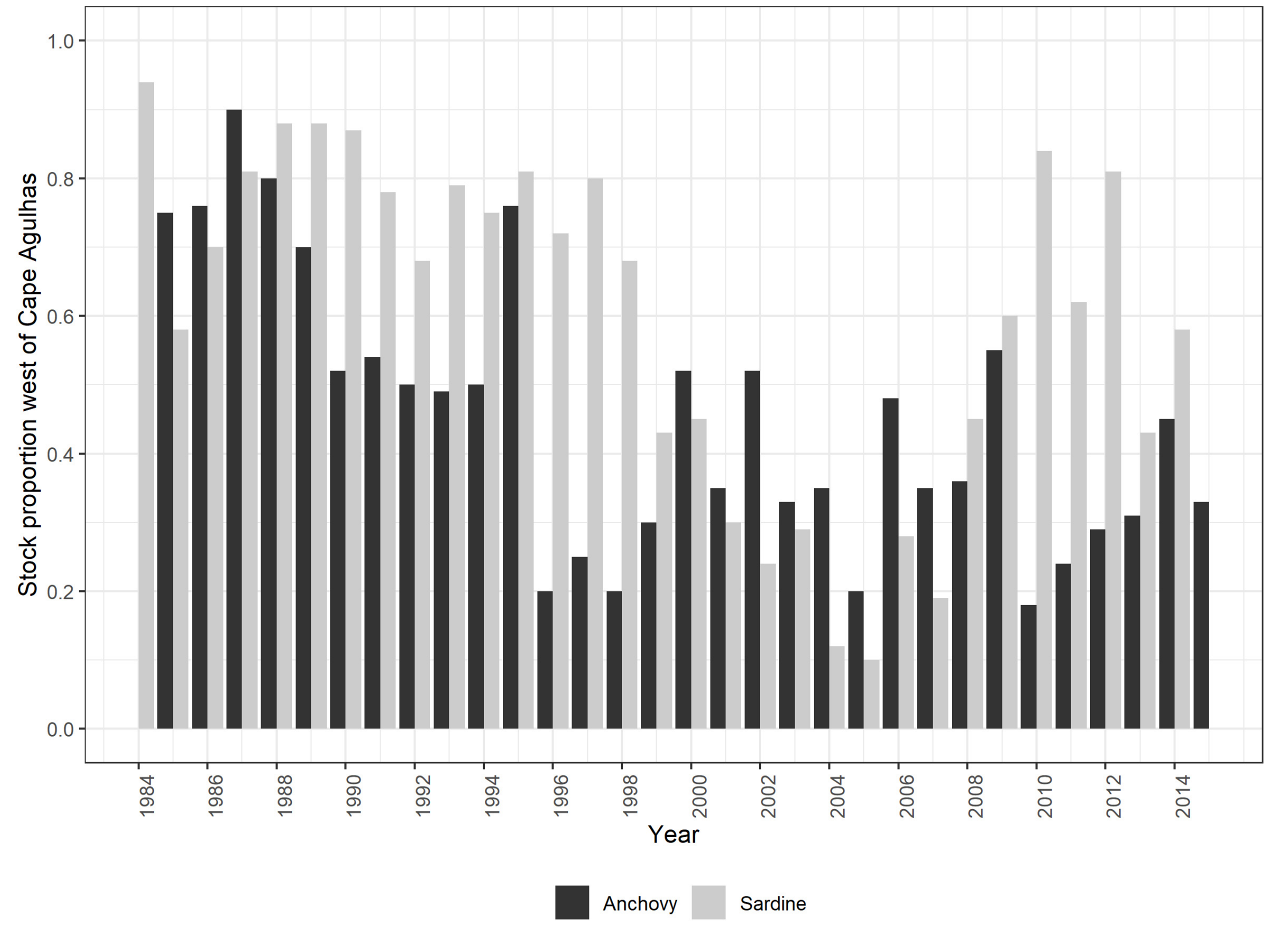


FIGURE 3 | Relative proportion of the total spawner biomass found to the west of Cape Agulhas: based on November survey biomass series for anchovy (from **Figure 1** of FISHERIES/2016/JUL/SWG-PEL/22REV2) and model-predicted sardine south coast component in November each year (based on the aforementioned divided by survey bias, Carryn de Moor, personal communication).

series (refer to explanation in section "Initial Sequential Model Fitting Incorporating an Upwelling Anomaly").

Further Exploring Alternative Weighting of Time Series

Under different weightings of the relative importance of time series in fitting the Southern Benguela model, the following simulation procedure was adopted once the fishing effort/mortality time series had been read in:

- Total cumulative upwelling (*Upwell*) was used to directly force large-celled phytoplankton production and the most sensitive predator-prey interactions were identified and vulnerability of prey to predators estimated to improve model fit to data series of field observations
- A small, additional, hypothetical environmental anomaly was fitted to small-celled phytoplankton to refine model fits, especially to anchovy biomass data series.

All in all, results of 17 different model fitting scenarios are reported and discussed in an attempt to achieve an acceptable fit of the temporal ecosystem model to observed time series of catch and abundance. In each scenario, factors such as weighting of time series, vulnerability of a prey group to a predator, and environmental anomalies affecting primary productivity were sequentially added in attempts to improve model fit to observations.

RESULTS

The Revised 1978 Southern Benguela Food Web

Parameters (input to the model or estimated by the model) for the revised and updated model of the Southern Benguela ecosystem in 1978 are tabulated (**Table 2** and **Supplementary Tables S1–S4**). As part of the "prebal" process, parameter spread and ecosystem characteristics in terms of flow rates were checked for consistency with general trophic principles and ecosystem characteristics from global models using the Prebal model routine in Ecopath, and found to be consistent with

TABLE 2 | Balanced parameters for the revised model of the Southern Benguela in 1978.

Group name	Trophic level	Biomass (t.km^{-2})	Total mortality (y^{-1})	P/B (y^{-1})	Q/B (y^{-1})	EE	P/Q (y^{-1})
Phytoplankton 1	1.000	35.000		200.000		**0.328**	
Phytoplankton 2	1.000	40.000		154.400		**0.028**	
Microzooplankton	2.053	**2.178**		482.000	1928.000	0.950	0.250
Mesozooplankton	2.526	**8.875**		40.000	133.333	0.950	0.300
Macrozooplankton	2.866	**13.737**		13.000	31.707	0.950	0.410
Gelatinous Zooplankton	3.293	4.545		0.584	1.669	**0.321**	0.350
Anchovy							
Anchovy recruits	2.526	4.535	1.200		19.042	**0.976**	0.063
Anchovy spawners	3.547	7.063	1.200		14.400	**0.323**	0.083
Sardine							
Juvenile sardine	2.526	0.228	1.400		21.819	**0.984**	0.064
Adult sardine	2.910	0.600	1.200		12.371	**0.979**	0.097
Redeye	3.662	5.555		1.300	13.000	**0.787**	0.100
Other small pelagics	3.604	**0.493**		1.000	10.000	0.990	0.100
Horse mackerel							
Juvenile Hmack	3.611	0.937	1.200		19.076	**0.247**	0.063
Adult Hmack	3.773	1.618	1.000		10.000	**0.890**	0.100
Chub mackerel	3.984	0.284		0.800	8.000	**0.837**	0.100
Lanternfish	3.730	**4.433**		1.200	12.000	0.990	0.100
Lightfish	3.639	**4.392**		1.200	12.000	0.990	0.100
Snoek	4.372	**0.198**		0.500	5.000	0.900	0.100
Tuna and Swordfish	4.562	**0.029**		0.470	**9.400**	0.900	0.050
Large Sparids	3.913	**0.012**		0.500	**5.000**	0.900	0.100
Medium Sparids	3.795	**0.027**		0.500	**5.000**	0.900	0.100
Sciaenids	4.273	**0.021**		0.500	**5.000**	0.900	0.100
Yellowtail	4.232	**0.033**		0.500	**5.000**	0.900	0.100
Other linefish	3.029	**0.019**		0.500	**5.000**	0.900	0.100
Mullet	2.393	**0.063**		0.500	5.000	0.900	0.100
Chokka Squid	3.807	0.455		3.500	**10.000**	**0.988**	0.350
Other cephalopods	3.825	0.900		3.500	**10.000**	**0.969**	0.350
M. capensis							
Small *M. capensis*	4.004	1.076	2.000		15.008	**0.940**	0.133
Large *M. capensis*	4.614	0.823	0.800		4.400	**0.845**	0.182
M. paradoxus							
Small *M. paradoxus*	3.957	1.293	2.000		16.030	**0.960**	0.125
Large *M. paradoxus*	4.525	0.989	0.800		4.700	**0.931**	0.170
PF Demersals	4.159	**1.912**		0.700	3.500	0.900	0.200
BF Demersals	3.450	**4.464**		0.700	3.500	0.900	0.200
Agulhas Sole	3.242	**0.006**		0.700	3.500	0.990	0.200
PF Chondrichthyans	4.821	0.582		0.500	4.545	**0.266**	0.110
BF Chondrichthyans	3.590	0.873		1.000	10.000	**0.820**	0.100
Apex Chondrichthyans	4.898	0.045		0.500	5.000	**0.000**	0.100
Seals	4.626	0.133		0.250	19.306	**0.961**	0.013
Cetaceans	4.435	**0.083**		0.150	10.000	0.900	0.015
African Penguin	4.064	0.002		0.201	96.980	**0.612**	0.002
Cape Gannet	4.394	0.002		0.199	99.917	**0.485**	0.002
Cape Cormorant	3.771	0.003		0.199	125.274	**0.039**	0.002
Other seabirds	4.535	0.053		0.199	125.882	**0.633**	0.002

(Continued)

TABLE 2 | Continued

Group name	Trophic level	Biomass (t.km^{-2})	Total mortality (y^{-1})	P/B (y^{-1})	Q/B (y^{-1})	EE	P/Q (y^{-1})
Benthic Producers	1.000	**6.218**		15.000		0.500	
Meiobenthos	2.000	**11.663**		4.000	33.000	0.950	0.121
Macrobenthos	2.161	**54.177**		1.200	10.000	0.950	0.120
WC rock lobster*	2.498	0.500		0.420	1.900	0.990	0.221
SC rock lobster	2.498	**0.981**		1.200	4.000	0.990	0.300
Detritus	1.000	50.000				**0.243**	

Values that were estimated by the model are indicated in bold font. For details of model groups, refer to ***Table 1*** *and* ***Supplementary Table S2****. P/B, Production/Biomass (y^{-1}); Q/B, Consumption/biomass (y^{-1}); P/Q, Production/consumption; EE, Ecotrophic Efficiency. *Biomass accumulation was estimated to be –0.603 t.km^{-2}.*

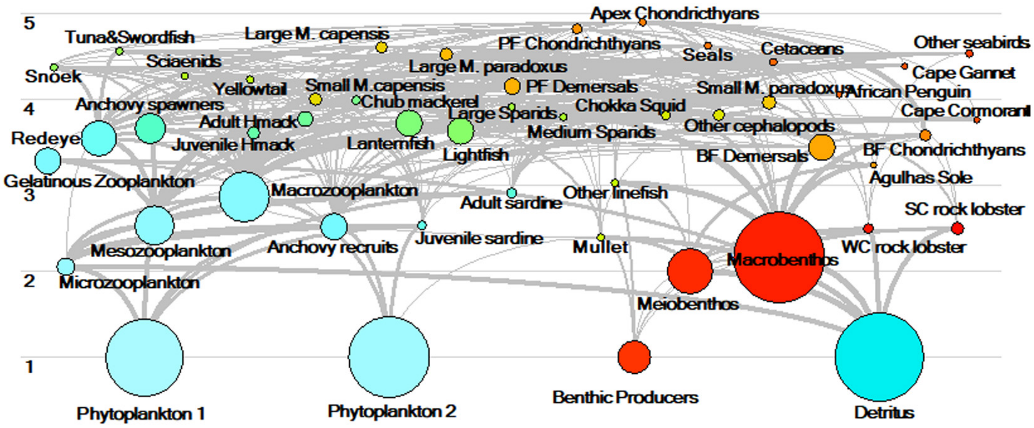


FIGURE 4 | Schematic of the trophic flows through the Southern Benguela food web estimated for 1978. Circles representing functional groups and are proportionally scaled according to biomass in 1978.

the guiding principles proposed by Link (2010) and Heymans et al. (2016) (for details, see **Supplementary Material section 6**). The trophic flow diagram summarizes the complex trophic web between trophic level 3 and 5, reflecting the importance of forage fish for a diverse assemblage of predatory species in this system (**Figure 4**). A discrepancy between isotope-derived and stomach content-derived estimates of trophic levels of anchovy, sardine and redeye in the Benguela was previously noted by van der Lingen and Miller (2011). Isotope studies showed greater trophic separation between redeye and the other two species in the period 2008–2010, than between anchovy and sardine, whereas assumed diet compositions previously modeled redeye to be feeding from a similar trophic level to anchovy (Shannon et al., 2003, 2004a). In the current revised model where anchovy are modeled in two stanzas each (**Supplementary Table S1**), anchovy recruits are feeding low in the food web (at the same level as juvenile sardine, **Table 1**), whereas adult anchovy are feeding higher but still slightly lower in the food web than redeye, so that overall, anchovy and redeye comparisons are more in line with the initial isotope studies. It should be noted that trophic levels are dynamic, and those of small pelagics depend greatly on the structure of the phyto-and zoo-plankton communities over the period being examined. For example, simply comparing modeled trophic levels between the 1978 base model and the end of the fitted period, viz. 2015, we see that the trophic level of small pelagics can vary by up to 21% (detailed results not shown).

Fitting the Model to Data Time Series

Through automated, stepwise fitting, the "best" model [lowest Akaike information criterion (AIC) and Sum of Squares (SS)] was obtained when fishing was incorporated, vulnerability estimates for the 40 most sensitive predator-prey interactions made, and an environmental anomaly with 18 spline points estimated and applied to the small phytoplankton model group to improve model fits to time series data. These numbers of vulnerabilities and spline points were used in subsequent model fitting as reported below. The time series were given equal weightings in this exploratory, automated model fitting (scenario 1, **Table 3**).

Initial Sequential Model Fitting Incorporating an Upwelling Anomaly

With *Total Upwelling* used to force large-celled phytoplankton production, estimating vulnerabilities for the 40 most sensitive predator-prey interactions enabled SS to be reduced by 83% (under equal weighting of time series, scenario 2, **Table 3**). Nevertheless, fits of birds and large pelagics were not good (plots not shown).

Weighting of Time Series Corresponding to Focus Model Groups

As intended, the weighting strategy aimed to improve pelagic fish-predator model representation (weightings1 in **Supplementary Table S8**) improved model fits to most line

TABLE 3 | Scenarios examined to improve model fit to data, when the data-derived upwelling anomaly (*upwell* – see footnote) is applied to large phytoplankton (apart from in Scenario 1), 40 vulnerabilities are fitted for the most influential predator-prey interactions (40vs) and a hypothetical environmental anomaly (18 spline points) is applied to small phytoplankton (Anomaly on PP1).

Scenario	Factors fitted	AIC	Cumulative reduction in SS
1a	Equal weightings	n/a	n/a
	Equal weightings + 40vs	182.7	74%
	Equal weightings + 40vs + Anomaly on PP1	46.19	76%
1b	Equal weightings + 40vs + Upwell + revised Anomaly on PP1	42.66	76%
2	Equal weightings + Upwell	n/a	n/a
	Equal weightings + Upwell + 40vs	87.28	83%
	Equal weightings + Upwell + 40vs + Anomaly on PP1	−79.92	84%
3	Weighting1	n/a	n/a
	Weighting1 + 40vs	8346	23%
	Weighting1 + 40vs + Anomaly on PP1	7943	40%
4	Weighting1 + 40vs + Anomaly on PP1 + Upwell	n/a	n/a
	Weighting1 + 40vs + Upwell + refitted Anomaly on PP1	8080	34%
5	Weighting1 + upwell	n/a	n/a
	*Weighting1 + upwell + 40vs	7887	44%
	Weighting1 + upwell + 40vs + Anomaly on PP1	7584	53%
6	Weighting1 + upwell + 40vs	n/a	n/a
	Weighting1 + upwell + 40vs + Anomaly on PP1 plus FF on sardine + revised Anomaly on PP1	7773	47% (only a further 3% reduction from scenario 5* above, but some better pelagic predator fits to biomass series- see **Supplementary Table S10**)
Preferred	Equal weightings + upwell + FF on sardine	n/a	n/a
	Equal weightings + upwell + FF on	92.88	84%
	sardine + 40vs	−6.096	85%
	Equal weightings + upwell + FF on sardine + 40vs + PP1 anomaly		
7	Weighting2 + upwell	n/a	n/a
	Weighting2 + upwell + 40vs	1628	62%
	Weighting2 + upwell + 40vs + Anomaly on PP1	1493	65%
8	Weighting3 + upwell	n/a	n/a
	Weighting3 + upwell + 40vs	2476	55%
	Weighting3 + upwell + 40vs + Anomaly on PP1	2337	59%
9	Weighting4 + upwell	n/a	n/a
	Weighting4 + upwell + 40vs	2350	55%
	Weighting4 + upwell + 40vs + Anomaly on PP1 ***(west coast scenario)***	2222	59%
10	Weighting5 + upwell	n/a	n/a
	Weighting5 + upwell + 40vs	2439	55%
	Weighting5 + upwell + 40vs + Anomaly on PP1 ***(south coast scenario)***	2284	59%
11	Weighting6 + upwell	n/a	n/a
	Weighting5 + upwell + 40vs	1772	61%
	Weighting5 + upwell + 40vs + Anomaly on PP1	1613	64%
12	Equal weightings + upwell + FF on sardine + FF on anchovy	n/a	n/a
	Equal weightings + upwell + FF on sardine + FF on anchovy + 40vs	−85.97	86%
	Equal weightings + upwell + FF on sardine + FF on anchovy + 40vs + PP1 anomaly	−190.2	87%
13	Equal weightings + upwell + FF on sardine + PC2 on anchovy + Penguin mortality	n/a	n/a
	Equal weightings + upwell + FF on sardine + PC2 on anchovy + Penguin mortality + 40vs	−129.2	86.6%
	Equal weightings + upwell + FF on sardine + PC2 on anchovy + Penguin mortality + 40vs + PP1 anomaly	−258.0	87.4%
14	Equal weightings + upwell + FF on sardine + PC2 on anchovy + Penguin mortality	n/a	n/a

(Continued)

TABLE 3 | Continued

Scenario	Factors fitted	AIC	Cumulative reduction in SS
	Equal weightings + upwell + FF on sardine + PC2 on anchovy + Penguin mortality + 25vs (As in scenario 13 above but where ***vulnerabilities for 25 predators were fitted*** in place of 40 most vulnerable predator-prey interactions)	−357.7	87.6% (88% if PP1 anomaly is also added)
15	Equal weightings + upwell + FF on sardine + PC2 on anchovy + Penguin mortality	n/a	n/a
	Equal weightings + upwell + FF on sardine + PC2 on anchovy + Penguin mortality + 25vs (As in scenario 13 above but where ***vulnerabilities were fitted for the 25 predators for which time series were used in model fitting***)	−334.7	87.6% (88% if PP1 anomaly also added)

*The hypothetical environmental anomaly applied to small phytoplankton was revised after each series of fittings as a final "tuning" of the model to data series and the fitting factors appear in the order in which the fitting proceeded. In the preferred scenario and scenarios 12, 13, and 14, data-derived forcing functions were applied as indicated to consumption of sardine, consumption of anchovy and African penguin mortality (FF and PC). Reduction in sum of squares (SS) of model fits to data series are sequentially reported for each scenario. Akaike's information criterion (AIC) is a measure of model quality (Symonds and Moussalli, 2011). The number of AIC data points was 1410. Weighting of time series are documented as reported in **Supplementary Table S8** and these together with forcing functions (upwell and FF) are summarized below. Equal weightings indicates that all data time series used for model fitting were equally weighted. Weighting1 was selected to heavily prioritize key groups in the model fitting (see text). Weighting2 was based on model group pedigree. Weighting3 was based on pedigree of the model time series where catches and effort are weighted at a high value of 10. Weighting4 and Weighting5 apply to west coast (WC) versus south coast (SC) time series; where WC and SC biomass or effort is available for a single group, only the WC or SC series is used. Linefish CPUE series are afforded higher weighting (4) in Weighting6, which is otherwise the same as Weighting3 and based on pedigrees allocated to model time series. Weighting details are provided in **Supplementary Table S8**.*

fish data series as well as to the endangered African Penguin. When fishing effort series alone drove temporal dynamics of model groups, the overall model fits were still poor for most groups, but were reduced by 44% (scenario 5, **Table 3**) when vulnerability of prey to predators was fine-tuned (for the 40 most sensitive interactions) under observed fisheries and total upwelling driver series. A further 9% reduction in SS was achieved when a hypothetical anomaly was fitted to small phytoplankton, yielding an overall reduction of 53% in sum of squares (**Table 3**). As expected, model fits were not improved to the same extent when vulnerabilities were tuned before upwelling was incorporated (scenario 4).

Refined Fitting Process to Include Sardine and Anchovy Availability on the West Coast

The simple sardine availability function applied to sardine-predator interactions assuming equally weighted time series (preferred scenario) yielded the same% reduction in SS of model fits to data series as obtained under Scenario 2 (85% SS reduction, **Table 3**). However, closer inspection of model plots (**Figure 5**) showed that modeled anchovy and sardine adults and recruit series were up to 37% better correlated to data series in the preferred scenario than without the sardine availability function (**Supplementary Table S9**). Similarly, African penguins and adult hake of both species showed greatly improved model fits to data. Most model linefish groups on the west coast correlated more closely with data when sardine availability function was included, but this was not the case for some south coast linefish groups; only large sparids on the south coast improved in model fit.

By contrast, under weighting1 to strengthen importance on focus model groups (weighting 1 in **Supplementary Table S7**; Scenario 6 in **Table 3**), SS of fits of the model to time series was reduced by only 47% (**Table 3**). However, model fits to data were improved for several sardine predators, in particular penguins, adult *M. paradoxus* and yellowtail which increased in model-data correlations by 39, 80, and 71% respectively (**Supplementary Table S10**). Nevertheless, model fit to data series for anchovy and sardine, and several other predators deteriorated despite efforts to enhance these groups by heavier weighting of their data time series.

When, in addition to a sardine availability function, an availability function was applied to anchovy consumption across all predators, based on the proportion of anchovy spawner biomass surveyed west versus south of Cape Agulhas (Coetzee et al., 2016), model fits to data series of anchovy and sardine recruits, medium sparids and yellowtail improved (**Table 3**, scenario 12 and **Supplementary Table S11**). However, model fits to anchovy and sardine spawner biomass, penguins, adult hake, large sparids and sciaenids were much poorer (**Supplementary Table S11** and **Supplementary Figures S3, S4**).

Extensive model scenarios (details not shown) were run in an attempt to best incorporate information contained in the Food Availability Index of Crawford et al. (2019). Initially, a forcing function based on this index was applied only to sardine and/or anchovy – bird interactions, but model fits were most improved when the simple sardine availability index used in the previous scenarios was retained, the Food Availability Index (Crawford et al., 2019) applied to availability of anchovy across all model predators, and the inverse of this function applied to "other mortality" of African Penguins (Scenario 13, **Table 3**). However, although incorporation of this index in this way greatly improved model fits to data series for penguins and medium sparids on the south coast, and to a lesser extent for gannets, fits were poorer for most other groups in this scenario (**Supplementary Table S11** and **Supplementary Figures S5, S6**).

Further Exploring Alternative Weighting of Time Series

Model trajectories of biomass and landings outputs for 1978–2015 were compared to time series (**Supplementary Table S5**) of catches, biomass (with the exception of survey-based spawner biomass series for anchovy and sardine, as above) and mortality time series, and model AIC and Sum of Squares (SS) (**Table 3**) as well as data-model plots per functional group (not shown apart from the "preferred scenario" in **Figure 6**) were examined for different time series weightings. None of the selected and carefully reasoned time series weighting scenarios improved overall models fits; SS of model fits to data were reduced by a maximum of 65% in scenario 7 (weighting2 based on model pedigree), and 64% in scenario 11 (weighting6 in which linefish CPUE series are afforded higher weighting), compared to an 84% and 85% reduction in SS respectively in scenario 2 and the preferred scenario, both of which assume equal weighting of time series. Furthermore, including only west coast series or only south coast series for model groups where coast-disaggregated series were available did not improve model fits overall either (SS reduction remained at 59%, scenarios 3–5, **Table 3**).

Where indicated by *upwell*, a forcing function is applied to large phytoplankton based on Lamont et al. (2018) cumulative upwelling series (**Table 3**). In the *preferred* scenario and scenarios 12 and 13, forcing factors derived from the proportion of sardine and anchovy respectively modeled or surveyed west of Cape Agulhas (Coetzee et al., 2016; Carryn de Moor, personal communication) are applied to juvenile and adult sardine and anchovy interactions with their predators (FF). In scenario 13, a forcing function/its inverse derived from the Food Availability

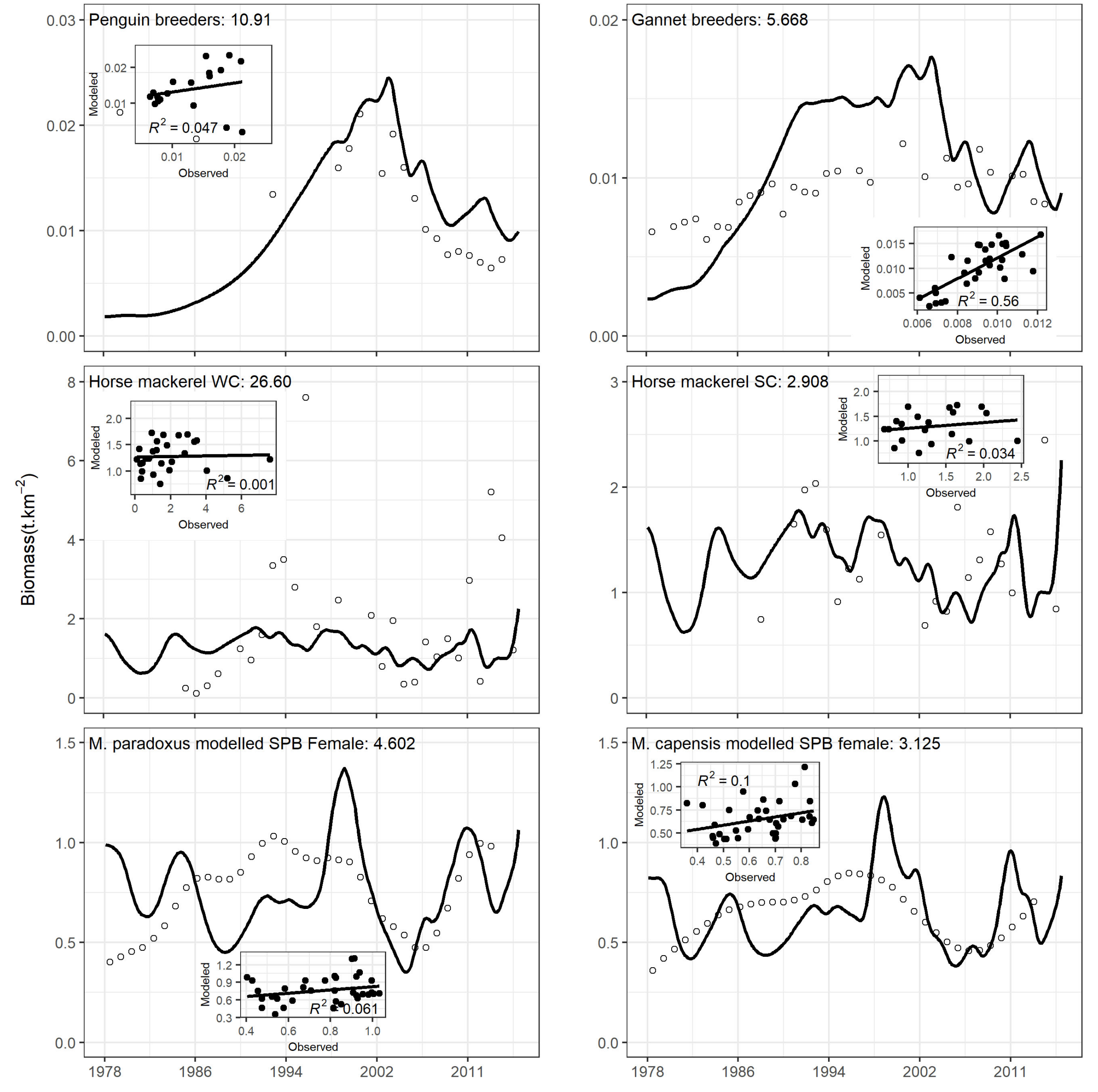
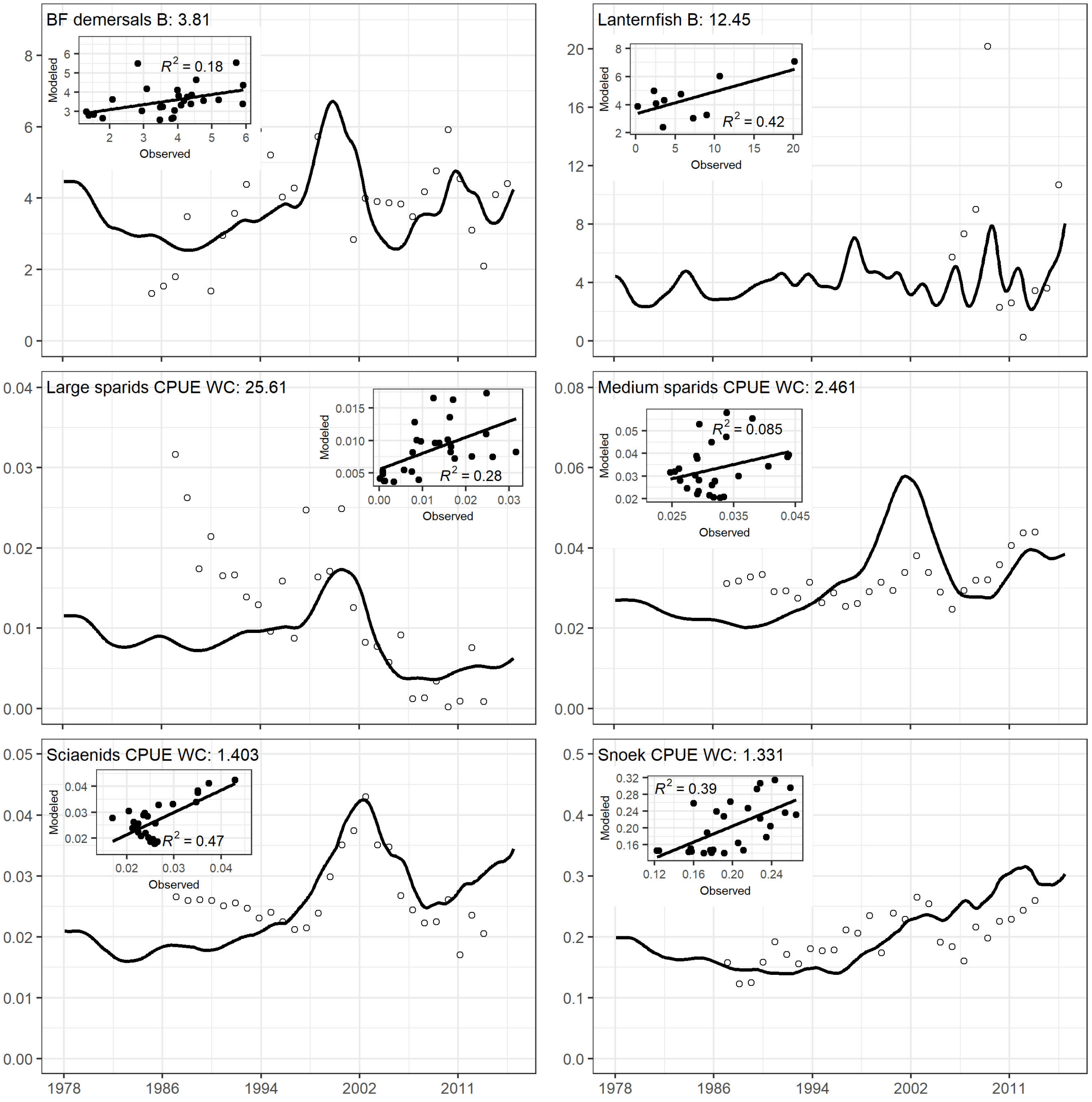


FIGURE 5 | Continued

Index of Crawford et al. (2019) is applied to juvenile and adult anchovy consumption by predators/African penguin mortality respectively (PC2).

Flow Control

Sardine dominated 40% of the 40 most sensitive predator-prey interactions searched for during model fitting. Vulnerability estimation found sardine to exert top-down flow control on small phytoplankton, whereas microzooplankton exerted bottom-up control on sardine in model fitting (**Supplementary Table S12**). In the absence of any forcing functions, model fitting requires that sardine and anchovy control microzooplankton trophically. Bottom–up control emerged for sardine on Sciaenids, African penguins, Cape gannet, Cape Cormorant and other seabirds (**Supplementary Table S12**). Several predators exerted top-down control on sardine, including horse mackerel, yellowtail, small hake, other cephalopods and pelagic-feeding chondrichthyans. No interactions between anchovy and its predators were found when searching for the 40 most sensitive predator-prey interactions with or without environmental forcing incorporated into the model fits (**Supplementary Table S12** and others not shown). An additional two vulnerability scenarios were explored in which the same vulnerability setting was applied to interactions between a specific predator and all its prey groups. Firstly,



BF demersals B: 3.81

Lanternfish B: 12.45

Large sparids CPUE WC: 25.61

Medium sparids CPUE WC: 2.461

Sciaenids CPUE WC: 1.403

Snoek CPUE WC: 1.331

FIGURE 5 | Continued

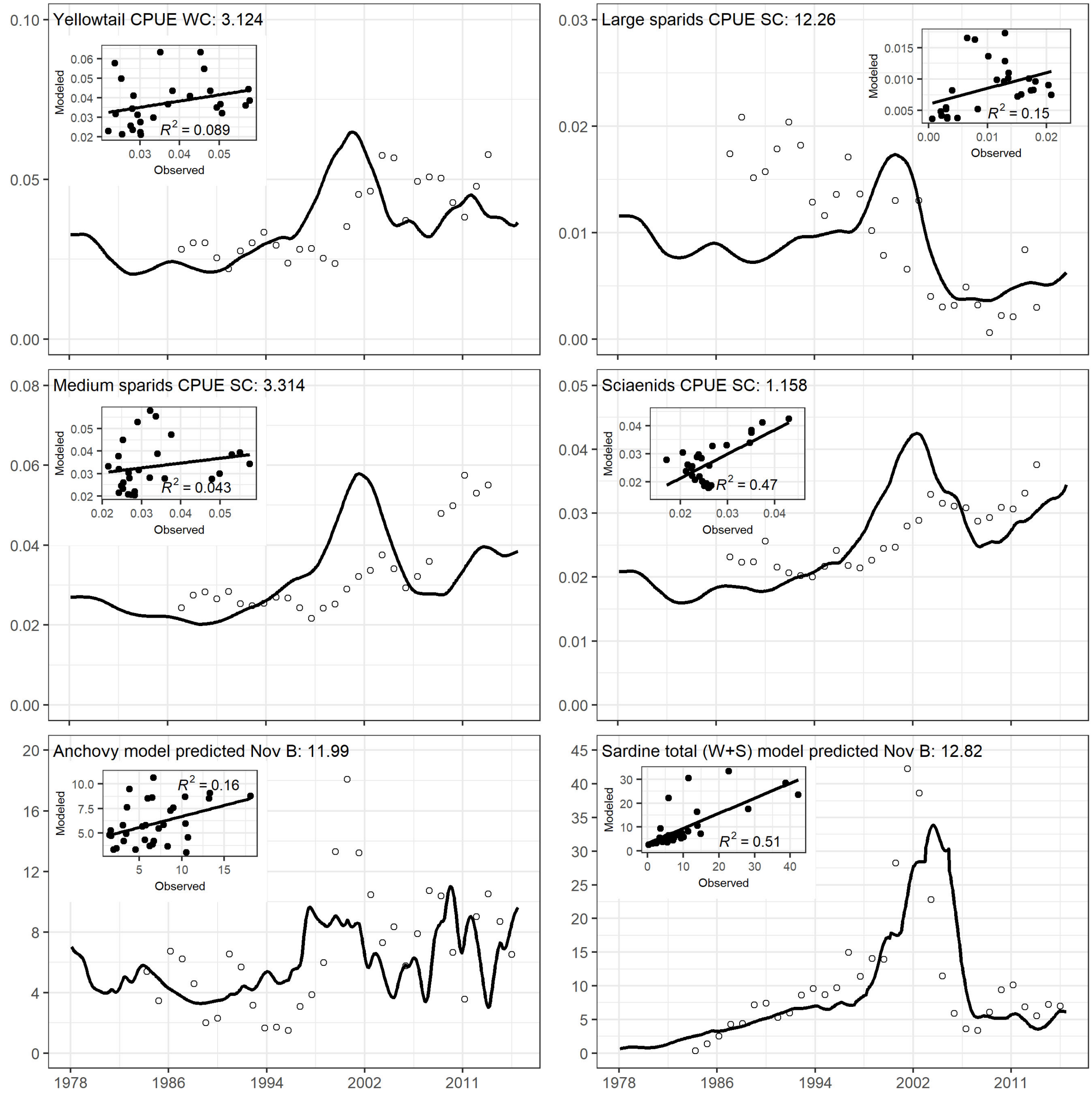


FIGURE 5 | Model fits of anchovy and sardine, and predators dependent on them in the preferred model fitting scenario. The contribution of each group to model sum of squares is provided on the plots. The figure is split into three sections to facilitate inclusion of scatterplots for each model-observation time series pair, and the R^2 of each correlation is provided.

vulnerabilities were fitted for 25 predators in place of the 40 most sensitive predator-prey interactions (scenario 14). In a second instance, vulnerabilities were fitted for the 25 predators for which time series were used in model fitting (scenario 15). These scenarios yielded poorer model fits of the key species anchovy and sardine, and unrealistic trajectories of tuna and swordfish in recent years, despite large reduction in overall model SS (**Table 3**). Further, model fits in scenario 14 were poorer for sciaenids, snoek, horse mackerel and hake. Nevertheless, fitted vulnerabilities in the first instance suggested bottom-up flow control for Sciaenids, African penguin, Cape gannet and deep-water hake, and top–down by yellowtail, snoek, small shallow water Cape hake and chondrichthyans, in good agreement with the 40v-scenarios modeled. In the second instance, bottom-up flow control was estimated for anchovy, sardine juveniles, horse mackerel, lightfish, large hakes, demersal fish, chokka squid and Cape gannet, whereas chub mackerel, adult sardine, lanternfish, snoek, yellowtail, small shallow-water Cape hake and African Penguins were estimated to exert top-down control on their prey. The outliers here compared to previous scenarios are top-down

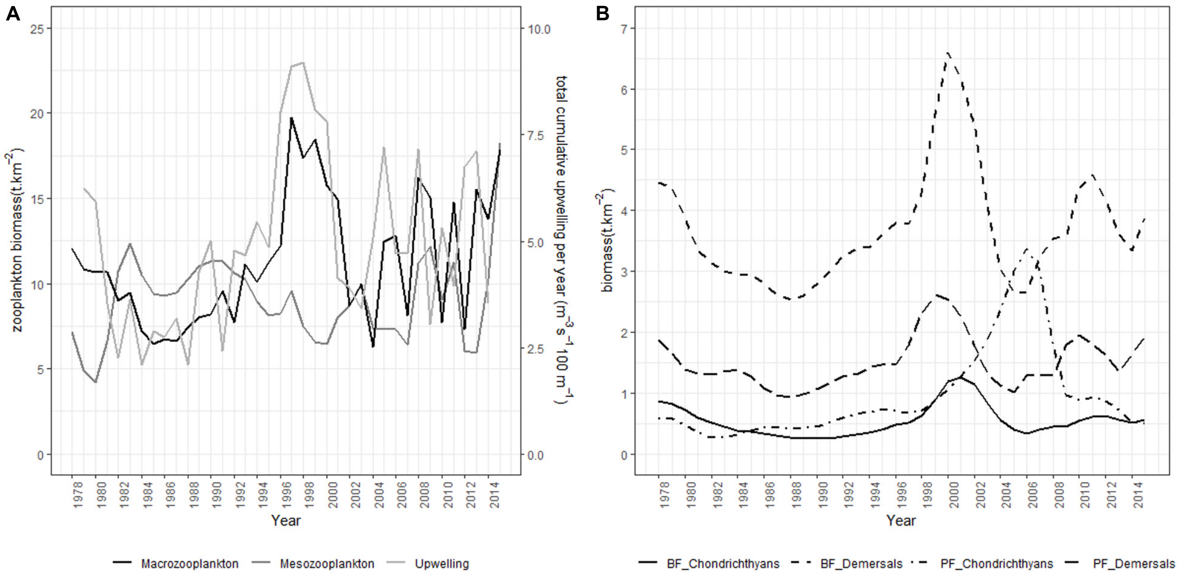


FIGURE 6 | Model trajectories from the preferred Southern Benguela model fitting scenario showing **(A)** meso-and macro-zooplankton dynamics in relation to total cumulative upwelling, and **(B)** demersal and chondrichthyan stock dynamics.

control by African penguin ($v = 19$) and lanternfish ($V > 1000$), suggesting these two groups may be far from their carrying capacities in this model configuration.

DISCUSSION

To date, the dual, interacting contributions of both fishing and environmental variability in driving observed dynamics in the Southern Benguela ecosystem have been highlighted by means of ecosystem modeling (Shannon et al., 2004b; Travers-Trolet et al., 2014; Ortega-Cisneros et al., 2018b) and using survey-based (Shannon et al., 2010) and modeled-derived (Fu et al., 2018) indicators. Building on previous Ecosim modeling (Shannon et al., 2004a, 2008; Smith et al., 2011), a more detailed disaggregation of the southern Benguela food web was possible given the more extensive abundance and catch time series data available. These expanded data series were used to improve the model resolution of the Southern Benguela ecosystem, and to further explore food web processes underpinning observed ecosystem dynamics. In our study, internal model food web dynamics were modeled in two ways, namely by means of parameterizing predator-prey interactions described in terms of vulnerabilities of prey to predators, and by means of direct forcing of sardine and anchovy availability to its predators. These internal predator-prey dynamics are themselves affected by, and interact with, both environmental and fishing drivers. Here, estimated fishing effort series were used to drive over half of the 31 model fishing fleets, and upwelling effects were modeled by forcing applied to large phytoplankton production. Together, modeling these three key drivers produced model ecosystem dynamics that compared favorably to several of the observed catch, abundance and mortality time series data available for the Southern Benguela.

To elaborate further, reasonable overall fit of small pelagic predators to available catch and abundance time series data was obtained by (i) allocating equal weightings to all time series used (while excluding modeled anchovy and sardine recruitment in billions, and excluding coast-specific modeled anchovy and sardine November biomass series), (ii) incorporating an upwelling anomaly based on annual means of TCU reported in Lamont et al. (2018) applied to large phytoplankton productivity, and iii) applying a forcing function derived from the relative proportion of sardine spawner biomass on the west coast (based on Coetzee et al., 2016, modified to account for survey bias, Carryn de Moor, personal communication) to modify availability of sardine (juveniles and adults) to predators. Subsequently, the 40 most sensitive predator-prey interactions were parameterized in terms of vulnerability to predation, to improve model fits. Finally a small, model-estimated hypothetical forcing function was fitted to small phytoplankton *in lieu* of non-specified environmental variability, in an attempt to further improve model fit to data series.

Upwelling intensity and variability both increased on the west and south coasts of South Africa in the first part of the 1990s (Blamey et al., 2012). Upwelling drives productivity in the Benguela, affecting prey abundance of fish and top predators (Hutchings et al., 2009), specifically mediated through small pelagic fish which link plankton productivity to predators in upwelling food web (e.g., Cury et al., 2000; Roy et al., 2001). van der Sleen et al. (2018) successfully fitted a GAM model to describe the relationship between anchovy recruitment and the December-March cumulative upwelling in the southern Benguela. In our modeling study, this same upwelling index, averaged annually (Lamont et al., 2018), was incorporated through forcing of large phytoplankton productivity, which feeds through the model food web via zooplankton dynamics. Copepod abundance on the west coast of South Africa increased between 1950 and the late 1990s, likely reflecting reduced predation pressure by small pelagic fish over the period, together with long-term intensification of coastal upwelling (Verheye and Richardson, 1998; Verheye et al., 1998). Between 1988 and 2003, a decline in abundance of large copepods was measured off South Africa, with a concomitant increase in abundance of small copepods (Huggett et al., 2009), likely related to both offshore warming and increased predation pressure exerted by small pelagics in the early 2000s when forage fish abundance was unusually high (Hutchings et al., 2009). In our non-spatialized model, small copepods are included in the mesozooplankton model group, which indeed showed a three-fold increase between 2000 and 2015, as well as a slight long-term increase over the modeled time period (1978–2015) despite west and south coast trajectories not being separated in our model (**Figure 6A**).

Southern Benguela ecosystem dynamics were fitted for the period 1978 to 2015, spanning the period of ecosystem changes including ecosystem regime shifts. Since the 1980s, declines and geographical shifts in distribution have been observed in several species off South Africa, and have been related to fishing and environmental changes (Blamey et al., 2014). For example, as recommended by Griffiths (2000), line fishing effort was severely reduced from 2000 onward following declaration of an emergency in this fishery. There have been indications that silver kob *Argyrosomus inodorus* and carpenter *Argyrozona argyrozona* are responding positively to reduced catches (Winker et al., 2013). These trends are captured by increasing Ecosim model abundances of Sciaenidae and medium Sparids respectively (**Figure 5**). Demersal fish off South Africa's west coast have exhibited changes over time, with indications of ecosystem shifts in the early 1990s and mid-2000s (Atkinson et al., 2011). These authors found increases in some fast-growing species of eels and fish, and declines in slow-growing, long-lived species such as chondrichthyans, attributing the changes to environmental drivers (temperature being the key) in combination with indirect trophic effects of fishing (Atkinson et al., 2011). In the fitted Ecosim model, increases in benthic-feeding and pelagic-feeding demersal fish and pelagic-feeding demersal chondrichthyans were captured in the 1990s, whereas demersal fish and benthic-feeding chondrichthyans declined in the early 2000s and model pelagic-feeding chondrichthyans increased (**Figure 6B**). Both species of Cape hake have been showing mixed trends since the 1960s (Rademeyer et al., 2008; Atkinson et al., 2011), but the ecosystem model fitted passably to stock assessment model series for recent decades (**Figure 5**). Relative abundances of anchovy and sardine were recorded to have shifted from predominantly west coast to greater proportions being found off the south and east coasts of South Africa (van der Lingen et al., 2002; Fairweather et al., 2006). Watermeyer et al. (2016) showed parallel, although smaller increases in the proportion of redeye, chub mackerel, kingklip, yellowtail, and chokka squid located east of Cape Agulhas between 1985 and 2008, and deduced from system connectivity indices that the period 2003–2008 was likely one of change. This supported the early signals of change previously reported in demersal fish data series (Atkinson et al., 2011), winds, upwelling and bottom oxygen depletion levels (Howard et al., 2007; Blamey et al., 2012; Jarre et al., 2015).

By considering the ecosystem holistically and elucidating key interactions, this modeling study has expounded on several of the key predator-prey relationships in the southern Benguela food web, which have been receiving careful attention by other colleagues in the area. Our study underlines the strong influence of sardine on the food web dynamics of the Southern Benguela. Predator-prey interactions involving sardine accounted for 40% of the 40 most sensitive predator-prey interactions in the Southern Benguela model, emphasizing the pivotal role that sardine play in controlling flow of energy in the Southern Benguela food web. This was captured in the model fitting process through applying a forcing function on all interactions between sardine as prey, and their predators; here, a simple forcing was invoked that was based on the proportion of sardine spawners located west of Cape Agulhas each year. Anchovy-predator interactions were absent from the 40 most sensitive predator-prey interactions identified in this study. The greater relative importance of sardine trophically compared to anchovy was further highlighted by our finding that a similar availability function explored in the case of anchovy, based on proportion of anchovy spawner biomass surveyed west of Cape Agulhas, only improved model fit for penguins and anchovy, but reduced model fit for adult sardine, hake adults and most linefish groups (**Supplementary Table S11**).

Availability of forage fish to predators needs further careful consideration. In the Benguela, seabirds particularly are closely associated with the dynamics of small pelagic fish. All three seabird species that rely heavily on sardine and anchovy as key prey species have been classified as endangered (Cape gannets, Cape cormorants and African penguins). Crawford et al. (2019) have undertaken Principal Component (PC) analyses of South African seabird diet and life history measures. PC1 showed an alternation between sardine and anchovy in the diet; PC2 contrasted good (when either anchovy or sardine was available) and poor (when gannets needed to eat saury offshore, or hake offal) foraging regimes. PC2 was significantly related to numbers of gannet and Cape cormorant breeders, and to adult penguin survival. Using PCA results (PC2 in particular, which captures prey availability), the authors proposed a Forage Availability Index. As expected, this seabird-focused index was found to be helpful in improving model fits for African penguin and Cape gannet, and via unexpected ecosystem feedbacks also medium sparids, but did not improve model fits to data series for small pelagics or linefish (**Supplementary Table S11** and **Supplementary Figures S5, S6**), emphasizing the importance of establishing a series of species-specific functional response relationships based on empirical data, to be incorporated to improve ecosystem model fits across several key functional groups simultaneously. A particular future focus research area should be closer examination of the functional responses of predatory fish to their prey.

In our study, predatory fish showed top-down (e.g., snoek) and bottom-up (e.g., Sciaenids) flow control (**Supplementary Table S12**). Further, a functional relationship capturing both bottom-up and top–down interactions has been found between geelbek (a Sciaenid) and sardine availability on the south west coast of South Africa (Parker et al., 2020). In addition, a weaker although still significant relationship between anchovy and yellowtail has also been identified by these authors (Parker et al., 2020). Our model fitting results support their finding: when an anchovy availability function was applied to anchovy consumption by predators, model fits to data series of both anchovy and yellowtail improved (**Table 3**, scenario 12 and **Supplementary Table S11**), and top-down flow control was estimated for yellowtail on its pelagic prey (scenarios 14 and 15). Ways to incorporate these newly found functional responses should be explored in future ecosystem modeling work.

Despite helpful guidelines in fitting Ecosim models to time series data (Shannon et al., 2004a; Heymans et al., 2016; amongst others), the model fitting process is very much dependent on one's understanding of the food web in question, and appreciation of the quality and intricacies in the data series available. What may be a sensible sequence of fitting in one system may well not be the most appropriate in another. Different ways of accounting for and incorporating process concepts into an Ecosim model of a given system need to be tested and aligned to current understanding of that ecosystem. The importance of local knowledge and experts in facilitating most sensible or "best" model fit should not be underestimated, as has been demonstrated similarly in the case of applying and interpreting ecosystem indicators (Shannon et al., 2010). Further, ecosystem type and the objective of the model in question dictate model group aggregations, which in turn influence some of the characteristics used as general guidelines in pre-balancing Ecopath models (Link, 2010; see discussion in **Supplementary Material S6**).

As the model currently stands, it is not yet fully suited as a management tool, yet it could be usefully applied in a scenario testing mode. This study provides documentation of an updated, detailed baseline trophic model for the southern Benguela ecosystem, from which functional predator-prey responses, spatialized modeling, and management strategy evaluation can be explored. For instance, improved parameterization of anchovy and sardine in the new model could facilitate investigation into whether predator-fishery competition may be reduced if fisheries differentially target different size classes of anchovy and sardine to those selected by predatory fish. Furthermore, as may be the case for seabirds elsewhere, it could be investigated whether fisheries targeting adult forage fish negatively impact seabirds by changing availability of juvenile fish relied upon as prey for our resident breeding seabirds (Field et al., 2010; Sydeman et al., 2017). On the contrary, data constraints encountered for some functional groups such as cetaceans will limit the usefulness of the model in answering detailed questions pertaining to dolphins and whales.

In particular, Ecospace and the novel modeling applications within (Steenbeek et al., 2013; Christensen et al., 2014) will be used to extend the current temporal model presented here to better capture spatial aspects of trophic interactions in the southern Benguela. Ecospace model configuration will also facilitate additional environmental drivers to be incorporated. For example, it will be possible to directly incorporate sea surface temperature fields (Dufois et al., 2012; Rouault et al., 2010), to use TCU divergence between September and January as a proxy for oxygen depletion, as proposed by Jarre et al. (2015) and to explore incorporating further seasonality [recall that van der Sleen et al. (2018) demonstrated a stronger relationship between anchovy recruitment and December–March cumulative upwelling when anchovy spawner biomass located west of Cape Agulhas was above a certain threshold level]. These avenues will help define spatial habitat capacity for each functional group modeled. Productivity of sardine and anchovy differ between the west and south coasts, and at least in the case of sardine, depend strongly on spatial distribution of fishing pressure (Watermeyer et al., 2018). A fully spatialized Southern Benguela Ecospace model would support spatially explicit advice on fishing strategies under long-term climate variability and change and has been identified as a key research area in several recently launched international projects.

To reiterate, in this study in which the Benguela ecosystem is modeled as a single unit using a non-spatial trophic model, the observed spatial changes have been approximated simply through internal food web dynamics by (i) estimating vulnerability parameters of most sensitive predator-prey interactions based on existing data time series, (ii) forcing changes in availability of sardine as prey to predators based on the surveyed proportion of sardine on the west coast, and (iii) by annual cumulative upwelling driving phytoplankton productivity. Attempting to fit the model to either west coast or south coast time series rather than mixing spatial series did not improve overall model fits, highlighting the limitations of the current non-spatialized model in describing coast-specific dynamics. Nevertheless, the model presented is an important contribution toward a platform from which climate scenarios could be explored with respect to fisheries management measures under global change, such as the work that is being undertaken by the Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP) using several different types of ecosystem modeling approaches in numerous regions of the world (Tittensor et al., 2018).

Timing of concluding this revised, fitted, temporal Ecosim model as a basis from which to extend into a spatialized Ecospace model of the Southern Benguela is ideal in the light of the recent National Biodiversity Assessment 2018 (NBA 2018; Skowno et al., 2019). The NBA 2018 has collated and assessed multiple spatial layers and pressures in the ocean spaces off South Africa, and incorporates expert knowledge and interpretation of these data and maps. This assessment, and in view of the new expanded array of 41 marine protected areas recently gazetted for South Africa, provides enormous opportunity for expanding Ecopath with Ecosim modeling of the Southern Benguela spatially, and will guide extensive spatial-temporal scenario testing using Ecospace in support of ecosystem-based management of our marine social-ecological systems.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

LS conceived the study, developed and ran the model simulations, and wrote the manuscript. All the authors provided comments on and inputs to the manuscript. KO-C provided substantial inputs to both text and figures. TL provided the upwelling index. HW provided the line fish data series and advised on model structure. RC provided the Forage Availability Index. AJ helped in framing the study and provided the inputs to the manuscript structure and focus. MC contributed to development of the 1978 model.

FUNDING

L' Institut de Recherche pour le Développement (IRD), CRH, Research Unit MARBEC (UMR 248), avenue Jean Monnet, CS 30171, 34203 Sète Cedex, France, is thanked for providing core funding for the revision of the Southern Benguela EwE model. Funding for this study through the South African Research Chairs Initiative, funded by DSI and administered by NRF, through the Research Chair in Marine Ecology and Fisheries (Grant No. 65238) is also gratefully acknowledged. In addition, this work is also a contribution to the EU-Horizon 2020 project "TRIATLAS" (Grant No. 817578) and the One Ocean Hub.

ACKNOWLEDGMENTS

D. Merkle, T. Fairweather, and A. Makhado from the Department of Environment, Forestry and Fisheries (DEFF), South Africa, are thanked for making catch and abundance data available for small pelagic fish, demersal fish and seabirds, respectively. C. de Moor is thanked for sharing earlier stock assessment model series of small pelagics. We are grateful to V. Christensen for comments on an earlier draft of the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00540/full#supplementary-material

REFERENCES

ANON (2016). *Fisheries_2016_APR_SWG_PEL_16*. Mesopelagic Experiment Application Submitted to DAFF. Cape Town: Department of Agriculture, Forestry and Fisheries.

Atkinson, L. J., Leslie, R. W., Field, J. G., and Jarre, A. (2011). Changes in demersal fish assemblages on the west coast of South Africa, 1986–2009. *African J. Mar. Sci.* 33, 157–170. doi: 10.2989/1814232x.2011.572378

Blamey, L. K., Howard, J. A. E., Agenbag, J., and Jarre, A. (2012). Regime-shifts in the southern Benguela shelf and inshore region. *Prog. Oceanogr.* 106, 80–95. doi: 10.1016/j.pocean.2012.07.001

Blamey, L. K., Plagányi, ÉE., and Branch, G. M. (2014). Was overfishing of predatory fish responsible for a lobster-induced regime shift in the Benguela? *Ecol. Modell* 273, 140–150. doi: 10.1016/j.ecolmodel.2013.11.004

Blamey, L. K., Shannon, L. J., Bolton, J. J., Crawford, R. J. M., Dufois, F., and Evers-King, H. (2015). Ecosystem change in the southern Benguela and the underlying processes. *J. Mar. Syst.* 144, 9–29. doi: 10.1016/j.jmarsys.2014.11.006

Bolton, J. J., Anderson, R. J., Smit, A. J., and Rothman, M. D. (2012). South African kelp moving eastwards: the discovery of Ecklonia maxima (Osbeck) Papenfuss at De hoop nature reserve on the south coast of South Africa. *African J. Mar. Sci.* 34, 147–151. doi: 10.2989/1814232x.2012.675125

Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., and Walters, C. J. (2014). Representing variable habitat quality in a spatial food web model. *Ecosystems* 17, 1397–1412. doi: 10.1007/s10021-014-9803-3

Christensen, V., and Walters, C. J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Modell.* 172, 109–139. doi: 10.1016/j.ecolmodel.2003.09.003

Cochrane, K. L., Augustyn, C. J., Fairweather, T., Japp, D., Kilongo, K., and Iitembu, J. (2009). Benguela current large marine ecosystem—governance and management for an ecosystem approach to fisheries in the region. *Coast. Manag.* 37, 235–254. doi: 10.1080/08920750902851187

Cockcroft, A. C., van Zyl, D., and Hutchings, L. (2008). Large-scale changes in the spatial distribution of South African West Coast rock lobsters: an overview. *African J. Mar. Sci.* 30, 149–159. doi: 10.2989/AJMS.2008.30.1.15.465

Coetzee, J., Merkle, D., Geja, Y., Mushanganyisi, K., and Shabangu, F. (2016). *Results of the 2016 Spawner Biomass Survey*. Report No FISHERIES/2016/DEC/SWG-PEL/79. Cape Town: Department of Agriculture, Forestry and Fisheries.

Coetzee, J., Merkle, D, Shabangu, F., Geja, Y., and Petersen, J. (2018). *Results of the 2018 Pelagic Biomass Survey.* Report No FISHERIES/2018/DEC/SWG-PEL/38. Cape Town: Department of Agriculture, Forestry and Fisheries.

Corrales, X., Coll, M., Ofir, E., Heymans, J. J., Steenbeek, J., and Goren, M. (2018). Future scenarios of marine resources and ecosystem conditions in the Eastern Mediterranean under the impacts of fishing, alien species and sea warming. *Sci. Rep.* 8:14284. doi: 10.1038/s41598-018-32666-x

Crawford, R. J. M., Ryan, P. G., and Williams, A. J. (1991). Seabird consumption and production in the Benguela and western agulhas ecosystems. *South African J. Mar. Sci.* 11, 357–375. doi: 10.2989/025776191784287709

Crawford, R. J. M., Sydeman, W. J., Thompson, S. A., Sherley, R. B., and Makhado, A. B. (2019). Food habits of an endangered seabird indicate recent poor forage fish availability off western South Africa. *ICES J. Mar. Sci.* 76, 1344–1352. doi: 10.1093/icesjms/fsz081

Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quiñones, R. A., and Shannon, L. J. (2000). Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES J. Mar. Sci.* 57, 603–618. doi: 10.1006/jmsc.2000.0712

Dufois, F., Penven, P., Peter Whittle, C., and Veitch, J. (2012). On the warm nearshore bias in pathfinder monthly SST products over eastern boundary upwelling systems. *Ocean Model.* 47, 113–118. doi: 10.1016/j.ocemod.2012.01.007

Fairweather, T. P., van der Lingen, C. D., Booth, A. J., Drapeau, L., and van der Westhuizen, J. J. (2006). Indicators of sustainable fishing for South African sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*. *African J. Mar. Sci.* 28, 661–680. doi: 10.2989/18142320609504215

Field, J. C., MacCall, A. D., Bradley, R. W., and Sydeman, W. J. (2010). Estimating the impacts of fishing on dependent predators: a case study in the California Current. *Ecol. Appl.* 20, 2223–2236. doi: 10.1890/09-0428.1

Fu, C., Travers-Trolet, M., Velez, L., Grüss, A., Bundy, A., and Shannon, L. J. (2018). Risky business: the combined effects of fishing and changes in primary productivity on fish communities. *Ecol. Modell.* 368, 265–276. doi: 10.1016/j.ecolmodel.2017.12.003

Grémillet, D., Pichegru, L., Kuntz, G., Woakes, A. G., Wilkinson, S., and Crawford, R. J. M. (2008). A junk-food hypothesis for gannets feeding on fishery waste. *Proc. R. Soc. B Biol. Sci.* 275, 1149–1156. doi: 10.1098/rspb.2007.1763

Griffiths, M. H. (2000). Long-term trends in catch and effort of commercial linefish off South Africa's Cape Province: snapshots of the 20th century. *South African J. Mar. Sci.* 22, 81–110. doi: 10.2989/025776100784125663

Heymans, J. J., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., Christensen, V., et al. (2016). Best practice in ecopath with ecosim food-web models for ecosystem-based management. *Ecol. Modell.* 331, 173–184. doi: 10.1016/j.ecolmodel.2015.12.007

Howard, J. A. E., Jarre, A., Clark, A. E., and Moloney, C. L. (2007). Application of the sequential t-test algorithm for analysing regime shifts to the southern Benguela ecosystem. *African J. Mar. Sci.* 29, 437–451. doi: 10.2989/AJMS.2007.29.3.11.341

Huggett, J., Verheye, H., Escribano, R., and Fairweather, T. (2009). Copepod biomass, size composition and production in the Southern Benguela: spatio–temporal patterns of variation, and comparison with other eastern boundary upwelling systems. *Prog. Oceanogr.* 83, 197–207. doi: 10.1016/j.pocean.2009.07.048

Huggett, J. A., Batyi-Nkwenkwe, K., Mdazuka, Y., Setati, S., and Wright, E. (2019). "Long-term variability in copepods off the South Coast during Spring, 1988–2018," in *South Africa's Oceans and Coasts Annual Science Report, 2018, Report No: 18*, eds S. P. Kirkman, J. A. Huggett, and R. J. M. Crawford (Pretoria: Department of Environmental Affairs), RP188/2019, ISBN: 987-0-621-47469-5.

Hutchings, L., Jarre, A., Lamont, T., van den Berg, M., and Kirkman, S. P. (2012). St Helena Bay (southern Benguela) then and now: muted climate signals, large human impact. *African J. Mar. Sci.* 34, 559–583. doi: 10.2989/1814232X.2012.689672

Hutchings, L., van der Lingen, C. D., Shannon, L. J., Crawford, R. J. M., Verheye, H. M. S., Bartholomae, C. H., et al. (2009). The Benguela current: an ecosystem of four components. *Prog. Oceanogr.* 83, 15–32. doi: 10.1016/j.pocean.2009.07.046

Jarre, A., Hutchings, L., Kirkman, S. P., Kreiner, A., Tchipalanga, P. C. M., and Kainge, P. (2015). Synthesis: climate effects on biodiversity, abundance and distribution of marine organisms in the Benguela. *Fish. Oceanogr.* 24, 122–149. doi: 10.1111/fog.12086

Koehn, L. E., Essington, T. E., Marshall, K. N., Kaplan, I. C., Sydeman, W. J., and Szoboszlai, A. I. (2016). Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current ecosystem. *Ecol. Modell.* 335, 87–100. doi: 10.1016/j.ecolmodel.2016.05.010

Lamont, T., García-Reyes, M., Bograd, S. J., van der Lingen, C. D., and Sydeman, W. J. (2018). Upwelling indices for comparative ecosystem studies: variability in the Benguela upwelling system. *J. Mar. Syst.* 188, 3–16. doi: 10.1016/J.JMARSYS.2017.05.007

Link, J. S. (2010). Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. *Ecol. Modell.* 221, 1580–1591. doi: 10.1016/j.ecolmodel.2010.03.012

Lockerbie, E. M., and Shannon, L. (2019). Toward exploring possible future states of the southern Benguela. *Front. Mar. Sci.* 6:380. doi: 10.3389/fmars.2019.00380

Ortega-Cisneros, K., Cochrane, K. L., Fulton, E. A., Gorton, R., and Popova, E. (2018a). Evaluating the effects of climate change in the southern Benguela upwelling system using the Atlantis modelling framework. *Fish. Oceanogr.* 27, 489–503. doi: 10.1111/fog.12268

Ortega-Cisneros, K., Shannon, L., Cochrane, K., Fulton, E. A., and Shin, Y.-J. (2018b). Evaluating the specificity of ecosystem indicators to fishing in a changing environment: a model comparison study for the southern Benguela ecosystem. *Ecol. Indic.* 95, 85–98. doi: 10.1016/J.ECOLIND.2018.07.021

Parker, D., Coetzee, J. D., Winker, H., and van der Lingen, C. D. (2020). Accounting for linefish dependency in the management of South African small pelagic fisheries. *Afr. J. Mar. Sci.* doi: 10.2989/1814232X.2020.1788160

Probyn, T. A. (1992). The inorganic nitrogen nutrition of phytoplankton in the southern Benguela: new production, phytoplankton size and implications for pelagic foodwebs. *South Afr. J. Mar. Sci.* 12, 411–420.

Rademeyer, R. A., Butterworth, D. S., and Plagányi, ÉE. (2008). Assessment of the South African hake resource taking its two-species nature into account. *African J. Mar. Sci.* 30, 263–290. doi: 10.2989/AJMS.2008.30.2.7.557

Rouault, M., Pohl, B., and Penven, P. (2010). Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. *African J. Mar. Sci.* 32, 237–246. doi: 10.2989/1814232X.2010.501563

Roy, C., van der Lingen, C. D., Coetzee, J. C., and Lutjeharms, J. R. E. (2007). Abrupt environmental shift associated with changes in the distribution of Cape anchovy Engraulis encrasicolus spawners in the southern Benguela. *African J. Mar. Sci.* 29, 309–319. doi: 10.2989/AJMS.2007.29.3.1.331

Roy, C., Weeks, S., Rouault, M., Nelson, G., Barlow, R., and van der Lingen, C. (2001). Extreme oceanographic events recorded in the Southern Benguela during the 1999-2000 summer season. *S. Afr. J. Sci.* 97, 465–471.

Ryan, P. G., and Moloney, C. L. (1988). Effect of trawling on bird and seal distributions in the southern Benguela region. *Mar. Ecol. Prog. Ser.* 45, 1–11. doi: 10.3354/meps045001

Scott, E., Serpetti, N., Steenbeek, J., and Heymans, J. J. (2016). A Stepwise Fitting Procedure for automated fitting of Ecopath with Ecosim models. *SoftwareX* 5, 25–30. doi: 10.1016/j.softx.2016.02.002

Serpetti, N., Baudron, A. R., Burrows, M. T., Payne, B. L., Helaouët, P., and Fernandes, P. G. (2017). Impact of ocean warming on sustainable fisheries management informs the ecosystem approach to fisheries. *Sci. Rep.* 7:13438. doi: 10.1038/s41598-017-13220-7

Shannon, L. J., Christensen, V., and Walters, C. J. (2004a). Modelling stock dynamics in the southern Benguela ecosystem for the period 1978–2002. *African J. Mar. Sci.* 26, 179–196. doi: 10.2989/18142320409504056

Shannon, L. J., Field, J. G., and Moloney, C. L. (2004b). Simulating anchovy–sardine regime shifts in the southern Benguela ecosystem. *Ecol. Modell.* 172, 269–281. doi: 10.1016/j.ecolmodel.2003.09.011

Shannon, L. J., Coll, M., and Neira, S. (2009). Exploring the dynamics of ecological indicators using food web models fitted to time series of abundance and catch data. *Ecol. Indic.* 9, 1078–1095. doi: 10.1016/j.ecolind.2008.12.007

Shannon, L. J., Coll, M., Yemane, D., Jouffre, D., Neira, S., and Bertrand, A. (2010). Comparing data-based indicators across upwelling and comparable systems for communicating ecosystem states and trends. *ICES J. Mar. Sci. J. Cons.* 67, 807–832. doi: 10.1093/icesjms/fsp270

Shannon, L. J., Moloney, C. L., Jarre, A., and Field, J. G. (2003). Trophic flows in the southern Benguela during the 1980s and 1990s. *J. Mar. Syst.* 39, 83–116. doi: 10.1016/S0924-7963(02)00250-6

Shannon, L. J., Neira, S., and Taylor, M. (2008). Comparing internal and external drivers in the southern Benguela and the southern and northern Humboldt upwelling ecosystems. *African J. Mar. Sci.* 30, 63–84. doi: 10.2989/AJMS.2008.30.1.7.457

Shannon, V., Hempel, G., Malanotte-Rizzoli, P., Moloney, C., and Woods, J. (2006). *Benguela: Predicting a Large Marine Ecosystem. Large Marine Ecosystem Series 14*. Amsterdam: Elsevier.

Sherley, R. B., Crawford, R. J. M., Dyer, B. M., Kemper, J., Makhado, A. B., and Masotla, M. (2019). The status and conservation of the cape gannet morus capensis. *Ostrich* 90, 335–346. doi: 10.2989/00306525.2019.1684396

Skowno, A., Poole, C., Raimondo, D., Sink, K., Van Deventer, H., Van Niekerk, L., et al. (2019). *National Biodiversity Assessment 2018: The Status of South Africa's Ecosystems and biodiversity. Synthesis Report*. Pretoria: South African National Biodiversity Institute.

Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., and Kaplan, I. C. (2011). Impacts of fishing low–trophic level species on marine ecosystems. *Science* 333, 1147–1150. doi: 10.1126/science.1209395

Steenbeek, J., Coll, M., Gurney, L., Mélin, F., Hoepffner, N., and Buszowski, J. (2013). Bridging the gap between ecosystem modeling tools and geographic information systems: driving a food web model with external spatial–temporal data. *Ecol. Modell.* 263, 139–151. doi: 10.1016/J.ECOLMODEL.2013.04.027

Sydeman, W. J., Thompson, S. A., Anker-Nilssen, T., Arimitsu, M., Bennison, A., and Bertrand, S. (2017). Best practices for assessing forage fish fisheries-seabird resource competition. *Fish. Res.* 194, 209–221. doi: 10.1016/j.fishres.2017.05.018

Symonds, M. R. E., and Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* 65, 13–21. doi: 10.1007/s00265-010-1037-6

Tittensor, D. P., Eddy, T. D., Lotze, H. K., Galbraith, E. D., Cheung, W., Barange, M., et al. (2018). A protocol for the intercomparison of marine fishery and ecosystem models: fish-MIP v1.0. *Geosci. Model Dev.* 11, 1421–1442. doi: 10.5194/gmd-11-1421-2018

Travers, M., and Shin, Y.-J. (2010). Spatio-temporal variability in fish-induced predation mortality on plankton. A simulation approach using a coupled trophic model of the Benguela ecosystem. *Prog. Oceanogr.* 84, 118–120. doi: 10.1016/j.pocean.2009.09.014

Travers-Trolet, M., Shin, Y.-J., Shannon, L. J., Moloney, C. L., and Field, J. G. (2014). Combined fishing and climate forcing in the southern Benguela upwelling ecosystem: an end-to-end modelling approach reveals dampened effects. *PLoS One* 9:e94286. doi: 10.1371/journal.pone.0094286

van der Lingen, C., and Miller, T. (2011). ""Trophic dynamics of pelagic nekton in the Southern Benguela current ecosystem: calibrating trophic models with stable isotope analysis," in *Interdisciplinary Studies on Environmental Chemistry- Marine Environmental Modeling & Analysis*, eds J. Omori, X. Guo, N. Yoshie, N. Fujii, I. Handoh, A. Isobe, et al. Tokyo, 85–94.

van der Lingen, C. D., Coetzee, J. C., and Hutchings, L. (2002). Temporal shifts in the spatial distribution of anchovy spawners and their eggs in the Southern Benguela: Implications for recruitment. *GLOBEC Rep.* 16, 46–48.

van der Lingen, C. D., Hutchings, L., Lamont, T., and Pitcher, G. C. (2016). Climate change, dinoflagellate blooms and sardine in the southern Benguela current large marine ecosystem. *Environ. Dev.* 17, 230–243. doi: 10.1016/j.envdev.2015.09.004

van der Sleen, P., Rykaczewski, R., Turley, B., Sydeman, W., García-Reyes, M., Bograd, S., et al. (2018). Non-stationary responses in anchovy (Engraulis encrasicolus) recruitment to coastal upwelling in the Southern Benguela. *Mar. Ecol. Prog. Ser.* 596, 155–164. doi: 10.3354/meps12567

Verheye, H. M., Lamont, T., Huggett, J. A., Kreiner, A., and Hampton, I. (2016). Plankton productivity of the Benguela current large marine ecosystem (BCLME). *Environ. Dev.* 17, 75–92. doi: 10.1016/j.envdev.2015.07.011

Verheye, H. M., and Richardson, A. J. (1998). Long-term increase in crustacean zooplankton abundance in the southern Benguela upwelling region (1951–1996): bottom-up or top-down control? *ICES J. Mar. Sci.* 55, 803–807.

Verheye, H. M., Richardson, A. J., Hutchings, L., Marska, G., and Gianakouras, D. (1998). Long-term trends in the abundance and community structure of coastal zooplankton in the southern Benguela system, 1951–1996. *South African J. Mar. Sci.* 19, 317–332. doi: 10.2989/025776198784126728

Walters, C., Christensen, V., and Pauly, D. (1997). Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fish.* 7, 139–172. doi: 10.1023/A:1018479526149

Walters, C., Pauly, D., and Christensen, V. (1999). Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2, 539–554. doi: 10.1007/s100219900101

Walters, C., Pauly, D., Christensen, V., and Kitchell, J. F. (2000). Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. *Ecosystems* 3, 70–83. doi: 10.1007/s100210000011

Watermeyer, K. E., Hutchings, L., Jarre, A., and Shannon, L. J. (2016). Patterns of distribution and spatial indicators of ecosystem change based on key species in the Southern Benguela. *PLoS One* 11:e0158734. doi: 10.1371/journal.pone.0158734

Watermeyer, K. E., Jarre, A., Shannon, L. J., Mulumba, P., and Botha, J. (2018). A frame-based modelling approach to understanding changes in the distribution and abundance of sardine and anchovy in the southern Benguela. *Ecol. Modell.* 371, 1–17. doi: 10.1016/j.ecolmodel.2017.12.017

Watermeyer, K. E., Shannon, L. J., and Griffiths, C. L. (2008). Changes in the trophic structure of the southern Benguela before and after the onset of industrial fishing. *African J. Mar. Sci.* 30, 351–382. doi: 10.2989/AJMS.2008.30.2.11.561

Watkins, B. P., Petersen, S. L., and Ryan, P. G. (2008). Interactions between seabirds and deep-water hake trawl gear: an assessment of impacts in South African waters. *Anim. Conserv.* 11, 247–254. doi: 10.1111/j.1469-1795.2008.00192.x

Wickens, P. A., Japp, D. W., Shelton, P. A., Kriel, F., Goosen, P. C., and Rose, B. (1992). Seals and fisheries in South Africa — competition and conflict. *South African J. Mar. Sci.* 12, 773–789. doi: 10.2989/02577619209504741

Winker, H., Kerwath, S. E., and Attwood, C. G. (2013). Comparison of two approaches to standardize catch-per-unit-effort for targeting behaviour in a multispecies hand-line fishery. *Fish. Res.* 139, 118–131. doi: 10.1016/j.fishres.2012.10.014

Winker, H., Kerwath, S. E., and Attwood, C. G. (2014). Proof of concept for a novel procedure to standardize multispecies catch and effort data. *Fish. Res.* 155, 149–159. doi: 10.1016/j.fishres.2014.02.016

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.

frontiers in Marine Science

REVIEW
published: 03 September 2020
doi: 10.3389/fmars.2020.569258

Harp Seals: Monitors of Change in Differing Ecosystems

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Harp seals are the most abundant marine mammal in the north Atlantic. As an ice obligatory predator, they reflect changes in their environment, particularly during a period of climatic change. As the focus of a commercial hunt, a large historic data set exists that can be used to quantify changes. There are three populations of harp seals: White Sea/Barents Sea, Greenland Sea and Northwest Atlantic. The objective of this paper is to review their current status and to identify the factors that are influencing population dynamics in different areas. Although important historically, recent catches have been low and do not appear to be influencing trends in either of the two northeast Atlantic populations. Massive mortalities of White Sea/Barents Sea seals occurred during the mid 1980s due to collapses in their main prey species. Between 2004 and 2006, pup production in this population declined by 2/3 and has remained low. Body condition declined during the same period, suggesting that ecosystem changes may have resulted in reduced reproductive rates, possibly due to reduced prey availability and/or competition with Atlantic cod. The most recent estimate of pup production in the Greenland Sea also suggests a possible decline during a period of reduced hunting although the trend in this population is unclear. Pupping concentrations are closer to the Greenland coast due to the reduction in ice in the traditional area and increased drift may result in young being displaced from their traditional feeding grounds leading to increased mortality. Reduced ice extent and thickness has resulted in major mortality of young in the Northwest Atlantic population in some years. After a period of increase, the population remained relatively stable between 1996 and 2013 due to increased hunting, multiple years with increased ice-related mortality of young seals, and lower reproductive rates. With a reduction in harvest and improved survival of young, the population appears to be increasing although extremely large interannual variations in body condition and fecundity have been observed which were found to be influenced by variations in capelin biomass and ice conditions. Each of these populations has been impacted differently by changes in their ecosystems and hunting practices. By identifying the factors influencing these three populations, we can gain a better understanding of how species may respond to changes that are occurring in their ecosystems.

Keywords: ***Pagophilus groenlandicus*, north Atlantic, ice seal, Arctic indicator, climate change, seal hunt**

Edited by:
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Specialty section:
This article was submitted to
Marine Fisheries, Aquaculture
and Living Resources,
a section of the journal
Frontiers in Marine Science

Received: *03 June 2020*
Accepted: *13 August 2020*
Published: *03 September 2020*

Citation:
Stenson GB, Haug T and
Hammill MO (2020) Harp Seals:
Monitors of Change in Differing
Ecosystems.
Front. Mar. Sci. 7:569258.
doi: 10.3389/fmars.2020.569258

INTRODUCTION

Under marine ecosystem-based management (EBM), understanding how species are adapted to their environment and how they response to environmental change is critical for the successful management of species and their ecosystems. However, such knowledge is extremely difficult to obtain in natural systems. One way to improve our understanding of the factors that influence the distribution, habitat use and population dynamics of a species is to compare how populations that occur in similar ecosystems may be impacted by different changes (e.g., Murawski et al., 2010; Drinkwater and Pepin, 2013; Drinkwater et al., 2013; Moore et al., 2019). This technique has been successfully applied in many areas (see Drinkwater and Pepin, 2013 for references) and can provide insights into the fundamental processes impacting species.

The northern Atlantic is undergoing a period of tremendous change with adjoining Arctic areas expected to show the most rapid change with modifications in temperature, ocean circulation, pH balance, ice cover, and sea level (McCarthy et al., 2001; Walsh, 2008; Intergovernmental Panel on Climate Change [IPCC], 2014; Haug et al., 2017). The potential impact of climate change on Arctic marine mammals, both directly through ice habitat loss or indirectly through changes in foraging ecology, has been reviewed by a number of authors (e.g., Kovacs and Lydersen, 2008; Laidre et al., 2008, 2015; Kovacs et al., 2011; Hoover et al., 2013; Stenson and Hammill, 2014). The expectation that a warmer (more ice-free) ocean will lead to higher primary productivity could result in higher concentrations of zooplankton, to the benefit of some marine mammals (e.g. bowhead whales, *Balaena mysticetus*), but the loss of prey species that depend on ice, especially polar cod (*Boreogadus saida*) and amphipods, could have negative impacts on other marine mammals that feed extensively upon them, such as harp (*Pagophilus groenlandicus*) and ringed (*Pusa hispida*) seals (Eamer et al., 2013). These changes are likely to be most severe on the ice dependent marine mammals and particularly those that inhabit the southern ice edge of the Arctic pack ice which is changing rapidly (Walsh, 2008).

Given the extensive changes that have occurred, comparing ecosystems across the north Atlantic can provide important insights into the factors impacting ecosystem components. The northwest Atlantic (NWA) and northeast Atlantic (NEA) have a number of features in common. Both are transition zones between temperate and Arctic ecosystems which is reflected in both the physical and biological components. They have similar composition of species and face similar challenges including a variety of anthropomorphic activities (e.g., fishing, oil and gas exploration, contaminants, shipping) and the impact of climate change (e.g., Stenson and Hammill, 2014; CAFF, 2017). Both regions are characterized by cold water from the Arctic in the north, and warmer water from the south, experience seasonal ice cover, the most common zooplankton is *Calanus finmarchicus* and both generally have wasp-waist ecosystems with capelin (*Mallotus villosus*) as the dominant forage fish (Astthorsson et al., 2007; Drinkwater and Pepin, 2013; Buren et al., 2014). Both areas have also had major fisheries for Atlantic cod (*Gadus morhua*) but while the cod stock in the Barents Sea has increased significantly over the past decade, the major stocks in the NWA have collapsed and remain low (Bogstad et al., 2015; Pedersen et al., 2017, 2020). The objective of this paper is to review the information available on an abundant, wide-ranging species, the harp seal (*Pagophilus groenlandicus*), to improve our understanding of how anthropogenic and environmental factors can influence the population dynamics of this high trophic level predator in differing ecosystems across the north Atlantic.

HARP SEALS AS AN INDICATOR SPECIES

Harp seals (*Pagophilus groenlandicus*) are the most abundant pinniped in the North Atlantic. They are a pelagic, migratory species that occurs from the coast of Canada in the west to the Barents Sea in the east and northward to Arctic waters (**Figure 1**). Three putative populations of harp seals, based upon their whelping (pupping) locations, have been identified. The NWA population whelps on the pack ice off Newfoundland (referred to as 'The Front') and in the Gulf of St. Lawrence ('Gulf'); the Greenland Sea ('West Ice') population whelps off the east coast of Greenland, and the White Sea/Barents Sea ('East Ice') population whelps in the White Sea (Sergeant, 1991). Relationships among the three North Atlantic populations of harp seals have been examined in studies of cranial measurements (Yablokov and Sergeant, 1963), underwater vocalizations (Perry and Terhune, 1999), serum transferrins (Møller et al., 1966; Nñvdal, 1969, 1971), blood serum proteins (Borisov, 1966), allozymes (Meisfjord and Nñvdal, 1994) and DNA (Meisfjord and Sundt, 1996; Perry et al., 2000). These studies have revealed significant differences between the NEA and NWA populations, but no evidence of differences between Greenland Sea and White Sea/Barents Sea harp seals. However, a recent study (Carr et al., 2015) suggests that harp seals comprise three genetically distinguishable breeding populations in the White Sea, Greenland Sea, and Northwest Atlantic. Satellite tracking studies (Folkow et al., 2004; Nordøy et al., 2008) and tag returns (Øien and Øritsland, 1995) indicate that individuals from the Greenland Sea and White Sea/Barents Sea populations mix during the non-breeding period. Similarly, non-breeding seals from the Northwest Atlantic and Greenland Sea populations overlap, particularly in southeast Greenland (Øien and Øritsland, 1995; Stenson and Sjare, 1997). This suggests that the populations may occasionally overlap, particularly in the NEA, which would explain the lack of a clear differentiation among the populations. However, for management purposes, the three populations are considered separately (International Council for the Exploration of the Sea [ICES], 2019b).

Harp seals whelp on drifting, first-year pack ice from late February through early April, depending upon location (Sergeant, 1991). In the NEA, pupping generally takes place between late February through mid-March in the White Sea (Potelov et al., 2003), and late March through early April in the Greenland Sea (Øigård et al., 2014). The NWA population pups in late February in the southern Gulf of St. Lawrence and a little

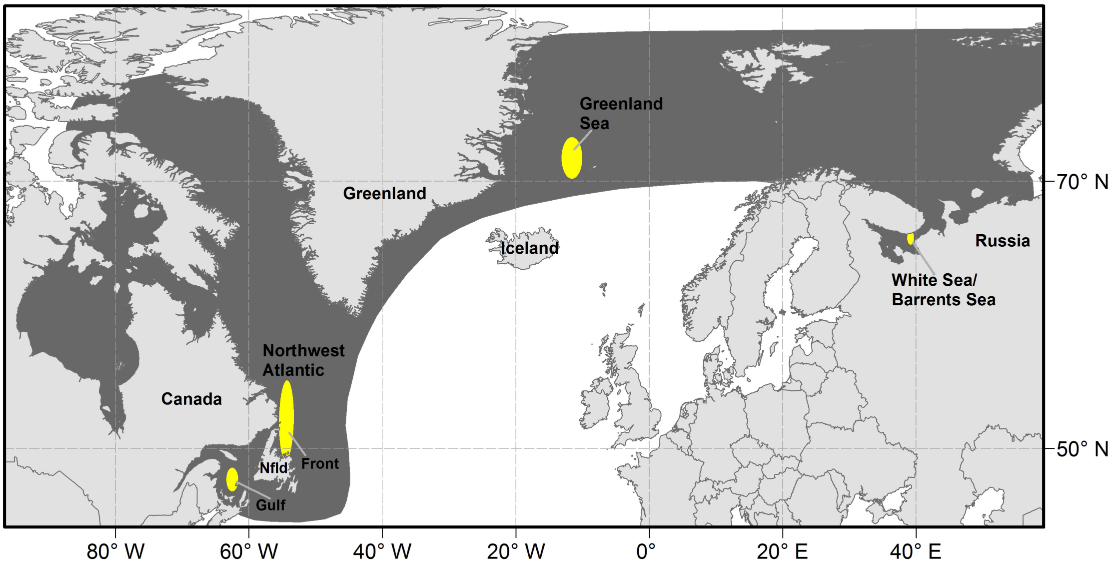

FIGURE 1 | Location of whelping concentrations (yellow) and range (dark shading) of harp seals in the north Atlantic.

later (early to mid-March) in the northern Gulf and at the Front (i.e., the same timing as the White Sea) (Stenson et al., 2002, 2003, 2020b). Pups are nursed for approximately 12 days, after which the females wean their pups, mate and disperse to feed. Molting of adults and immatures takes place north of each whelping location approximately 3-4 weeks after weaning with immature seals and adult males molting before adult females (Sergeant, 1991). Suitable ice is necessary for pupping and during lactation, and young of the year (YOY) harp seals require ice to haul out on for a period of 4–6 weeks while they develop the physiological capability for swimming and diving (Sergeant, 1991; Burns et al., 2007; Stenson and Hammill, 2014).

As an obligatory ice-dependent species that relies on pack ice for at least part of the year and an abundant, high trophic level predator, climate change can impact harp seals directly through the loss of ice as a platform and indirectly through changes in prey availability (e.g., Stenson and Hammill, 2014; Stenson et al., 2016). Thus, harp seals are well situated to reflect changes in their environment and act as an indicator species for monitoring north Atlantic and Arctic marine biodiversity (Department of Fisheries and Oceans [DFO], 2012; CAFF, 2017). Also, harp seals have been the focus of commercial hunts across their range which has resulted in an extensive historic data set that can be used to quantify changes that may have occurred. In order to review the current status of harp seals across the north Atlantic and to identify the factors that are influencing their population dynamics in different areas, we start with an overview of the history of harvesting, abundance, environmental conditions and harp seal responses to these conditions as reflected in productivity. We then finish by discussing how anthropogenic and environmental factors appear to be affecting the dynamics of each population within the context of a changing environment. Such a review is timely and will provide us with a better understanding of how this key indicator species is being impacted by ongoing environmental change.

WHITE SEA/BARENTS SEA HARP SEALS

Following pupping and breeding in the northern portion of the White Sea, harp seals from the White Sea/Barents Sea population molt during April and May in the White Sea and south-eastern parts of the Barents Sea (Haug et al., 1994; Nordøy et al., 2008). When the molt is over, seals disperse in small herds to feed, primarily around Svalbard and in the northern Barents Sea. They follow the receding ice edge during summer, gradually moving northwards and north-eastwards in the Barents Sea throughout the summer. In November-December, White Sea/Barents Sa harp seals move southward towards the breeding areas, spending the winter in the southeastern Barents Sea and White Sea.

Harvest

Historically, the harvests of White Sea/Barents Sea harp seals were initially shore based and presumably small-scale, taking place along the coasts of the White Sea and around the Kanin Peninsula, and presumably of a very small magnitude (Sergeant, 1991). Norwegian vessels began hunting offshore in 1867 (Iversen, 1927), followed by Soviet vessels during the 1920s. Initially, catches quite small, perhaps a few hundred annually (Iversen, 1927), but after 1875 the total catches increased, with annual harvests of 15,000 – 60,000 animals up to around 1900. Following the turn of the century exploitation increased further with the largest catches being taken in the 1920s and 1930s (annual average of 200,000 – 300,000 animals, maximum in 1925 when nearly 470,000 seals were taken) (Iversen, 1927; Sivertsen, 1941; Nakken, 1988; Skaug et al., 2007).

While exploitation was low during World War II, hunting pressure increased from 1946 until 1955 with average catches between 150,000 and 200,000 seals (International Council for the Exploration of the Sea [ICES], 2019b; **Figure 2**). Quotas of 100,000 were introduced unilaterally for Soviet catches in 1955 (Yakovenko, 1963) and were gradually reduced to a total (Soviet and Norwegian) catch quota of 34,000 seals by 1965. Adult females were protected in the whelping patches starting in 1963, and Soviet catches of 1+ seals were stopped in 1965 (Kjellqwist et al., 1995). Catches increased during the late 1970s and 1980s (annual quotas increased to a maximum of 82,000 in 1983) but since the late 1980s, quotas were reduced, declining to 35,000 by 2009. Following a decline in pup production after 2003 (see below), quotas were further reduced to 7,000 during the 2010-2014 period. Since 2017, the current annual quota has been set at approximately 10,000 animals one year and older (referred to as 1+), assuming that two YOY equals one older seal. However, catches over the past decade have been well below the recommended quotas, and therefore also well below estimated sustainable levels. With the exception of 2018 and 2019, when 2,241 and 602 seals, respectively, were taken, annual catches have been below 30 animals since 2012 (International Council for the Exploration of the Sea [ICES], 2019b).

Abundance

Based upon a population model that incorporates data on annual age-specific reproductive rates, removals and independent estimates of pup production (e.g., Hammill et al., 2015; International Council for the Exploration of the Sea [ICES], 2019b), the high catches before and after World War II resulted in a declining harp seal population until the early 1960s when the population may have been as low as 500,000 (Sergeant, 1991; Skaug et al., 2007; International Council for the Exploration of the Sea [ICES], 2019b). Reductions in catches and protection of females allowed the population to increase until the 1980s (**Figure 3**; International Council for the Exploration of the Sea [ICES], 2019b). However, the collapse of forage fish (capelin, polar cod, Atlantic herring [*Clupea harengus*]) in the Barents Sea during the mid 1980s led to the an 'invasion' of seals in very poor condition along the Norwegian coast from 1986-1988 (Haug et al., 1991) and the apparent complete loss of a number of cohorts (Kjellqwist et al., 1995). A small, but similar 'invasion' of

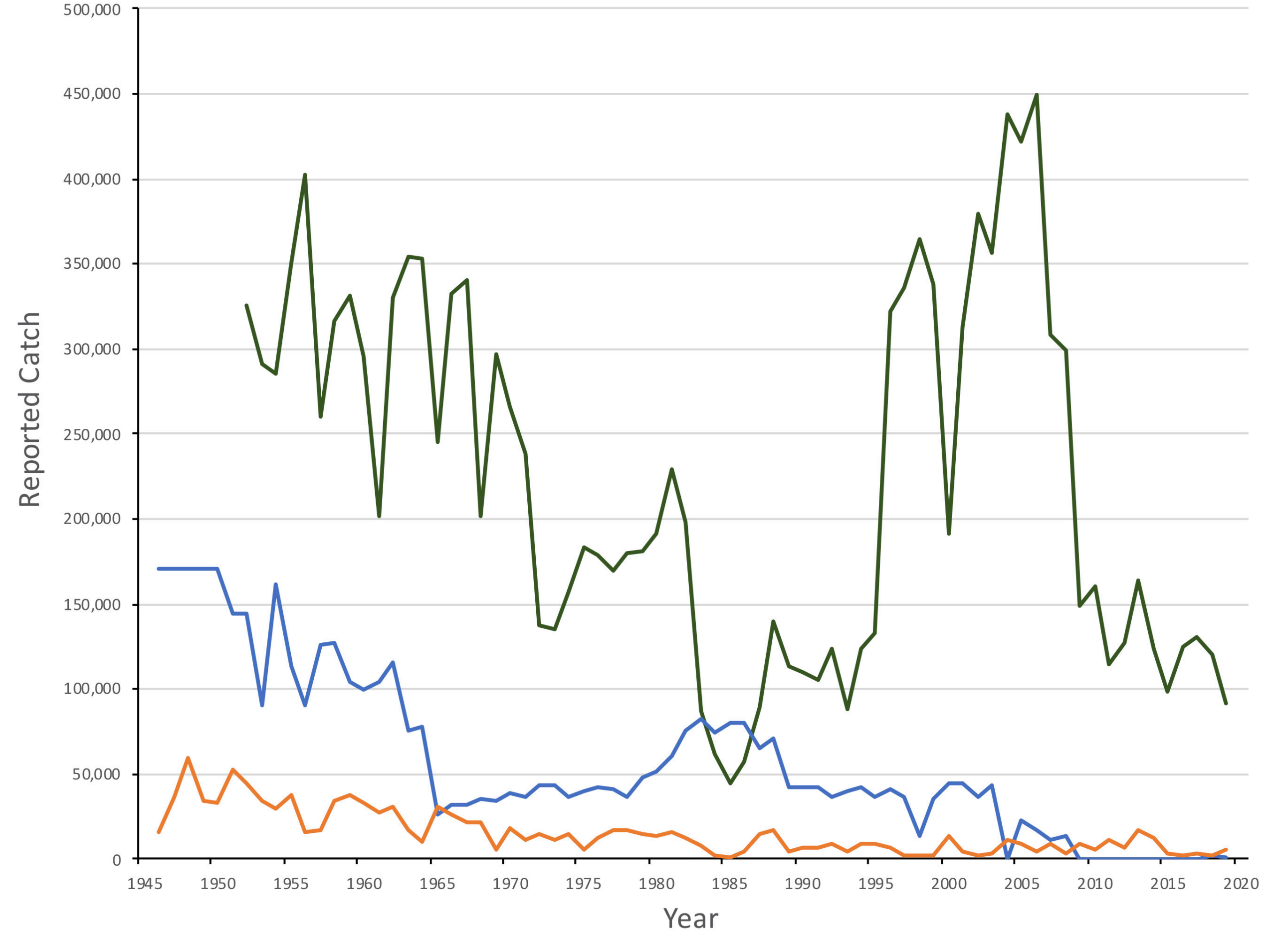

FIGURE 2 | Reported catches of Northwest Atlantic (green), White Sea/Barents Sea (blue) and Greenland Sea (orange) harp seals, 1950–2019. Catches in the White Sea/Barents Sea from 1946-50 is a 5 year average.

FIGURE 3 | Estimated abundance of Greenland Sea (orange), White Sea/Barents Sea (blue) and Northwest Atlantic (green) harp seals and 95% C.I. Data from International Council for the Exploration of the Sea [ICES], 2019b and Hammill et al., 2020.

seals occurred again during the period of low capelin abundance in the mid 1990s (Nilssen et al., 1998).

Aerial surveys of the White Sea between 1998 and 2013 indicate that this population went through a significant and rapid decline in pup production from ca 330,000 pups from 1998-2003 to ca 130,000 since 2005 (Potelov et al., 2003; International Council for the Exploration of the Sea [ICES], 2019b). Although a variety of explanations were examined, the cause of this decline is unknown, but does not appear to be related to harvest levels or population inertia due to the loss of several cohorts in the mid 1980s. The most likely explanation is a decline in pregnancy rates (International Council for the Exploration of the Sea [ICES], 2016), potentially resulting from worsening body condition due to changes in prey (primarily capelin) abundance and distribution (Øigård et al., 2013). Thus, it appears that the population dynamics of Barents Sea/White Sea harp seals over the past eight decades have been influenced by both environmental change and changing harvest regimes.

The most recent population model indicates that the White Sea/Barents Sea population declined from the 1980s until around 2007 (**Figure 3**). From 2007 to present the model suggests a slow increase, but this is uncertain due to due a scarcity of data on vital rates and pup production for this population in the last decade. The current estimate for population size in 2019 is 1.5 million (95% CI 1.3 – 1. 7 million) seals (International Council for the Exploration of the Sea [ICES], 2019b).

The Ice Habitat

The Barents Sea is an inflow shelf sea (mean depth ca 200 m) where Atlantic and Arctic waters meet. Warm, nutrient rich Atlantic water from the North Atlantic Current enters the Barents Sea from the Norwegian Sea primarily through its western entrance and influences the southern region, while cold Arctic water penetrates from the east and north and dominates the northern Barents Sea (see Hunt et al., 2013). Some Atlantic water also enters the Arctic Ocean through the Fram Strait and continues eastward north of Svalbard (Haug et al., 2017). Water temperature has increased within the Barents Sea as a result of increased Atlantic inflow, particularly over the past decade (Spielhagen et al., 2011; International Council for the Exploration of the Sea [ICES], 2019a). Historically, the White and Barents Seas (northern and eastern sections) have been characterized by the presence of drifting sea ice. In the Barents Sea, extensive seasonal variations were observed, particularly in the eastern areas, with maximum ice cover in March /April and minimum in August/September (Wassmann et al., 2006; Hunt et al., 2013). Increasing water temperature over recent decades has been associated with dramatic reductions in sea ice mass and coverage (see Haug et al., 2017). Laidre et al. (2015) found that the Barents Sea had the largest decline in the average annual days with sea ice among all of the circumpolar regions they examined, with an estimated three week per decade reduction in the period of ice cover between 1970 and 2013. Overall, the ice extent in the Barents Sea has decreased more than 60% over the last 200 years (Vinje, 2001; Wassmann et al., 2006), although there is high interannual variability.

Harp seals traditionally pup on relatively close pack ice, approximately 6/10 coverage or greater (Sergeant, 1991). To determine how ice cover in the White Sea has changed over the past three decades, we examined the extent of ice during the peak of pupping using data from the Norwegian Ice Service. The first surveys to estimate pup production in the White Sea were carried out in 1998. Therefore, we downloaded archived Norwegian Ice Service ice charts (Norwegian Meteorological Institute, 2020) for 10 March (+/− 1 day), 1998 to 2020, from the Norwegian Meteorological Institute Cryo web portal[1] and the extent of the ice classes Open Drift Ice (4-6/10 coverage), Close Drift Ice (7-9/10), and Very Close Drift Ice (9-10/10) in the area of the White Sea (including the main basin, three inner bays, and the Gorlo) were identified (**Figure 4**). Because of the way in which the data were presented, we calculated the area of greater than 4/10 sea ice, which was rounded to the nearest 1000 km^2 to account for digitizing error, using QGIS (QGIS Development Team, 2019). Examining the total ice extent, expressed as an anomaly from the 2000-2010 average, indicates that there is a general decline in the extent of suitable ice in the White Sea between 1998 and 2020, but ice cover was particularly low in 2003, 2015 and 2020 (**Figure 5**). While no pup production surveys have been carried out in the White Sea since 2013, decreases in ice cover of this magnitude have been found to be associated with increased pup mortality in the NWA (Stenson and Hammill, 2014; Hammill et al., 2015).

Diet/Feeding Ecology

Due to seasonal variation in food availability, the ability to store large amounts of energy and sustain significant periods of fasting is an essential adaptation for most Arctic mammals. Harp seals exhibit a regular seasonal pattern of lipid deposition in their subcutaneous blubber layer (which also serves other purposes such as insulation and buoyancy, see Iverson et al., 2002) to take advantage of periods of high productivity to store energy required for pupping, breeding and molting. Monitoring these changes in body mass provides a metric by which changes in food availability can be measured. White Sea/ Barents Sea harp seals are generally thin in spring and early summer (May – June). They improve their condition over the summer and become quite fat by September – October (Nilssen et al., 1997). The energy stores built up during the summer and autumn are maintained until February, before seals again lose mass as blubber stores are rapidly depleted during the breeding and molting period (March-June). An average adult (165 cm long) harp seal weighs ∼80 kg after in June but and increases its mass by 81.5% to ∼145 kg in October (Nilssen et al., 1997).

The diet of Barents Sea harp seals varies seasonally and geographically, but is mostly comprised of relatively few species, in particular capelin, polar cod, Atlantic herring*)*, krill (*Thysanoessa spp.*) and the pelagic amphipod *P. libellula* (Nilssen et al., 2000; Lindstrøm et al., 2013). Polar cod and crustaceans appear to be of particular importance during summer and autumn feeding in the northern parts of the Barents Sea (May-October). As ice cover expands southwards in late autumn and winter, the diet of southward migrating seals appear to switch from mostly crustaceans to mainly fish, particularly capelin and polar cod (Nilssen et al., 1995; Lindstrøm et al., 1998). In the southernmost areas of the Barents Sea, where the seals occur during winter and early spring, herring is also an important prey (Nilssen et al., 1995). Several fish species may serve as prey for harp seals during late autumn and winter. Low capelin biomass, such as that observed in 1993-1996, was associated with a dietary switch to other fish species, in particular polar cod, other gadoids and herring (Bogstad et al., 2000).

Changes in Prey Assemblages

The Barents Sea has undergone a number of shifts in the abundance of important fish species resulting from changes in environmental conditions which may also have had an impact on predator-prey relationships as well. In the mid 1980s, there was a simultaneous collapse in capelin, Atlantic herring, and polar cod stocks (**Figure 6**). More recently, the increase in Atlantic inflow and an overall warming trend has also resulted in a slight increase in primary productivity and a shift in community structure, particularly a reduction in the area of the Barents Sea occupied by Arctic species. Boreal species have been expanding northward with a resultant change in the structural properties and links between the boreal and the Arctic food webs (Fossheim et al., 2015; Kortsch et al., 2015). Decreases in the biomass of large mesozooplankton, particularly *Themisto libellula*, in Arctic waters have led to a strong decline and recruitment failure of polar cod which is currently at its lowest abundance since 1990 (International Council for the Exploration of the Sea [ICES], 2019a). Following a second collapse in the mid 1990s (1993-1996), capelin stocks recovered somewhat only to collapse again in the middle of the mid 2000s (2003-2006) and then in 2014 (**Figure 6**). These collapses were all primarily caused by recruitment failures (Gjøsæter et al., 2009). There is an overlap between capelin spawning areas and Norwegian spring spawning herring nursery areas in the southern Barents Sea, and the presence of strong year classes of young herring, which feed on capelin larvae, may have contributed significantly to the capelin collapses (Gjøsæter and Bogstad, 1998). In contrast, after a period of relative low abundance around 2000, the Barents Sea Atlantic cod stock has increased to the highest biomass ever observed by 2014 and extended its range northwards (International Council for the Exploration of the Sea [ICES], 2019a). This increase in cod abundance may have also contributed to the relatively low levels

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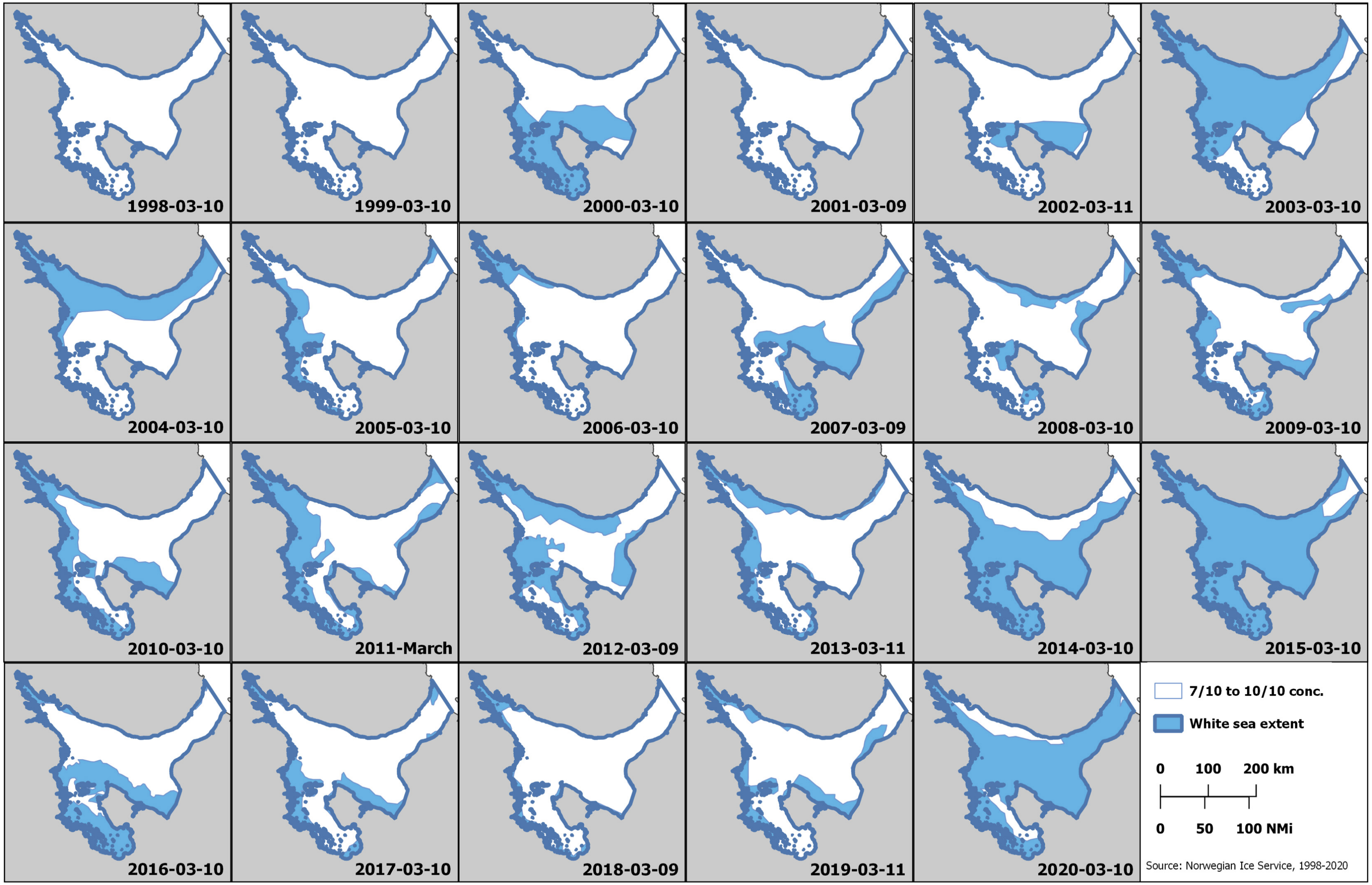
[1] https://cryo.met.no/archive/ice-service/icecharts/quicklooks/



Source: Norwegian Ice Service, 1998-2020

FIGURE 4 | Occurrence of drift ice (4+/10 coverage) in the White Sea on 10 March 1998-2020. Data from the Norwegian Meteorological Institute Cryo web portal (https://cryo.met.no/archive/ice-service/icecharts/quicklooks/).

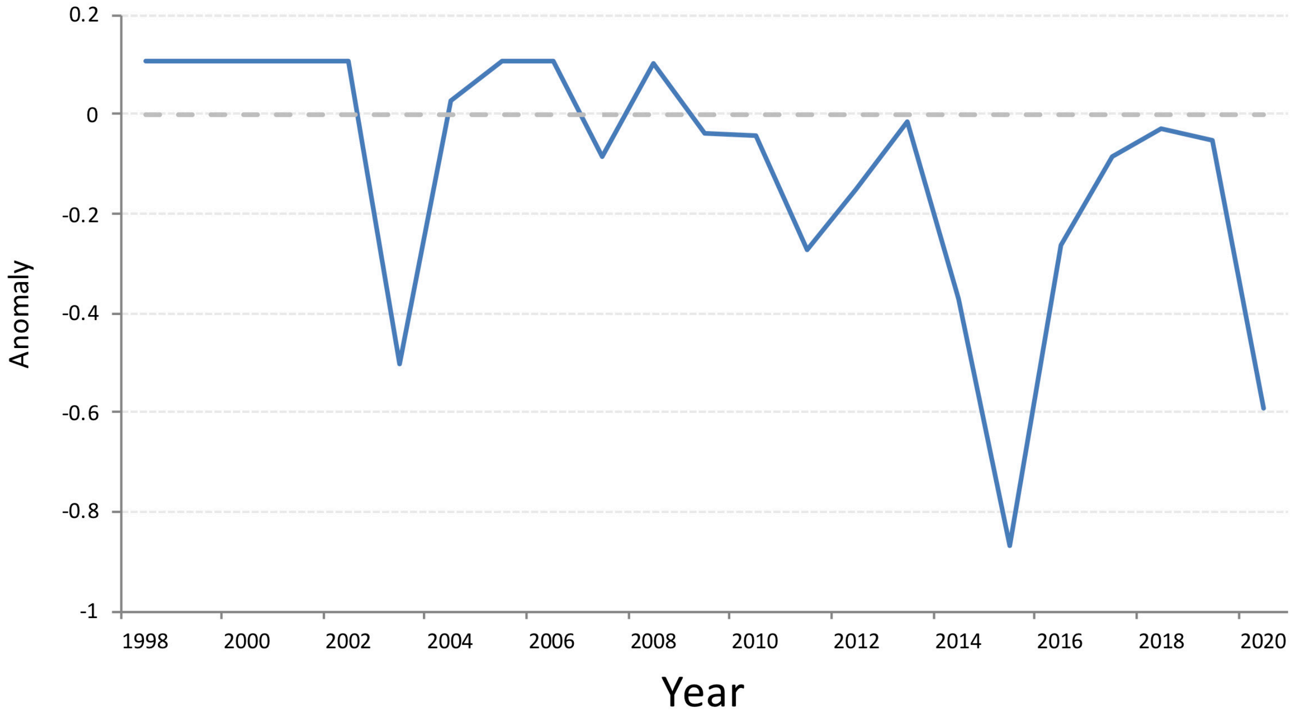


FIGURE 5 | Extent of drift ice, 4/10 and greater, coverage in the White Sea 1998-2020, expressed as anomalies from the average ice coverage 2000-2010. Data obtained from the Norwegian Ice Service (https://cryo.met.no/archive/ice-service/icecharts/quicklooks/).

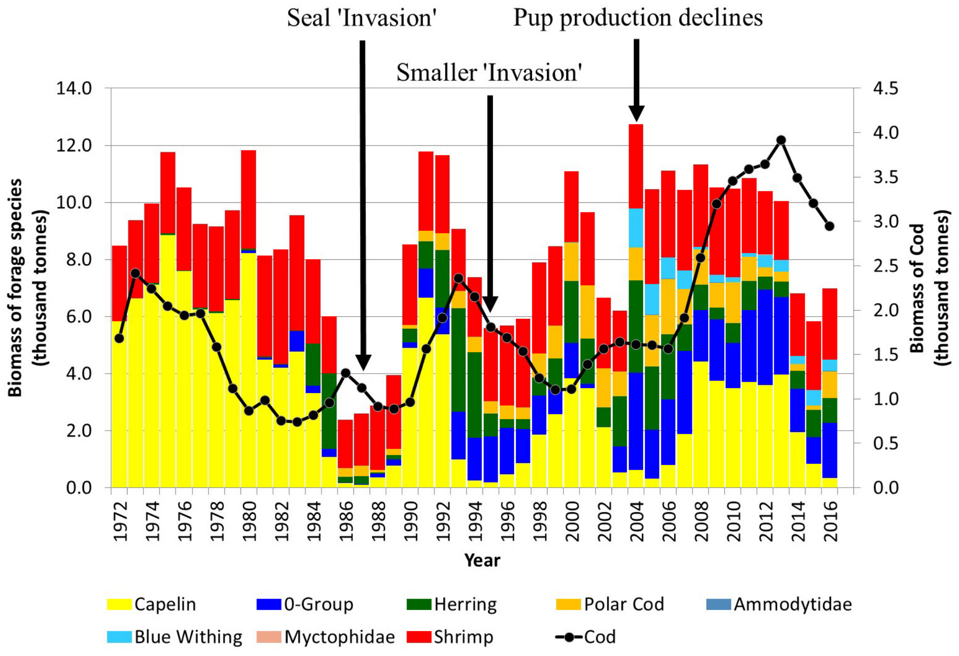


FIGURE 6 | Estimated biomass of forage species and Atlantic cod in the Barents Sea. The timing of seal 'invasion' along the Norwegian coast and an abrupt decline in pup production are indicated (modified from Haug et al., 2017; Protozorkevich and van der Meeren, 2020).

of two major harp seal prey species, capelin and polar cod, during the past decade.

Environmental Impacts on Body Condition and Reproduction

The impact of changes in prey availability have been observed among White Seal/Barents Sea harp seals. As outlined above, catches have declined markedly over the last several decades. However, in spite of reduced harvesting, there was a significant drop in pup production in 2004 and 2005. Øigård et al. (2013) found that harp seal body condition was significantly lower in 2011 than it was 10–15 years previous. They identified possible links between seal body condition and the abundance of several spatially overlapping potential competitors and prey including Atlantic cod, polar cod and capelin.

Changes in reproductive rates within a population are also often an indicator of their ecosystem, often reflecting changes in foraging success and body condition (e.g., Stenson et al., 2020a). The mean age at sexual maturity of White Sea/Barents Sea harp seals increased from approximately 5.5 years in the early 1960s, to 8.2 years in the early 1990s (Frie et al., 2003). In the 2000s, the mean age of maturity was estimated to be ∼7 years in 2018 which is not significantly different from a previous estimate from 2006, but still higher than observed among the other two harp seal populations (International Council for the Exploration of the Sea [ICES], 2019b). It is possible that increases in population size (see below), may have contributed to the observed changes in age at maturity. However, Frie et al. (2003) proposed that the observed changes may also be due to changes in the Barents Sea ecosystem, in particular occasional low availability of important forage fish such as capelin and polar cod during winter and early spring.

GREENLAND SEA HARP SEALS

Greenland Sea harp seals form whelping concentrations along the ice edge north of the Norwegian island of Jan Mayen. Historically the Jan Mayen current creates a gyre that forms and retains a tongue shaped ice feature, known as the Odden, during the spring (Wilkinson and Wadhams, 2005). This persistent ice feature provided a suitable platform for nursing and resting during the post weaning fast. In recent years, the ice edge has shifted westward towards the Greenland coast which has resulted in a shift in the location of pupping (see below). As in the other populations, molting occurs approximately a month later at the fringe of winter ice laying seawards of the heavier Arctic ice off the east Greenland pack, located between the latitudes 69°N and 75°N (Øritsland and Øien, 1995; Haug et al., 2006). Satellite tracking studies suggest that a large proportion of the Greenland Sea stock migrates into the Barents Sea during summer and autumn, then return to spend the winter off south-east Greenland, in the Denmark Strait (Folkow et al., 2004).

Harvest

The Greenland Sea (West Ice) stock of harp seals has been subject to commercial exploitation for centuries (Iversen, 1927; Nakken, 1988; Sergeant, 1991). Knowledge of the Greenland Sea catches by Dutch, British, German, and Danish ships prior to the 1870s, is poor. Norwegian sealers sailed to the Greenland Sea for the first time in 1846 and have been active ever since. Exploitation levels reached a historical maximum in the 1870s and 1880s when annual catches (pups and adults) varied between 50,000 and 120,000 (Iversen, 1927). It was evident that these catch levels were unsustainable, and regulatory measures (mainly designed to protect adult females) were introduced in 1876 (Iversen, 1927). Annual catches varied between 10,000 and 20,000 animals throughout the first decades of the 20th century, before increasing to around 40,000 seals per year by the 1930s (Iversen, 1927; Sergeant, 1991). Following a pause in sealing during World War II, total annual catches by Norway and the Soviet Union quickly rose to a postwar maximum of about 70,000 in 1948, but then followed a decreasing trend until quotas were imposed in 1971 (Sergeant, 1991; International Council for the Exploration of the Sea [ICES], 2019b). Since 1989, catches have been generally less than 10,000 seals with no Russian takes since 1995 (**Figure 2**; International Council for the Exploration of the Sea [ICES], 2019b).

Abundance

The Greenland Sea population was heavily hunted, particularly in the late 19th Century which resulted in a population decline (Iversen, 1927). As the catches declined since the 1950s, the Greenland Sea population was thought to have been increasing slowly (**Figure 3**; International Council for the Exploration of the Sea [ICES], 2019b). However, due to a series of conflicting estimates from mark-recapture experiments in the 1980s and a ∼40% drop in estimated pup production from 2012 to 2018, it is difficult to determine the overall population trend. The estimate of current (2019) population size is relatively robust to a variety of model assumptions and indicates a total population size of 427,000 (95% CI 313,000 −541,000), making the Greenland Sea population the smallest of the three harp seal populations (International Council for the Exploration of the Sea [ICES], 2019b). Given the low level of catches in this population, this decline in pup production and lack of increase in the population cannot be accounted for by hunting and is most likely a result of ecological changes.

The Ice Habitat

The Greenland Sea and surrounding areas are influenced by a mix of cold and warm currents. The East Greenland Current, which runs along the Greenland coast, and East Icelandic Current which is further offshore, bring colder water from the north. The North Atlantic Current and the Irminger Current bring warmer waters from the south, mixing with the colder Arctic water in the area of the Denmark Strait and north of Iceland (Astthorsson et al., 2007; Rigét et al., 2019). The East Greenland Current carries multiyear Arctic ice from the Fram Strait southward along the Greenland coast which remains ice-bound throughout much of the year. However, increasing inflow of relatively warm Atlantic waters has resulted in reduced ice coverage in recent years. In their study of historical variability of sea ice position in the Nordic Seas, Divine and Dick (2006) concluded that the spring ice edge retreated approximately 250–375 km in the Greenland

Sea between the periods 1870-1920 and 1989-2002. The edge of the ice in March/April, which historically extended all the way to the island of Jan Mayen where the Odden sea ice feature regularly formed, is now situated 270–360 km west of the island (**Figure 7**; Wilkinson and Wadhams, 2005; Øigård et al., 2014).

Since harp seals pup near the ice edge, this change in ice extent has resulted in a shift in the location of their whelping patches closer the Greenland coast (**Figure 7**). While the ice itself still appears to be suitable for nursing (International Council for the Exploration of the Sea [ICES], 2019b), the seals are now pupping on pack ice that is being carried quickly southward within the East Greenland Current, rather than remaining relatively stationary north of Jan Mayen in the Odden. These new conditions may have a negative impact on first year survival if they result in earlier loss of ice for seals to rest on or if the ecological conditions encountered by YOY during the first few months of independent feeding differ from those encountered in the traditional area of the Odden.

Pupping and breeding closer to the Greenland coast may also increase mortality of young and adults as they would be more vulnerable to predation from species such as polar bears (*Ursus maritimus*). Recent studies from Greenland suggest that polar bear diets are changing from being dominated by ringed seals (*Phoca hispida*) to include a larger proportion of hooded and harp seals (McKinney et al., 2013). Harp and hooded seal pups also appear more frequently in the diet of killer whales in East Greenland coastal waters compared to previously (Foote et al., 2013; International Council for the Exploration of the Sea [ICES], 2013).

Diet/Feeding Ecology

Recent observations of the diet of harp seals in the Greenland Sea pack ice suggests a relatively narrow range of prey taxa. This is consistent with other studies that have found that food webs in Greenland waters are generally relatively simple with few species (Rigét et al., 2019). The pelagic amphipod *P. libellula,* polar cod, and capelin dominated the harp seal diet (63–99% of the observed diet, Haug et al., 2004; Enoksen et al., 2017). Greenland Sea and Barents Sea harp seals overlap in their feeding range during summer and autumn in Spitsbergen waters (Haug et al., 1994; Folkow et al., 2004), an area where crustaceans dominate their diet (Nilssen et al., 1995; Lindstrøm et al., 2013). Harp seals examined in coastal waters of northern Iceland during the period February-May had a varied diet which consisted mainly of sand eels (*Ammodytes* sp.), gadoids, capelin, and other fishes; crustaceans (amphipods and krill) and other invertebrates were also observed to a lesser extent (see Hauksson and Bogason, 1997).

Changes in Prey Assemblages

The increase in water temperature in the Nordic Seas and reduced ice cover has resulted in an increase in primary productivity in Icelandic waters and a change in distribution and abundance of a number of species. Warm water species such as Atlantic mackerel (*Scomber scombrus*) and haddock (*Melanogrammus aeglefinus*) have extended their range while the abundance of migratory cetaceans, such as fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*), has increased (International Council for the Exploration of the Sea [ICES], 2019c; Moore et al., 2019). Christiansen et al. (2016) reported the first occurrence of Atlantic cod, beaked redfish (*Sebastes mentella*), and capelin in northeast Greenland. In contrast, warming waters has led to a decline in the abundance and distribution of many cold water species such as polar cod which use sea ice for spawning and feeding (Christiansen, 2017; International Council for the Exploration of the Sea [ICES], 2019c). While capelin have moved westward from Icelandic waters into the cooler Greenland waters, Beaugrand et al. (2009) found a clear movement of warm water zooplankton species in the NEA associated with a decrease in colder water species in response to regional climate warming in the southern part of Iceland. They found that subarctic species, which tend to have a higher energy content decreased, while lower energy containing cold-temperate mixed water species increased. It is likely that the decrease in lipid content of zooplankton may affect both lipid dynamics and the trophodynamics of the entire biological and ecological system (Beaugrand et al., 2009).

Environmental Impacts on Body Condition and Reproduction

Unlike the White Sea/Barents Sea harp seals, the mean age of sexual maturity in Greenland Sea seals, appears to be relatively stable at around 5–6 years, with no discernible trend over time (Frie et al., 2003; International Council for the Exploration of the Sea [ICES], 2019b). This difference between the two NEA harp seal stocks suggests that maturing animals from the two stocks have experienced different per capita food-availability in the 1980s and perhaps even before that time. This may be due to differences in overall food availability between the two ecosystems or simply a consequence of the smaller population size in the Greenland Sea. However, recent reproductive data for this population are limited and somewhat variable, so it is difficult to determine if the recent ecosystem changes are having an impact on vital parameters.

NORTHWEST ATLANTIC HARP SEALS

The NWA population summers in the eastern Canadian Arctic and Greenland. In the fall (November-December), most of the seals migrate southward to the Gulf of St. Lawrence and the Newfoundland Shelf. After a period of feeding, they give birth on the pack ice in the Gulf of St. Lawrence ("Gulf") or off northern Newfoundland ("Front") each spring. Following molting in April and May, harp seals disperse and eventually migrate northward during June (Stenson and Sjare, 1997). Small numbers of harp seals may remain in southern waters throughout the summer while others remain in the Arctic throughout the year. NWA harp seals are found primarily on the Canadian and Greenland continental shelves.

Harvest

Northwest Atlantic harp seals are taken by subsistence hunters in the Canadian Arctic and Greenland, and in a commercial hunt in the Gulf of St. Lawrence and off Newfoundland. Catches in Greenland occurred primarily along the west coast. Catches in the Canadian Arctic are poorly known but are assumed to be less than 1,000 annually (Stenson and Upward, 2020). Historically they were low in comparison to the Canadian commercial catch. However, beginning in 1980 Greenland catches increased relatively steadily to a peak of approximately 100,000 in 2000. Between 2011 and 2017, catches have declined with an average of 60,000 seals reported annually which is a similar level to that currently occurring in Canada (International Council for the Exploration of the Sea [ICES], 2019b).

Commercial hunting in Newfoundland began in the early 18th Century although only low numbers were taken until the 19th Century. Peak catches occurred between 1820 and 1860 when the average annual take was over 400,000 seals. The population could not sustain this level of removals and catches declined throughout the rest of the century to an annual average of 160,000 between 1914 and 1940. Following World War II, catches increased again. By 1965 regulations were first introduce to restrict the harvest in the Gulf and to protect breeding females. An average of 280,000 seals were harvest each year between 1946 and 971 when full quotas were introduced (**Figure 2**). Between 1972 and the demise of the large vessel hunt in 1982, an average of 166,000 seals were taken annually. Catches decreased after 1982 and remained low, averaging approximately 52,000 per year until 1995, at which time interest in the hunt increased significantly. Annual catches consisting almost exclusively of YOY increased to an average of 272,600 between 1996 and 2006, with a maximum of 366,000 in 2004. Since then catches have declined, averaging 63,000 per year between 2009 and 2019 (Stenson and Upward, 2020).

Abundance

The NWA harp seal population is one of the largest populations of pinnipeds in the world (Southwell et al., 2012; Laidre et al., 2015) and is significantly larger than the other populations (**Figure 3**). Following World War II, the population was subjected to high levels of hunting and by 1971, the population had declined to approximately 1.6 million (95% CI 1.5 – 1.7 million) animals (Hammill et al., 2020). With the imposition of a quota system and lower catches due to reduced demand,

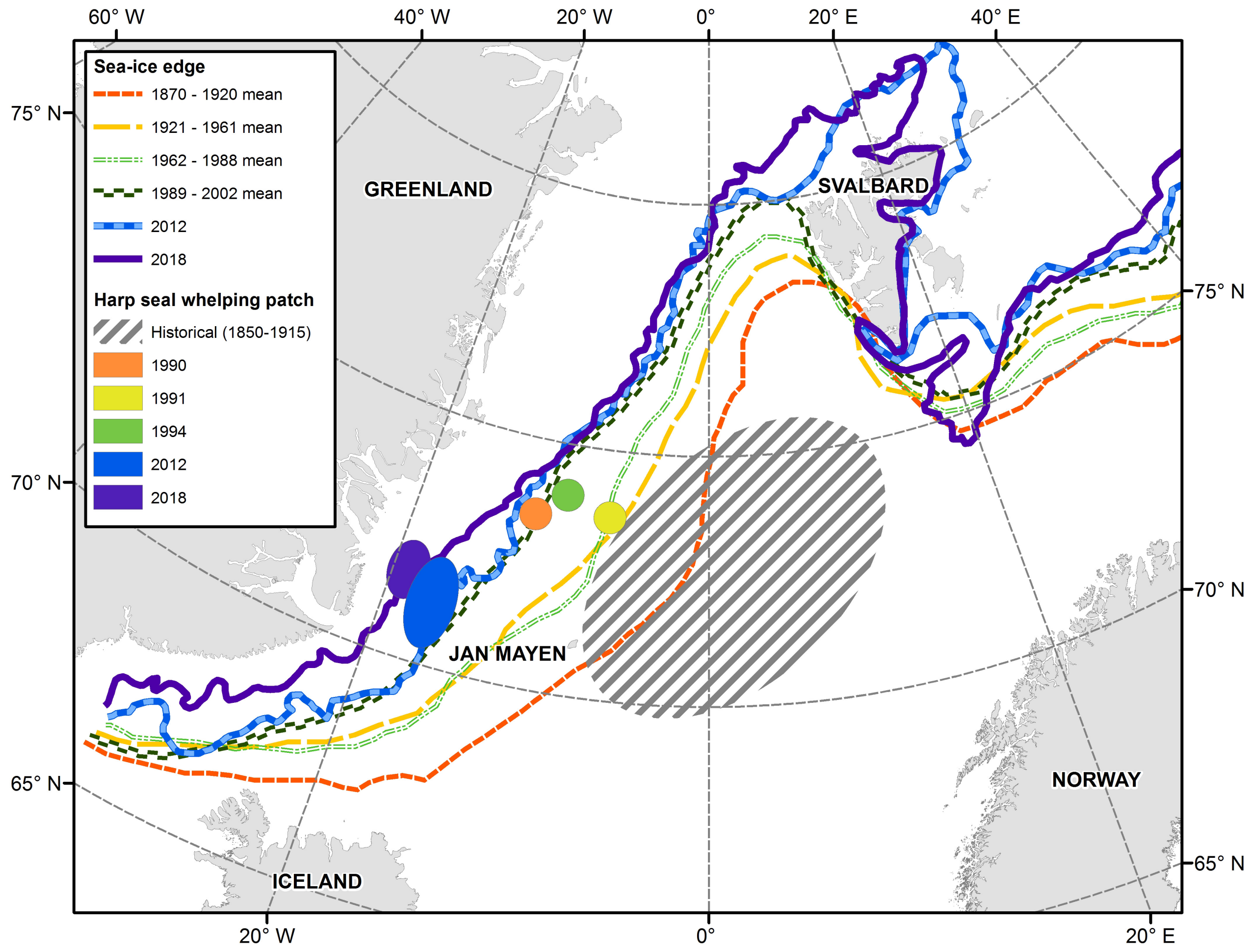


FIGURE 7 | Location of sea ice edge and the Greenland Sea harp seal whelping concentrations. Historical ice data from Divine and Dick (2006). Recent ice data and whelping locations from Øritsland and Øien (1995); Øigård et al. (2014) and International Council for the Exploration of the Sea [ICES] (2019b).

the population began to increase. From the mid 1990s until ~2014, the population appeared to be relatively stable around 5.5 million due to a combination of high catches in both Canada and Greenland, reduced reproductive rates and a series of years with high ice-related mortality of YOY (see below). Since 2014, however, the population appears to be increasing again as a result of several years with high reproductive rates and low mortality of YOY, and was estimated to be 7.6 million (95% CI 6.6 – 8.8 million) in 2019 (Stenson et al., 2020a; Hammill et al., 2020). It will take 6–10 years before the impact of the high catches of YOY will work itself through the population and be reflected in pup production. Therefore, another pup production survey will be needed before this increase can be confirmed and the recent population trend understood.

The Ice Habitat

The NWA is dominated by the Labrador current that brings cold Arctic water south along the Labrador and Newfoundland Shelves, the southernmost penetration of polar waters in the northern hemisphere (Rice, 2002). The Labrador current runs south along the outer edge of the shelves to the Grand Banks where it bifurcates into an 'inshore' and a larger, 'offshore' branch. This offshore branch meets the warm Gulf Stream waters coming from south, resulting in a rich mixing environment that provides an area of high productivity. Relatively warm water also enters the Labrador Sea through the West Greenland Current that runs along the Greenland shelf. Around the Davis Strait, it branches into a westward component that crosses over to Baffin Island and a northward current that continues around Baffin Bay.

During the winter, much of the Labrador Shelf, and parts of the west Greenland shelf may be covered by ice. In the west, ice can extend as far south as the northern Grand Banks (47^o N) and over a 100 km outward from the coast. Some of this ice enters the northern Gulf of St Lawrence through the Strait of Belle Isle while ice in the southern Gulf is primarily formed *in situ* or in the St. Lawrence river. While the NWA has undergone periods of relative cooling and warming even within recent times, the overall the trend has been towards warmer temperatures and a deterioration in ice conditions, particularly in the southern Gulf of St. Lawrence (Johnston et al., 2005, 2012; Friedlaender et al., 2010; Bajzak et al., 2011; Stenson and Hammill, 2014). Laidre et al. (2015) estimated that the spring break-up in the Labrador Sea was, on average, almost 10 days per decade earlier in 2013 than in 1979.

The loss of sea ice during, or shortly after, pupping has had a direct impact on mortality of YOY harp seals in the NWA. If ice cover or thickness is not sufficient during the nursing period or while the young seals develop the capacity for diving, it can break up during storms and the YOY seals may drown (**Figure 8**; Stenson and Hammill, 2014). Hammill et al. (2015) found that although ice cover varied considerably among years, there was a major change in ice conditions by the late 1990s with a significant declining trend in annual ice cover in the Gulf of St. Lawrence of 1940 km^2. The extent of ice at the Front also declined but the impact on harp seals was considered to be less due to the greater overall extent of ice in the area. However, they estimated that pup survival was reduced in a number of years, being as low as 50% in 2010 and 25% in 2011, as a result of less ice in both areas and therefore had to be included explicitly in the population model (**Figure 9**).

Diet/Feeding Ecology

As in other areas NWA harp seals also rely on invertebrates and polar cod in the north, and primarily forage fish in the south (e.g., Kapel, 1995; Finley et al., 1990; Lawson and Stenson, 1997; Ogloff et al., 2019). However, there is considerable geographic and seasonal variation in the prey species consumed (e.g., see Stenson, 2012). While capelin is the primary prey overall, the proportion in the diet varies among years with importance of individual prey species generally reflecting local abundance. For example, polar cod were an important prey during the early 1990s when their abundance on the Newfoundland shelf and Grand Banks increased during a period of cold water. A variety of other species including Atlantic herring, Atlantic cod, sand eels (*Ammodytes spp.*), sculpins (Cottidae), redfish (*Sebastes spp.*), Greenland halibut (*Reinhardtius hippoglossoides*), amphipods (*Hyperiidae*), mysids, shrimp (*Pandulas spp.*) and squid (Teuthoidea) are also consumed (Lawson et al., 1995; Lawson and Stenson, 1997; Tucker et al., 2009; Stenson, 2012). In the NWA, harp seals appear to gain some of their energy stores during the summer feeding in the Arctic regions, but reach their maximum weight in February after feeding in southern areas during the fall (Chabot et al., 1996; Chabot and Stenson, 2002). Approximately 50% of consumption by NWA harp seals occurred on the Newfoundland Shelf south of 55°N (Stenson, 2012) so changes in prey availability in both area Arctic and southern areas can have an impact on the ability of NWA harp seals to obtain the energy needed for successful reproduction.

Changes in Prey Assemblages

The NWA ecosystems have historically been dominated by demersal species, particularly Atlantic cod. However, they underwent an abrupt shift in community structure in the late 1980s and early 1990s as a result of a history of overfishing and changing environmental conditions that resulted in an extreme cold period during these years (Koen-Alonso et al., 2010; Department of Fisheries and Oceans [DFO], 2014; Koen-Alonso and Cuff, 2018). Although the collapse of the Atlantic cod stocks on the Newfoundland and Labrador shelves was the most visible change among groundfish, it was part of a synchronous decline in the biomass of a number of other commercial and non-targeted fish species, and a shift to an ecosystem dominated by shellfish such as northern shrimp (*Pandalus borealis)* and snow crab (*Chionoecetes opilio*). During the early 1990s, there was also an order of magnitude decline in biomass of capelin, the key forage fish in these ecosystems (Buren et al., 2014, 2019). These dramatic changes, recognized as a regime shift, caused a reorganization of the fish community, as well as loss of its spatial structure and functional diversity (Buren et al., 2014, 2019; Dempsey et al., 2017; Pedersen et al., 2017, 2020). Following the cold period in the late 1980s and early 1990s, the water has warmed. By the late 2000s there was some rebuilding of the demersal fish species along with signs of a modest recovery of capelin and major declines in demersal invertebrate stocks (Koen-Alonso and Cuff, 2018). In recent years, these ecosystems appear to be reverting back to a

FIGURE 8 | Whitecoat harp seal pups that drowned after a storm destroyed the ice on which they had been born, northern Gulf of St. Lawrence March 2010. Photo credit: G. Stenson.

community dominated by demersal fish, but not necessarily to the same pre-collapse state, with some warmer water species such as silver hake (*Merluccius bilinearis*) becoming more dominant in some southern areas. If this is any indication of future changes, the Newfoundland and Labrador shelf ecosystems may never fully return to their previous state. At present, the total biomass in these ecosystems remains well below levels observed prior to the collapse in the late 1980s, and since the mid 2010s, productivity appears to be reduced (Pedersen et al., 2017, 2020; Koen-Alonso and Cuff, 2018).

Environmental Impacts on Body Condition and Reproduction

While the ecosystem changes in the NWA impact harp seals directly through increased mortality of young, it has also impacted their population dynamics indirectly through changes in body condition and subsequent reproductive rates. Since the early 1980s, late-term pregnancy rates among mature females has declined while interannual variability increased, ranging from 20% to over 80%. Beginning in the late 1980s, females have been found to be aborting their foeti prematurely in some years (Stenson et al., 2016). During this same period, harp seals have undergone more than a 3-fold increase in abundance (**Figure 3**) and shown declines in growth rates (Chabot et al., 1996; Hammill and Sauvé, 2017; Hammill et al., 2020; Stenson and Buren, unpublished data). Stenson et al. (2016) found that while the general decline in fecundity is a reflection of density-dependent processes associated with increased population size, the large inter-annual variability is due to varying rates of late term abortions which are related to changes in capelin abundance and mid-winter ice coverage. Capelin biomass on the Newfoundland Shelf has been shown to be impacted by changes in the timing of ice retreat which influences the timing of the primary productivity bloom and, as a result, the amount of zooplankton available as prey for capelin (Buren et al., 2014; Lewis et al., 2019). This suggests that mid-winter ice extent reflects environmental conditions that influence a variety of harp seal prey species. Hammill et al. (2020) found that the fit of their population model to the observed pup production was improved by assuming that annual reproductive rates were a function of an index consisting of a variety of environmental measures (e.g., sea surface temperature, ice extent, bottom temperature, air temperature, etc.) (Colbourne et al., 2016) that reflect a changing carrying capacity in the ecosystem.

In their examination of changes in body condition since 1980, Stenson et al. (2020a) found that the average relative condition of pregnant females has remained consistently high while, that of non-pregnant and immature females varied considerably and showed a general decline since 2000. While condition did not

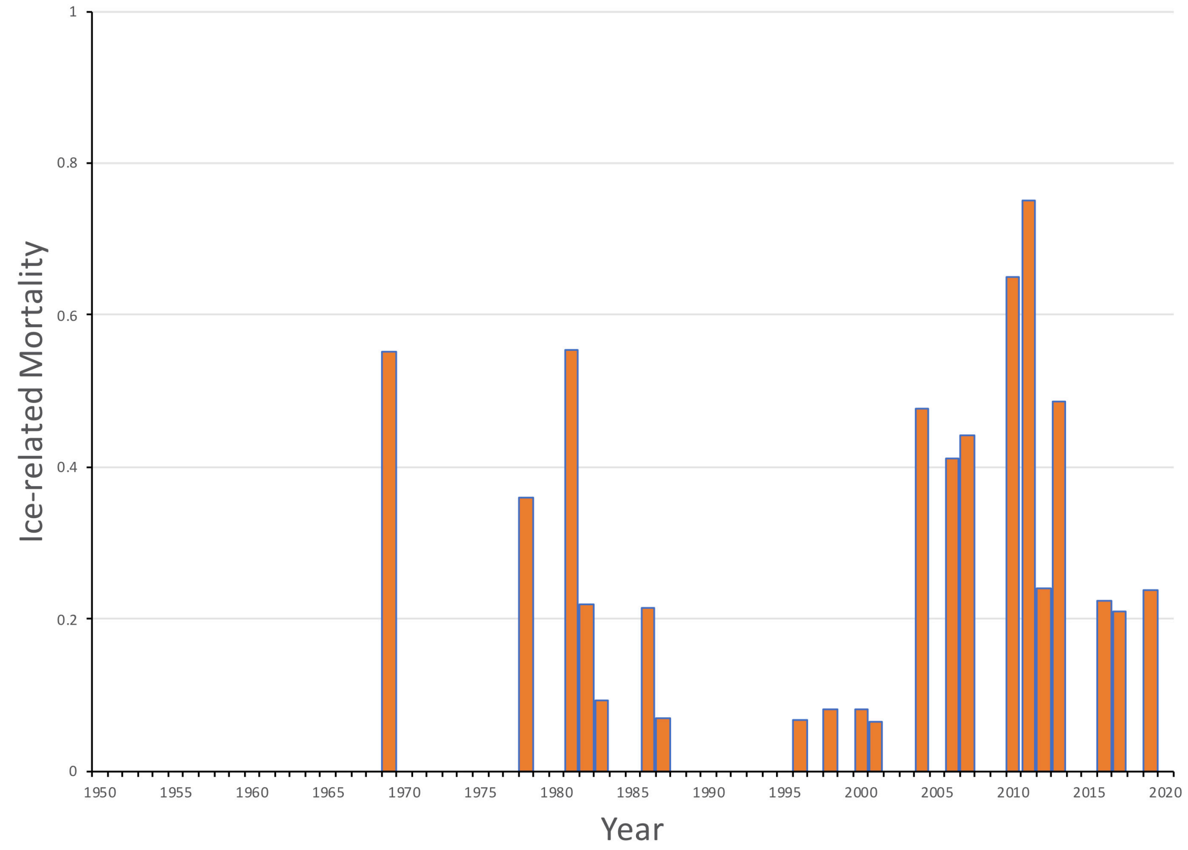


FIGURE 9 | Estimated ice-related mortality of NWA harp seal young of the year (1952-2019) based upon ice conditions in the Gulf of St. Lawrence and off Newfoundland (Hammill et al., 2020).

appear to influence fecundity rates directly, it affected the rate of late term abortions; relatively small reductions in average condition resulted in much higher abortion rates. They also found that body condition was related to capelin abundance and mid-winter ice extent. They proposed that as overall condition in the population declines, females that are able to attain sufficient energy (i.e., body condition) maintained their pregnancy while those that could not attain sufficient energy reserves terminate their pregnancy prematurely.

DISCUSSION

Because of their wide range and differential movements of age classes and sexes, total abundance of harp seals is estimated using a population model that incorporates information on annual reproductive rates, known or estimated sources of mortality, and independent estimates of pup production (e.g., Øigård et al., 2014; Hammill et al., 2015, 2020). Obtaining good estimates of these parameters that are comparable among populations can often be difficult. For example, while a time series of annual late term pregnancy rates are available from the NWA, only periodic estimates based upon samples collected during the molt (i.e., shortly after weaning) are available of the NEA populations (e.g., Kjellqwist et al., 1995; Frie et al., 2003; Stenson et al., 2016; International Council for the Exploration of the Sea [ICES], 2019b). Considerable effort has been made to ensure that comparable methods are used to estimate pup production for all three populations (e.g., Stenson et al., 2002, 2003, 2014, 2020b; Haug et al., 2006; Øigård et al., 2010, 2014) but surveys can only be carried out periodically and long-term time series are difficult to maintain. As such, there can be considerable uncertainty about the population trends among some of these populations which makes interpreting the impact of ecological changes difficult to identify.

The populations dynamics of North Atlantic harp seals has been heavily influenced by commercial hunts. All three populations underwent significant declines in the 19 Century and in the period since World War II (e.g., Iversen, 1927; Skaug et al., 2007; Hammill et al., 2011, 2020; International Council for the Exploration of the Sea [ICES], 2019b). However, lower catches and improved management have lessened the influence of hunting on the populations in recent years (e.g., Hammill et al., 2015, 2020; International Council for the Exploration of the Sea [ICES], 2019b). In the White Sea/Barents Sea, catches have been very low over the past decade, while catches in the Greenland Sea have remained low for the past thirty years. The primary reason for low catches in these areas is economical rather than biological as the catches have been well below the scientific advice for sustainable harvests in both populations

(International Council for the Exploration of the Sea [ICES], 2019b). In spite of these low catches, neither population is recovering in a manner that would be expected. Also, the declines in pup production observed in the White Sea in 2004-2005 and in the Greenland Sea in 2018 cannot be explained by hunting. This suggests that other factors may be limiting these populations.

The situation in the NWA is slightly different. Quotas and low harvest allowed the population to increase during the 1970s and 1980s at approximately 8% per year (Hammill et al., 2015). Between 1996 and 2008, however, harvests increased significantly with combined Canadian and Greenland catches being over 400,000 in some years (Stenson and Upward, 2020). During this period, there were also a number of years with poor ice conditions that resulted in mortality of young seals. As a result of the high harvests on YOY seals and increased mortality which continued until approximately 2011, the population remained relatively stable for almost two decades (1998-2013) (Hammill et al., 2020). Stenson and Upward (2020) found very few females from the 1996 – 2012 cohorts in their reproductive samples also suggesting that there may have been low survival over these years.

NWA harp seals are now estimated to be increasing (Hammill et al., 2020) due to a reduction in the hunt, together with a series of years with good survival of young, and relatively high reproductive rates. This suggests that this population may be less limited by changes in the either environment than the other two populations. This may be because the northwest Atlantic ecosystem is still being influenced by the cold Labrador current and seasonal ice cover, while the northeast Atlantic and the Barents Sea are more strongly influenced by increased inflow of warmer Atlantic waters. The relatively stable Greenland Sea pup production during the 2000s, when the Barents Sea/White Sea population experienced a dramatic decline, may be due to Greenland Sea seals spending at least part of the year in the western margin dominated by the cold East Greenland Current, while the White Sea/Barents Sea population is more confined to the Barents Sea, which is much more strongly influenced by the Atlantic inflow. The almost 40% drop in the most recent pup production estimate in the Greenland Sea may suggest that the ecosystem associated with cold Arctic waters along the western margin are now changing, and the resilience provided to seals by having access to two oceanic regimes has disappeared. This may suggest a gradient from (1) dramatic negative population response in the Barents Sea/White sea population exposed to rapid changes in the Barents Sea, via (2) delayed and potentially less dramatic negative response in the Greenland Sea population having access to both Barents Sea and Greenland Sea regimes, to (3) continued population increase in the Northwest Atlantic population which remains in waters dominated by Arctic conditions in the Labrador Sea.

Overall, climate change has resulted in dramatic changes in ecosystems across the north Atlantic, both with respect to changes in ice conditions and community structure. Reductions in sea ice associated with climate change is impacting all three harp seal populations. Laidre et al. (2015) found that among the twelve Arctic areas they examined, the largest increase in ice free days, both in the spring and in the fall, occurred in the Barents Sea while the second largest increase occurred in the Labrador Sea, both being important pupping areas for harp seals. The shift in timing of spring breakup and fall freeze-up has not been as dramatic in the Greenland Sea, but the changes are still significant (Laidre et al., 2015). Poor ice conditions have resulted in a number of years with high mortality among YOY seals in the NWA (Stenson and Hammill, 2014; Hammill et al., 2015, 2020). The same degree of ice loss is now being observed in the White Sea, suggesting that this population may also be impacted by increased mortality of young seals. While the population may not be impacted by the occasional year with poor pup survival, repeated years with even low levels of additional mortality can have serious consequences which will not be identified for over a decade at the current frequency of pup production surveys (Hammill and Stenson, 2010; Stenson and Hammill, 2014; Hammill et al., 2020).

Shifts in the whelping locations of Greenland Sea harp seals have occurred as the ice edge recedes towards the east Greenland coast (Rosing-Asvid, 2008). A shift in the location of whelping outside of the traditional pupping areas was also observed in the NWA during a year when ice conditions were extremely poor (Stenson and Hammill, 2014). Harp seals have traditionally pupped in areas where the ice persists in the same general area during the period of nursing and the post weaning fast. This was a feature of the Odden in the Greenland Sea and off the north coast of Newfoundland where ice is often retained. When pupping occurs outside of the traditional areas, the young may be exposed to ice that can break up quicker and to different prey fields during the period when they are first learning to find food. In areas such as the Greenland Sea and off Newfoundland, they can also encounter increased predation from polar bears which travel great distances to seek out the pupping concentrations (Peacock et al., 2013).

Comparing historical locations of NWA harp seal whelping patches during periods of good and poor ice conditions led Stenson and Hammill (2014) to conclude that females pupped in areas with suitable ice outside of their traditional whelping areas if no ice was present within these traditional areas. However, if any amount of ice was present in the traditional areas, females gave birth even if the ice was too thin to sustain the pups, resulting in high pup mortality. There was no evidence to indicate that harp seals pupped on land even in areas where ice was absent and young seals that drifted to shore had high levels of abandonment and mortality. They predicted that if the current warming trends continue, ice-breeding harp seals will encounter more years with poor ice conditions and may eventually adapt by moving north. Until then, they will continue to have increased levels of mortality that could result in the disappearance of the most southern breeding component in the Gulf of St Lawrence. Such a situation occurred in 2017 when poor ice in southern Gulf resulted in an almost complete collapse of pupping with only 2% of the total NWA pup production occurring in an area that traditionally accounts for 25–30%. There was evidence that suggests that some of the females moved to the Newfoundland area to give birth but whether these females will stay there or move back to the Gulf is unknown (Department of Fisheries and Oceans [DFO], 2020; Stenson et al., 2020b).

Historically the community structure of ecosystems in the NWA and NEA, particularly the Barents Sea, shared a number of traits. They were characterized by demersal fish dominated by Atlantic cod, and had a wasp-waist ecosystem with capelin or polar cod as the dominant forage fish. All areas are influenced by seasonal sea ice cover which will influence timing and strength of primary production. However, the NWA and NEA appear to be diverging with the NWA being more influenced by the cold Labrador current, while the increased Atlantic inflow is bringing warm water and temperate species to the NEA. The unidirectional warming trend in the NEA has been conducive to increased productivity and a recovery in fish groundfish productivity to very high levels (Bogstad et al., 2015; Haug et al., 2017). In contrast, in the NWA, the climate has alternated between warm and cold periods resulting in a decline in productivity and only minimal recovery of demersal species (Pedersen et al., 2017; Koen-Alonso and Cuff, 2018).

These ecological changes have been reflected in the changes observed in body condition and vital rates of harp seals. As abundance and/or distribution of many of the key prey species has changed, body condition in both White Sea/Barents Sea and NWA harp seals has declined.

Similar declines in body condition have been observed in common minke whales (*Balaenoptera acutorostrata*) that inhabit the Barents Sea (Haug et al., 2002). Solvang et al. (2017) reported a negative trend in body condition over the period 1992-2013, with particular low values in 2013. Bogstad et al. (2015) suggested that the current record high cod stock in the area may have outperformed the seal and whale stocks in competition for food (mainly capelin). It is possible that collapse of the Barents Sea capelin stock that occurred around 2003 resulted in a reduction in body condition and pregnancy rates as has been seen in the NWA (Stenson et al., 2016). This may account for the decline in White Sea pup production observed in 2004 and 2005 (Øigård et al., 2013). The continued lower level of births in this population may be due to increased ice mortality and competition with the large Atlantic cod stock for food as the capelin stocks rebounded.

Northwest Atlantic capelin stocks have not recovered significantly since the collapse in the early 1990s which has led to lower body condition and reduced, but highly variable pregnancy rates in NWA harp seals (Stenson et al., 2020a). The large increase in abundance this population has undergone over the past 40 years has contributed to the lower average reproductive rates (i.e., density dependent factors), but it appears that at a high population size, females are sensitive to relatively small changes in prey availability and respond to low prey abundance by aborting their foeti (Stenson et al., 2016). It is unknown if White Sea/Barents Sea harp seals respond, similarly, as later term pregnancy data are not available. However, the very high age of sexual maturity observed in this population (Kjellqwist et al., 1995; Frie et al., 2003) suggests that they may also be near the carrying capacity of the Barents Sea. If so, they may also be responding to relatively small changes in food availability.

Unfortunately, there are no data on body condition and only limited data on reproductive rates of Greenland Sea harp seals. However, the reduction in pup production observed in 2018 in the absence of a hunt suggests that this population may also be impacted by changes in food availability. This may not be unexpected as there have been major shifts in the distribution of capelin and reduction in polar cod in the area. Also, seals from this population spend part of the year in the Barents Sea feeding and so will be influenced the same changes in prey availability that impact the Barents Sea/White Sea seals (see Folkow et al., 2004; Nordøy et al., 2008).

In summary, the current population dynamics of harp seals from the White Sea/Barents Sea population is not influenced by harvests, but the population is being limited by ecological changes in the Barents Sea including (1) reduction in sea ice possibly resulting in increased mortality of young, (2) changes in prey availability, and (3) potential competition with Atlantic cod. The latter two would result in reduced female body condition which could increase late term abortion and/or reduced energy transfer to pups thereby reducing survival. Greenland Sea harp seals are being affected by changes in ice that are not known to be associated with increase pup mortality, but may reduce survival later in the year. They may also be impacted by changes in prey both in the Barents Sea, as well as around Iceland and Greenland. Until recently, the abundance of harp seals in the NWA was limited by catches and while these catches have been reduced, the population is still influenced by changes in the age structure. The high harvest levels of young seals and reduced survival due to poor ice conditions likely resulted in the severe reduction of some cohorts that are only now coming to an age where they will be reproducing. Climate change has also been shown to impact NWA harp seals directly through ice related mortality of YOY, as well as indirectly through changes in prey availability that influence body condition and reproductive rates. Each of the three harp seal populations has been impacted differently by changes in their ecosystems and hunting practices. As their ecosystems continue to change, it is important that we continue to monitor abundance and improve our data on vital rates to further understand how ecological and anthropogenic factors influence this important indicator species.

AUTHOR CONTRIBUTIONS

GS and TH conceived the article. All authors contributed to the writing.

FUNDING

This is a contribution of the CoArc project and received some funding from the Norwegian Foreign Ministry and its Arctic 2030 program.

ACKNOWLEDGMENTS

We would like to thank M. Koen-Alonso, L. Shepard, M. Biuw, and two reviewers for their editorial suggestions which have improved this paper considerably. We also thank J. Lawson for the map of harp seal distribution and P. Goulet for preparing the White Sea ice data.

REFERENCES

Astthorsson, O. S., Gislason, A., and Jonsson, S. (2007). Climate variability and the Icelandic marine ecosystem. *Deep Sea Res. II* 54, 2456–2477. doi: 10.1016/j.dsr2.2007.07.030

Bajzak, C. E., Hammill, M. O., Stenson, G. B., and Prinsenberg, S. (2011). Drifting away: implications of changes in ice conditions for a pack-ice breeding phocid, the harp seal (*Pagophilus groenlandicus*). *Can. J. Zool.* 89, 1050–1062. doi: 10.1139/z11-081

Beaugrand, G., Liczak, C., and Edwards, M. (2009). Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Global Change Biol.* 15, 1790–1803. doi: 10.1111/j.1365-2486.2009.01848.x

Bogstad, B., Gjøsæter, H., Haug, T., and Lindstrøm, U. (2015). A review of the battle for food in the Barents Sea: cod vs marine mammals. *Front. Ecol. Evol.* 3:29. doi: 10.3389/fevo.2015.00029

Bogstad, B., Haug, T., and Mehl, S. (2000). Who eats whom in the Barents Sea? *NAMMCO Sci. Publ.* 2, 98–119.

Borisov, V. I. (1966). Some data of the serological analysis of *Pagophilus groenlandicus* Erxleben colonies. *Zool. Zh. Ukr.* 45, 1890–1892.

Buren, A. D., Koen-Alonso, M., Pepin, P., Mowbry, F., Nakashima, B., Stenson, G., et al. (2014). Bottom-up regulation of capelin, a keystone forage species. *PLoS One* 9:e87589. doi: 10.1371/journal.pone.0087589

Buren, A. D., Murphy, H. M., Adamack, A. T., Davoren, G. K., Koen-Alonso, M., MontevDoiecchi, W. A., et al. (2019). The collapse and continued low productivity of a keystone forage fish species. *Mar. Ecol. Prog. Ser.* 616, 155–170. doi: 10.3354/meps12924

Burns, J. M., Lestyk, K. C., Folkow, L. P., Hammill, M. O., and Blix, A. S. (2007). Size and distribution of oxygen stores in harp and hooded seals from birth to maturity. *J. Comp. Physiol. B* 177, 687–700. doi: 10.1007/s00360-007-0167-2

CAFF (2017). *State of the Arctic Marine Biodiversity Report*. Akureyri: Conservation of Arctic Flora and Fauna International Secretariat. 978-9935-431-63–69.

Carr, S. M., Duggan, A. T., Stenson, G. B., and Marshall, H. D. (2015). Quantitative phylogenomics of within-species mitogenome variation: monte Carlo and non-parametric analysis of phylogeographic structure among discrete transatlantic breeding areas of harp seals (*Pagophilus groenlandicus*). *PLoS One* 10:e0134207. doi: 10.1371/journal.pone.0134207

Chabot, D., and Stenson, G. B. (2002). Growth and seasonal fluctuations in size and condition of male Northwest Atlantic harp seals (*Phoca groenlandica*): an analysis using sequential growth curves. *Mar. Ecol. Prog. Ser.* 227, 25–42. doi: 10.3354/meps227025

Chabot, D., Stenson, G. B., and Cadigan, N. B. (1996). Short-and long- term fluctuations in the size and condition of harp seal (*Phoca groenlandica*) in the northwest Atlantic. *NAFO Sci. Council Stud.* 26, 15–32.

Christiansen, J. S. (2017). No future for Euro-Arctic ocean fishes. *Mar. Ecol. Prog. Ser.* 575, 217–227. doi: 10.3354/meps12192

Christiansen, J. S., Bonsdorff, E., Byrkjedal, I., Fevolden, S. E., Karamushko, O. V., Lynghammar, A., et al. (2016). Novel biodiversity baselines outpace models of fish distribution in Arctic waters. *Sci. Nat.* 103, 8.

Colbourne, E., Holden, J., Senciall, D., Bailey, W., Snook, S., and Higdon, J. (2016). Physical Oceanographic Conditions on the Newfoundland and Labrador Shelf during 2015. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2016/079. v +40 p.

Dempsey, D. P., Koen-Alonso, M., Gentleman, W. C., and Pepin, P. (2017). Compilation and discussion of driver, pressure and state indictors for the Grand Bank ecosystem. *Northwest Atlantic. Ecol. Indicator.* 75, 331–339. doi: 10.1016/j.ecolind.2016.12.011

Department of Fisheries, and Oceans [DFO] (2012). Science advice for identifying indicators for monitoring arctic marine biodiversity in Canada. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep.* 2012/053, 23.

Department of Fisheries, and Oceans [DFO] (2014). Short-term stock prospects for cod, crab and shrimp in the newfoundland and labrador region (Divisions 2J3KL). *DFO Can. Sci. Adv. Sec. Sci. Resp.* 2014/049, 18.

Department of Fisheries, and Oceans [DFO] (2020). 2019 status of Northwest Atlantic harp seals, *Pagophilus groenlandicus*. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep.* 2020/020, 14.

Divine, D. V., and Dick, C. (2006). Historical variability of sea ice edge position in the nordic seas. *J. Geophys. Res.* 111:c01001. doi: 10.1029/2004jc002851

Drinkwater, K., Colbourne, E., Loeng, H., Sundby, S., and Kristiansen, T. (2013). Comparison of the atmospheric forcing and oceanographic responses between the Labrador Sea and the Norwegian and Barents seas. *Prog. Ocean* 114, 11–25. doi: 10.1016/j.pocean.2013.03.007

Drinkwater, K., and Pepin, P. (2013). Comparison of climate forcing on the marine ecosystems of the Northeast and Northwest Atlantic: a synthesis of the NORCAN Project. *Prog. Ocean* 114, 3–10. doi: 10.1016/j.pocean.2013.05.002

Eamer, J., Donaldson, G. M., Gaston, A. J., Kosobokova, K. N., Lárusson, K. F., Melnikov, I. A., et al. (2013). *Life Linked to Ice: A Guide to Sea-Ice-Associated Biodiversity ?in This Time of Rapid Change*. Iceland: Conservation of Arctic Flora and Fauna. CAFF Assessment Series No. 10.

Enoksen, S., Haug, T., Lindstrøm, U., and Nilssen, K. T. (2017). Recent summer diet of hooded *Cystophora cristata* and harp *Pagophilus groenlandicus* seals in the drift ice of the Greenland Sea. *Polar Biol.* 40, 931–937. doi: 10.1007/s00300-016-2002-2

Finley, K. J., Bradstreet, M. S. W., and Miller, G. W. (1990). Summer feeding ecology of harp seals (*Phoca groenlandica*) in relation to Arctic cod (Boreogadus saida) in the Canadian high Arctic. *Polar Biol.* 10, 609–618. doi: 10.1007/bf00239372

Folkow, L. P., Nordøy, E. S., and Blix, A. S. (2004). Distribution and diving behaviour of harp selas (*Pagophilus groenlandicus*) from the Greenland Sea stock. *Polar Biol.* 27, 281–298. doi: 10.1007/s00300-004-0591-7

Foote, A. D., Newton, J., Avila-Arcos, M. C., Kampmann, M. L., Samaniego, J. A., Post, K., et al. (2013). Tracking niche variation over millennial timescales in sympatric killer whale lineages. *Proc. R. Soc. B* 280:20131481. doi: 10.1098/rspb.2013.1481

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R., Aschan, M., and Dolgov, A. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat Clim. Change* 5, 673–677. doi: 10.1038/nclimate2647

Frie, A. K., Potelov, V. A., Kingsley, M. C. S., and Haug, T. (2003). Trends in age at maturity and growth parameters of female northeast Atlantic harp seals. Pagophilus groenlandicus (Erxleben, 1777). *ICES J. Mar. Sci.* 60, 1018–1032. doi: 10.1016/s1054-3139(03)00123-1

Friedlaender, A. S., Johnston, D. W., and Halpin, P. N. (2010). Effects of the North Atlantic Oscillation on sea ice breeding habitats of harp seals (*Pagophilus groenlandicus*) across the North Atlantic. *Prog. Ocean* 86, 261–266. doi: 10.1016/j.pocean.2010.04.002

Gjøsæter, H., and Bogstad, B. (1998). Effects of the presence of herring (*Clupea harengus*) on the stock-recruitment relationships of Barents Sea capelin (*Mallotus villosus*). *Fish. Res.* 38, 57–71. doi: 10.1016/s0165-7836(98)00114-3

Gjøsæter, H., Bogstad, B., and Tjelmeland, S. (2009). Ecosystem effects of the three capelin stock collapses in the Barents Sea. *Mar. Biol. Res.* 5, 40–53. doi: 10.1080/17451000802454866

Hammill, M. O., and Sauvé, C. (2017). Growth and condition in harp seals-evidence of density dependent and density independent influences. *ICES J. Mar. Sci.* 74, 1395–1407. doi: 10.1093/icesjms/fsw237

Hammill, M. O., Stenson, G. B., Doniol-Valcroze, T., and Mosnier, A. (2015). Conservation of northwest Atlantic harp seals: past success, future uncertainty? *Biol. Conserv.* 192, 181–191. doi: 10.1016/j.biocon.2015.09.016

Hammill, M. O., Stenson, G. B., and Kingsley, M. C. S. (2011). Historical Abundance of Northwest Atlantic harp seals (*Pagophilus groenlandicus*): influence of harvesting and climate. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2011/100. iv + 16 p.

Hammill, M. O., Stenson, G. B., Mosnier, A., and Doniol-Valcroze, T. (2020). Trends in harp seal, *Pagophilus groenlandicus*, abundance in the Northwest Atlantic, 1952-2019. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2020/in press. iv + 28 p.

Hammill, M. O., and Stenson, G. B. (2010). A preliminary evaluation of the performance of the Canadian management approach for harp seals using simulation studies. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2009/093. iv + 47 p.

Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallfredsson, E. H., Høines, ÅS., et al. (2017). Future harvest of living resources in the Arctic Ocean of the Nordic and Barents Seas: a review of possibilities and constraints. *Fish. Res.* 188, 38–57. doi: 10.11016/j.fishres.2016.12.002

Haug, T., Krøyer, A. B., Nilssen, K. T., Ugland, K. I., and Aspholm, P. E. (1991). Harp seal (*Phoca groenlandica*) invasions in Norwegian coastal waters: age composition and feeding habits. *ICES J. Mar. Sci.* 48, 363–371. doi: 10.1093/icesjms/48.3.363

Haug, T., Lindstrøm, U., and Nilssen, K. T. (2002). Variations in minke whale *Balaenoptera acutorostrata* diet and body condition in response to ecosystem changes in the Barents Sea. *Sarsia* 87, 409–422. doi: 10.1080/003648202100 0155715

Haug, T., Nilssen, K. T., and Lindblom, L. (2004). Feeding habits of harp and hooded seals in drift ice waters along the east coast of Greenland in summer and winter. *Polar Res.* 23, 35–42. doi: 10.3402/polar.v23i1.6264

Haug, T., Nilssen, K. T., Øien, N., and Potelov, V. (1994). Seasonal distribution of harp seals (*Phoca groenlandica*) in the Barents Sea. *Polar Res.* 13, 161–172.

Haug, T., Stenson, G. B., Corkeron, P. J., and Nilssen, K. T. (2006). Estimation of harp seal (*Pagophilus groenlandicus*) pup production in the North Atlantic completed: results from surveys in the Greenland Sea in 2002. *ICES J. Mar. Sci.* 63, 95–104. doi: 10.1016/j.icesjms.2005.07.005

Hauksson, E., and Bogason, V. (1997). Comparative feeding of grey (*Halichoerus grypus*) and common seals (*Phoca vitulina*) in coastal waters of Iceland, with a note on the diet of hooded (*Cystophora cristata*) and harp seals (*Phoca groenlandica*). *J. Northwe. Atlant. Fish. Sci.* 22, 125–135. doi: 10.2960/j.v22.a11

Hoover, C., Pitcher, T., and Christensen, V. (2013). Effects of hunting, fishing and climate change on the Hudson Bay marine ecosystem: II. Ecosystem model future projections. *Ecol. Model.* 264, 143–156. doi: 10.1016/j.ecolmodel.2013.01.010

Hunt, G. L. Jr., Blanchard, A. L., Boveng, P., Dalpadado, P., Drinkwater, K. F., Eisner, L., et al. (2013). The barents and chuckchi seas: comparison of two Arctic shelf ecosystems. *J. Mar. Sys.* 109-110, 43–68.

Intergovernmental Panel on Climate Change [IPCC] (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva: IPCC, 151.

International Council for the Exploration of the Sea [ICES] (2013). *Report of the ICES Working Group on Harp and Hooded Seals, 26-30 August 2013*. Murmansk: PINRO, 55. ICES CM 2013/ACOM: 20.

International Council for the Exploration of the Sea [ICES] (2016). *Report of the ICES/NAFO/NAMMCO Working Group on Harp and Hooded Seals, 26-30 September 2016*, ICES HQ, Copenhagen, Denmark. ICES CM 2016/ACOM: 21:1-81.

International Council for the Exploration of the Sea [ICES] (2019a). "Barents Sea Ecoregion – Ecosystem overview," in *Report of the ICES Advisory Committee, 2019*, (Copenhagen: ICES), doi: 10.17895/ices.advice.5747 ICES Advice 2019, Section 5.1.

International Council for the Exploration of the Sea [ICES] (2019b). *ICES/NAFO/NAMMCO Working Group on Harp and Hooded Seals (WGHARP)*. Copenhagen: ICES, 193. doi: 10.17895/ices.pub.5617 ICES Scientific Reports 1:72.

International Council for the Exploration of the Sea [ICES] (2019c). "Icelandic Waters ecoregion –Ecosystem overview," in *Report of the ICES Advisory Committee, 2019*, (Copenhagen: ICES), doi: 10.17895/ices.advice.5746 ICES Advice 2019, Section 11.1.

Iversen, T. (1927). *Drivis og selfangst. Årsberetning vedkommende Norges Fiskerier*, Vol. 1927. Diamanten: Norwegian, 1–84.

Iverson, S. J., Frost, K. J., and Lang, S. (2002).). Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: factors contributing to among and within species variability. *Mar. Ecol. Prog. Ser.* 241, 161–181. doi: 10.3354/meps241161

Johnston, D. W., Bowers, M. T., Friedlaender, A. S., and Lavigne, D. M. (2012). The effects of climate change on harp seals (*Pagophilus groenlandicus*). *PLoS One* 7:e29158. doi: 10.1371/journal.pone.0029158

Johnston, D. W., Friedlaender, A. S., Torres, L. G., and Lavigne, D. M. (2005). Variation in sea ice cover on the east coast of Canada from 1969 to 2002: climate variability and implications for harp and hooded seals. *Clim. Res.* 29, 209–222. doi: 10.3354/cr029209

Kapel, F. O. (1995). "Feeding ecology of harp and hooded seals in the Davis Strait - Baffin Bay region," in *Whales, Seals, Fish and man.* Developments in Marine Biology 4, eds A. S. Blix, L. Walløe, and Ø Ulltang (Elsevier: Amsterdam), 287–304. doi: 10.1016/s0163-6995(06)80031-4

Kjellqwist, S. A., Haug, T., and Øritsland, T. (1995). Trends in age- composition, growth and reproductive parameters of Barents Sea harp seals. *Phoca groenlandica*. *ICES J. Mar. Sci.* 52, 197–208. doi: 10.1016/1054-3139(95)80035-2

Koen-Alonso, M., and Cuff, A. (2018). *Status and Trends of the Fish Community in the Newfoundland Shelf (NAFO Div 2J3KL), Grand Bank (NAFO Div. 3LNO) and Southern Newfoundland Shelf (NAFO Div. 3Ps) Ecosystem Production Units*. Dartmouth: NAFO. NAFO SCR Doc. 18/70.

Koen-Alonso, M., Pepin, P., and Mowbry, F. (2010). *Exploring the Role of Environmental and Anthropogenic Drivers in the Trajectories of Core Fish Species in the Newfoundland-Labrador Marine Community*. Dartmouth: NAFO. NAFO SCR Doc. 10/37.

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., and Aschan, M. (2015). Climate change alters the structure of arc- tic marine food webs due to poleward shifts of boreal generalists. *Proc. R. Soc. Lond. B. Biol. Sci.* 282:20151546. doi: 10.1098/rspb.2015.1546

Kovacs, K., and Lydersen, C. (2008). Climate change impacts on seals and whales in the North Atlantic Arctic and adjacent shelf areas. *Sci. Progr.* 91, 117–150. doi: 10.3184/003685008x324010

Kovacs, K., Lydersen, C., Overland, J. E., and Moore, S. E. (2011). Impacts on changing sea-ice conditions on Arctic marine mammals. *Mar. Biodiv.* 41, 181–194. doi: 10.1007/s12526-010-0061-0

Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L. F., Moore, S. E., Regehr, E. V., et al. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conserv. Biol.* 29, 724–737. doi: 10.1111/cobi.12474

Laidre, K. L., Stirling, I., Lowry, L. F., Wiig, Ø. Heide-Jørgensen, M. P., and Ferguson, S. H. (2008). Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecol. Appl.* 18, S97–S125.

Lawson, J. W., and Stenson, G. B. (1997). Diet of northwest Atlantic harp seals (*Phoca groenlandica*) in offshore areas. *Can J. Zool.* 75, 2095–2106. doi: 10.1139/z97-844

Lawson, J. W., Stenson, G. B., and McKinnon, D. (1995). Nearshore diet of harp seals (*Phoca groenlandica*) in the northwest Atlantic during 1990-1993. *Can. J. Zool.* 75, 1805–1818. doi: 10.1139/z95-213

Lewis, K. P., Buren, A. D., Regular, P. M., Mowbray, F. K., and Murphy, H. M. (2019). Forecasting capelin *Mallotus villosus* biomass on the Newfoundland shelf. *Mar. Ecol. Prog. Ser.* 616, 171–183. doi: 10.3354/meps12930

Lindstrøm, U., Harbitz, A., Haug, T., and Nilssen, K. T. (1998). Do harp seals *Phoca groenlandica* exhibit particular prey preferences? *ICES J. Mar. Sci.* 55, 941–953. doi: 10.1006/jmsc.1998.0367

Lindstrøm, U., Nilssen, K. T., Pettersen, L. M. S., and Haug, T. (2013). Harp seal foraging behaviour during summer around Svalbard in the northern Barents Sea: diet composition and selection of prey. *Polar Biol.* 36, 305–320. doi: 10.1007/s00300-012-1260-x

McCarthy, J. J., Canzani, O. F., Leary, N. A., Dokken, D. J., and White, K. S. (eds) (2001). *Climate change 2001: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press. doi: 10.1007/s00300-012-1260-x

McKinney, M. A., Iverson, S. J., Fisk, A. T., Sonne, C., Riget, F. F., Letcher, R. J., et al. (2013). Global change effects on the long-term feeding ecology and contaminant exposures of East Greenland polar bears. *Global Change Biol.* 19, 2360–2372. doi: 10.1111/gcb.12241

Meisfjord, J., and Nñvdal, G. (1994). Using isoelectric-focusing to discern enzyme variation in northeast Atlantic stocks of the harp seal (*Phoca groelandica*). *Hereditas* 121, 273–281. doi: 10.1111/j.1601-5223.1994.00273.x

Meisfjord, J., and Sundt, G. (1996). Genetic variation between populations of the harp seal. Phoca groenlandica. *ICES J. Mar. Sci.* 53, 89–95. doi: 10.1006/jmsc.1996.0008

Møller, D. G., Nñvdal, G., and Valen, A. (1966). Rapport om arbeidet med blodanalyser for populasjonsundersuǏkelser. [Report on sero- logical work in population studies]. *Fisken Hav.* 1966, 1–17.

Moore, S. E., Haug, T., Víkingsson, G. A., and Stenson, G. (2019). Baleen Whale Ecology in Arctic and Subarctic Seas in an Era of Rapid Habitat Alteration. *Prog. Oceanog.* 2019:102118. doi: 10.1016/j.pocean.2019.05.010

Murawski, S. A., Steele, J. H., Taylor, P., Fogarty, M. J., Sissenwine, M. P., Ford, M., et al. (2010). Why compare marine ecosystems? *ICES J. Mar. Sci.* 67, 1–9. doi: 10.1093/icesjms/fsp221

Nakken, O. (1988). Fangsthistorikk. *Fiskets Gang.* 74, 14–15.

Nilssen, K. T., Haug, T., Grotnes, P. E., and Potelov, V. A. (1997). Seasonal variation in body condition of adult Barents Sea harp seals (*Phoca groenlandica*). *J. Northw. Atl. Fish. Sci.* 22, 17–25. doi: 10.2960/j.v22.a1

Nilssen, K. T., Haug, T., Øritsland, T., Lindblom, L., and Kjellqwist, S. A. (1998). Invasions of harp seals *Phoca groenlandica* Erxleben to coastal waters of Norway in 1995: ecological and demographic implications. *Sarsia* 83, 337–345. doi: 10.1080/00364827.1998.10413693

Nilssen, K. T., Haug, T., Potelov, V., and Timoshenko, Y. K. (1995). Food habits and food availability of harp seals (*Phoca groenlandica*) during early summer and autumn in the northern Barents Sea. *Polar Biol.* 15, 485–493.

Nilssen, K. T., Pedersen, O. P., Folkow, L., and Haug, T. (2000). Food consumption estimates of Barents Sea harp seals. *NAMMCO Sci. Publ.* 2, 9–28. doi: 10.7557/3.2968

Nordøy, E. S., Folkow, L. P., Potelov, V., Prischemikhin, V., and Blix, A. S. (2008). Seasonal distribution and dive behaviour of harp seals (*Pagophilus groenlandicus*) of the White Sea – Barents Sea stock. *Polar Biol.* 31, 1119–1135. doi: 10.1007/s00300-008-0453-9

Norwegian Meteorological Institute (2020). *Updated Daily. Norwegian Ice Service Archived Ice Charts*. Avaliable at: https://cryo.met.no/archive/ice-service/icecharts/quicklooks/. (accessed April 28, 2020)

Nñvdal, G. (1969). Blood protein polymorphism in harp seals in eastern Canada. *J. Fish. Res. Bd. Can.* 26, 1397–1399. doi: 10.1139/f69-128

Nñvdal, G. (1971). Serological studies on marine mammals. *Rapp ReA∧un Cons. Int. Explor. Mer.* 161, 136–138.

Ogloff, W. R., Yurkowski, D. J., Davoren, G. K., and Ferguson, S. H. (2019). Diet and isotopic overlap elucidate competition potential between seasonally sympatric phocids in the Canadian Arctic. *Mar. Biol.* 166:103. doi: 10.1007/s00227-019-3549-6

Øien, N., and Øritsland, T. (1995). "Use of mark-recapture experiments to monitor seal populations subject to catching," in *Whales, Seals, Fish and Man. Developments in Marine Biology 4*, eds A. S. Blix, L. Walløe, and Ø Ulltang (Amsterdam: Elsevier), 35–45. doi: 10.1016/s0163-6995(06)80007-7

Øigård, T. A., Haug, T., and Nilssen, K. T. (2014). From pup production to quotas: current status of harp seals in the Greenland Sea. *ICES J. Mar. Sci.* 71, 537–545. doi: 10.1093/icesjms/fst155

Øigård, T. A., Haug, T., Nilssen, K. T., and Salberg, A.-B. (2010). Estimation of pup production of hooded and harp seals in the Greenland Sea in 2007: reducing uncertainty using Generalized Additive Models. *J. Northwest Atl. Fish. Sci.* 42, 103–123. doi: 10.2960/j.v42.m642

Øigård, T. A., Lindstrøm, U., Haug, T., Nilssen, K. T., and Smout, S. (2013). Functional relationship between harp seal body condition and available prey in the Barents Sea. *Mar. Ecol. Prog. Ser.* 484, 287–301. doi: 10.3354/meps10272

Øritsland, T., and Øien, N. (1995). "Aerial surveys of harp and hooded seal pups in the Greenland Sea pack ice," in *Whales, Seals, Fish and Man. Developments in Marine Biology 4*, eds A. S. Blix, L. Walløe, and Ø Ulltang (Amsterdam: Elsevier), 77–87. doi: 10.1016/s0163-6995(06)80012-0

Peacock, E., Taylor, M. K., Laake, J., and Stirling, I. (2013). Population ecology of polar bears in Davis Strait, Canada and Greenland. *J. Wildl. Mange.* 77, 463–476. doi: 10.1002/jwmg.489

Pedersen, E. J., Koen-Alonso, M., and Tunney, T. D. (2020). Detecting regime shifts in communities using estimated rates of change. *ICES J. Mar. Sci.* 77, 1546–1555. doi: 10.1093/icesjms/fsaa056

Pedersen, E. J., Thompson, P. L., Ball, R. A., Fortin, M. J., Gouhier, T. C., Link, H., et al. (2017). Signatures of the collapse and incipient recovery of an overexploited marine ecosystem. *R. Doc. Open Sci.* 4:170215. doi: 10.1098/rsos.170215

Perry, E. A., Stenson, G. B., Bartlett, S. E., Davidson, W. S., and Carr, S. M. (2000). DNA sequence analysis identifies genetically distinguishable populations of harp seals (*Pagophilus groenlandicus*) in the northwest and northeast Atlantic. *Mar. Biol.* 137, 53–58. doi: 10.1007/s002279900248

Perry, E. A., and Terhune, J. M. (1999). Variation of harp seal underwater vocalisations among three breeding locations. *J. Zool. Lond.* 249, 181–186. doi: 10.1111/j.1469-7998.1999.tb00756.x

Potelov, V. A., Golikov, A. P., and Bondarev, V. A. (2003). Estimated pup production of harp seals *Pagophilus groenlandicus* in the White Sea. Russia, in 2000. *ICES J. Mar. Sci.* 60, 1012–1017. doi: 10.1016/s1054-3139(03)00095-x

Protozorkevich, D., and van der Meeren, G. I. (eds) (2020). *Survey Report From the Joint Norwegian/ Russian Ecosystem Survey in the Barents Sea and Adjacent Waters August-October 2019*. Bergen: Havforskningsinstituttet, 93. IMR/PINRO Joint Report Series, 1-2020.

QGIS Development Team (2019). *QGIS Geographic Information System*. Chicago: Open Source Geospatial Foundation Project.

Rice, J. (2002). "Changes to the large marine ecosystem of the Newfoundland-Labrador shelf," in *Large Marine Ecosystems of the North Atlantic*, eds K. Sherman and H. R. Skjoldal (Amsterdam: Elsevier Science B.V), 51–103. doi: 10.1016/s1570-0461(02)80055-6

Rigét, F., Mosbech, A., Boertmann, D., Wegeberg, S., Merkel, F., Aastrup, P., et al. (2019). "The seas around Greenland: an environmental status and future perspective," in *World seas: An Environmental Evaluation*, (Cambridge, MA: Academic Press), 45–68. doi: 10.1016/b978-0-12-805068-2.00001-2

Rosing-Asvid, A. (2008). A new harp seal whelping ground near South Greenland. *Mar. Mamm. Sci.* 24, 730–736. doi: 10.1111/j.1748-7692.2008.00216.x

Sergeant, D. E. (1991). Harp seals, man and ice. *Can. Spec. Publ. Fish. Aquat. Sci.* 114, 1–153.

Sivertsen, E. (1941). On the biology of the harp seal Phoca groenlandica Erxl. Investigations carried out in the White Sea 1925-1937. *Hvalradets Skr.* 26, 1–166.

Skaug, H. J., Frimannslund, L., and Øien, N. I. (2007). Historical population assessment of Barents Sea harp seals (*Pagophilus groenlandicus*). *ICES J. Mari. Sci.* 64, 1356–1365. doi: 10.1093/icesjms/fsm118

Solvang, H. K., Yanagihara, H., Øien, N., and Haug, T. (2017). Temporal and geographical variation in body condition of common minke whales (*Balaenoptera acutorostrata acutorostrata*) in the Northeast Atlantic. *Polar Biol.* 40, 667–683. doi: 10.1007/s00300-016-1992-0

Southwell, C., Bengston, J., Bester, M., Blix, A. S., Bornemann, H., Boveng, P., et al. (2012). A review of data on abundance, trends in abundance, habitat use and diet of ice-breeding seals in the southern ocean. *CCAMLR Sci.* 19, 49–74.

Spielhagen, R. F., Werner, K., Sørensen, S. A., Zamelczyk, K., Kandiano, E., Budeus, G., et al. (2011). Enhanced modern heat transfer to the Arctic by warm Atlantic water. *Science* 331, 450–453. doi: 10.1126/science.1197397

Stenson, G. B., Buren, A. D., and Koen-Alonso, M. (2016). The impact of changing climate and abundance on reproduction in an ice-dependent species, the Northwest Atlantic harp seal. *Pagophilus groenlandicus*. *ICES J. Mar. Sci.* 73, 250–262.

Stenson, G. B., and Hammill, M. O. (2014). Can ice breeding seals adapt to habitat loss in a time of climate change? *ICES J. Mar. Sci.* 71, 1977–1986. doi: 10.1093/icesjms/fsu074

Stenson, G. B., Hammill, M. O., Kingsley, M. C. S., Sjare, B., Warren, W. G., and Myers, R. A. (2002). Is there evidence of increased pup production in northwest Atlantic harp seals. *Pagophilus groenlandicus*? ICES J. Mar. Sci. 59, 81–92. doi: 10.1006/jmsc.2001.1129

Stenson, G. B., Hammill, M. O., Lawson, J. W., and Gosselin, J.-F. (2014). Estimating pup production of Northwest Atlantic harp seals, *Pagophilus groenlandicus*, in 2012. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2014/057. doi: 10.1006/jmsc.2001.1129

Stenson, G. B., Rivest, L.-P., Hammill, M. O., Gosselin, J.-F., and Sjare, B. (2003). Estimating pup production of harp seals, *Pagophilus groenlandicus*, in the northwest Atlantic. *Mar. Mammal. Sci.* 19, 141–160. doi: 10.1111/j.1748-7692.2003.tb01098.x

Stenson, G. B. (2012). Estimating consumption of prey by harp seals, *Pagophilus groenlandicus,* in NAFO divisions 2J3KL. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2012/156, 26. doi: 10.1111/j.1748-7692.2003.tb01098.x

Stenson, G. B., and Sjare, B. (1997). "Seasonal distribution of harp seals, (*Phoca groenlandica*)," in *the Northwest Atlantic*, 23. ICES C. M. 1997/CC:10, 23.

Stenson, G. B., and Upward, P. (2020). Updated estimates of harp seal bycatch and total removals in the Northwest Atlantic. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2020/014, 19.

Stenson, G. B., Buren, A. D., and Sheppard, G. L. (2020a). Updated estimates of reproductive rates in Northwest Atlantic harp seals and the influence of body condition. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2020/057, 21.

Stenson, G. B., Gosselin, J.-F., Lawson, J. W., Buren, A., Goulet, P., Lang, S. L. C., et al. (2020b). Estimating pup production of Northwest Atlantic Harp Seals, *Pagophilus groenlandicus*. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2020/056, 34.

Tucker, S., Bowen, W. D., Iverson, S. J., Blanchard, W., and Stenson, G. B. (2009). Sources of variation in diets of harp and hooded seals estimated from Quantitative Fatty Acid Signature Analysis (QFASA). *Mar. Ecol. Prog. Ser.* 384, 287–302. doi: 10.3354/meps08000

Vinje, T. (2001). Anomalies and trends of sea ice extent and atmospheric circulation in the Nordic Seas during the period 1864-1998. *J. Clim.* 14, 255–267.

Walsh, J. E. (2008). Climate of the Arctic marine environment. *Ecol. Appl.* 18, S3–S22.

Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M. L., Hop, H., et al. (2006). Food web and carbon flux in the Barents Sea. *Progr. Oceanogr.* 71, 232–287. doi: 10.1016/j.pocean.2006.10.003

Wilkinson, J. P., and Wadhams, P. (2005). A method of detecting change in the ice conditions of the central Greenland Sea by the whelping locations of harp seals. *J. Clim.* 18, 1216–1226. doi: 10.1175/jcli3325.1

Yablokov, A. V., and Sergeant, D. E. (1963). Cranial variation in the harp seal *Pagophilus groenlandicus* Erxleben, 1777). *Zool. Zh. Ukr.* 42, 1857–1865.

Yakovenko, M. Y. (1963). Bazvitie promysla i problema chislennosti Belomorskogo lysuna (The history of fishery development and assessment of the White Sea harp seal number). *Trudy PINRO* 15, 199–214.

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 11 September 2020
doi: 10.3389/fmars.2020.00641

Time-Dynamic Food Web Modeling to Explore Environmental Drivers of Ecosystem Change on the Kerguelen Plateau

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Specialty section:
This article was submitted to
Marine Fisheries, Aquaculture and
Living Resources,
a section of the journal
Frontiers in Marine Science

Received: 07 May 2020
Accepted: 13 July 2020
Published: 11 September 2020

Citation:
Subramaniam RC,
Melbourne-Thomas J, Corney SP,
Alexander K, Péron C, Ziegler P and
Swadling KM (2020) Time-Dynamic
Food Web Modeling to Explore
Environmental Drivers of Ecosystem
Change on the Kerguelen Plateau.
Front. Mar. Sci. 7:641.
doi: 10.3389/fmars.2020.00641

Understanding the impacts of climate and fishing on marine systems is important for ecosystem-based management in the Southern Ocean, but can be difficult to evaluate due to patchy data in space and time. We developed the first time-dynamic food web model for the Kerguelen Plateau using Ecopath with Ecosim to explore likely drivers of change in this relatively data-poor region. The Kerguelen Plateau is located at the centre of intersecting frontal systems and is inhabited by one of the largest populations of the commercially important Patagonian toothfish. We used this model to evaluate the environmental and human drivers of food web dynamics in the region by calibrating it with French and Australian fisheries data from 1997–2018 and biomass data for the period 1986–2018. Fishing was not identified as a driver of food web dynamics within this model, which could indicate that current management strategies are sustainable. A correlation analysis with environmental parameters likely to drive food web dynamics (sea surface temperature, zonal wind, Southern Annular Mode and chlorophyll *a* concentration) highlighted cool sea surface temperature, higher zonal wind speeds and negative phases of the Southern Annular Mode as important drivers of change, particularly during the summer. As the Southern Ocean is predicted to warm and winds are expected to intensify under future climate change, our study illustrates the importance of considering environmental change in ecosystem management.

Keywords: Ecosim, environmental drivers, ecosystem change, Kerguelen Plateau, Patagonian toothfish fishery

1. INTRODUCTION

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) uses an ecosystem-based approach to maintaining sustainability, therefore it is important to understand the environmental drivers of the food web (Constable et al., 2014). Food webs in the Southern Ocean are coupled to the environment at a multitude of timescales. Predator foraging for example, can occur on timescales of minutes to hours while environmental processes such as eddy dynamics can happen at monthly to yearly scales (Fulton et al., 2019). Food web dynamics themselves also vary;

energy gained through phytoplankton blooms can be tracked via peaks in zooplankton biomass and seen months or years later in mid-trophic levels (e.g., fish) and Southern Ocean predators (Bannister et al., 2015; Goedegebuure et al., 2017).

The Kerguelen Plateau, located in the sub-Antarctic Indian Ocean (**Figure 1**), intersects with the frontal systems of the Antarctic Circumpolar Current (ACC) (Park et al., 2014). Driven by strong westerly winds, the ACC brings water of varying temperatures (0.5–3°C) to the Kerguelen Plateau (Park et al., 2014; Mintenbeck, 2017). Upwelling leads to annual phytoplankton blooms that support breeding and foraging predators (Thiers et al., 2017) and the largest fishery for Patagonian toothfish (Brooks et al., 2016).

The plateau is divided into two regions: the northern region, denoted by the hatched area in **Figure 1** is a French Exclusive Economic zone (EEZ) while the southern region, denoted by the striped area in **Figure 1**, is an EEZ for Australia. Direct fishing for Patagonian toothfish (*Dissostichus eleginoides*) in the French EEZ began as a trawl fishery in 1985 and longline fishing began in 1991. The fishery has been longline only since 2001 and is active all year except late summer (February-March) to avoid seabird mortality (Duhamel et al., 2011). Australia also operates a commercial fishery from May to November in the southern region. Fishing for Patagonian toothfish in the Australian EEZ began as a trawl fishery in 1997, longline fishing began in 2003 and gradually replaced trawling. A trawl fishery for mackerel icefish (*Champsocephalus gunnari*) was initiated at the same time as the toothfish and continues today (from December–November). Both EEZs are located within the CCAMLR area and while Australian catch limits are agreed through consensus in CCAMLR (Mintenbeck, 2017), French catch limits are decided unilaterally.

There is limited understanding regarding how changes to the environment may impact the food web and commercial fishing (Rayfuse, 2018; Meredith et al., 2019). Sea surface temperature (SST) can affect the growth rate, population structure, prey availability, and breeding performance of predators in this region (e.g., Guinet et al., 1998; Lescroël and Bost, 2006; Pardo et al., 2017; Cristofari et al., 2018). Other observations reveal that strong westerly winds have improved foraging performance and breeding success of albatrosses in regions adjacent to the Kerguelen Plateau (Weimerskirch et al., 2012). SST and wind on the Kerguelen Plateau have been linked to large-scale climate processes such as the Southern Annular Mode (SAM) (e.g., Lovenduski and Gruber, 2005). The SAM index is an important climate driver in the Southern Ocean and is dictated by the position of strong westerly winds (Bost et al., 2015). However, the SAM has not yet been related to food web dynamics. Positive SAM phases indicate a contraction of the winds poleward and negative phases indicate an expansion of the wind belt toward the equator (Rogers et al., 2020). This strong band of wind affects SST and oceanographic processes on the Kerguelen Plateau via upwelling or downwelling (Su et al., 2020), influencing food web interactions.

Patagonian toothfish are a slow growing, long-lived species, which makes them vulnerable to over-fishing. Recruitment is influenced by the environment (such as SST) making them susceptible to future climate change (Mintenbeck, 2017). Correlating food web dynamics with climate requires consistent observations, which is difficult on the Kerguelen Plateau due to its remote location and harsh environmental conditions. Food web models are a useful medium for exploring potential climatic impacts on ecosystems and for informing ecosystem-based management practices (Fulton et al., 2019).

Ecopath with Ecosim (EwE, Christensen and Walters, 2004) is a useful tool to explore the combined environmental and human drivers of food web dynamics that are important for ecosystem-based management. EwE is suited to data-limited regions such as the Kerguelen Plateau as it estimates values where there are gaps in time-series data and uses food web interactions to generate trends for other functional groups where data are absent. Furthermore, this method can identify sensitive trophic interactions and approximates an environmental trend that can be assessed for correlation with climate trends.

In this study, we use EwE to calibrate the Ecopath model presented in Subramaniam et al. (2020) with time-series data to investigate environmental and human impacts on the Kerguelen Plateau food web.

2. METHODS

2.1. Ecosim

EwE is a commonly-used software for developing food web models. The Ecopath module of EwE provides a snapshot of the food web through two master equations that balance the energy input and output of the food web (see Subramaniam et al., 2020). The balanced Ecopath model can then be calibrated to time-series data in Ecosim.

Biomass dynamics in Ecosim are described through a series of coupled simultaneous equations:

$$\frac{\delta B_i}{\delta t} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i) * B_i \qquad (1)$$

where $\frac{\delta B_i}{\delta t}$ represents the growth rate of group i during the time period t, g_i is net growth efficiency (production/consumption), F_i is fishing mortality rate, M_i is other mortality rate, e_i is emigration rate, I_i is immigration rate and B_i is biomass. The consumption rates Q_{ij} and Q_{ji} are calculated based on a simple "foraging arena" model while biomasses (B_i) are split into components that are vulnerable and invulnerable to predation.

The performance of the model is assessed by calculating the weighted sum of squares (SS) between the log observed data and model output (Christensen et al., 2008).

2.2. Ecosim Input and Calibration

We used the balanced Ecopath model described in Subramaniam et al. (2020) as the baseline Ecosim model. The model is comprised of 28 functional groups, organized based on similar diets and life cycles. A visual representation of this model illustrates the structure of the food web and associated trophic levels (**Figure 2**) and balanced model parameters are provided in **Tables A1, A2**. As the Kerguelen Plateau is a data-poor system, Subramaniam et al. (2020) provided an analysis of food web

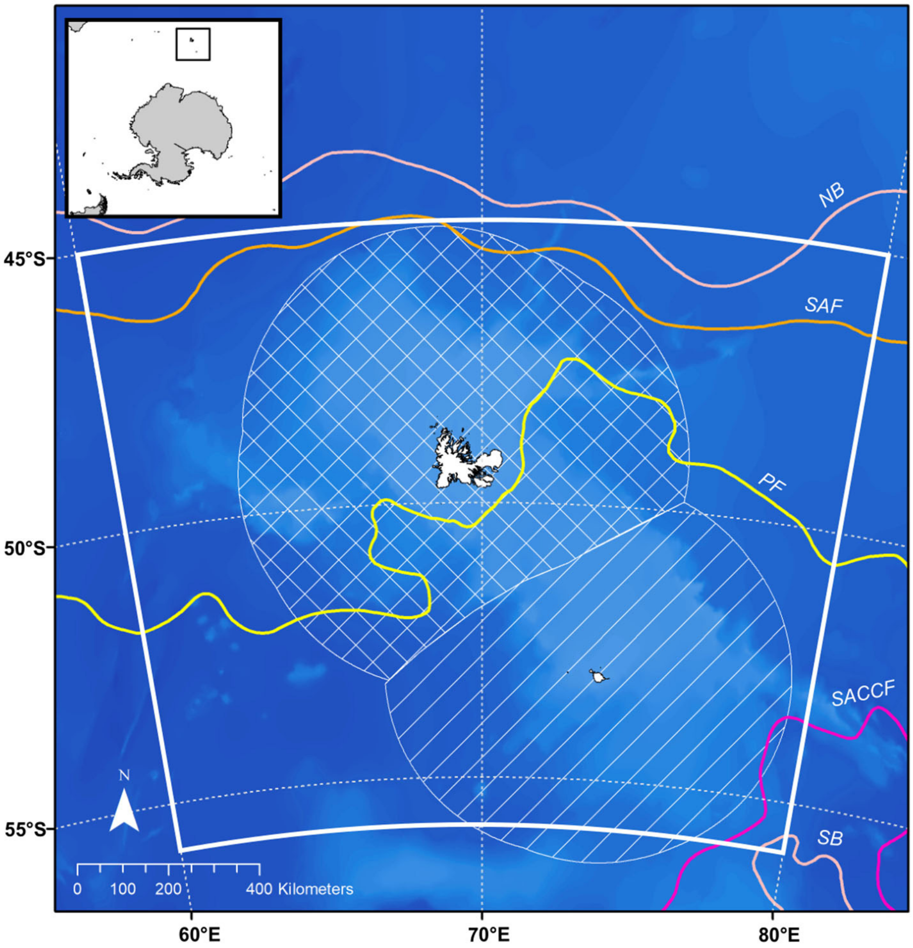

FIGURE 1 | Map of the Kerguelen Plateau, model domain (60°–80°E, 45°–56°S) is indicated by the white box, the hatched area indicates the French EEZ, striped area indicates the Australian EEZ. Front positions and boundaries of the Antarctic Circumpolar Current (ACC) as described in Park et al. (2014), bathymetry data are from https://www.gebco.net. NB, northern boundary of the ACC; SAF, subantarctic front; PF, polar front; SACCF, southern ACC front; SB, southern boundary of the ACC.

dynamics averaged over a period of 10 years, but also used data dating back to the late 1980s for some species. Therefore, this model can be seen as a representation of the mean state of the ecosystem from the late 1980s to 2018. A similar approach has been used for Ecosim models in other regions of the Southern Ocean (e.g., Dahood et al., 2019).

Trawl surveys on the Kerguelen Plateau have shown large fluctuations in the biomass of some fish species over this time period (e.g., *Notothenia rossii*, Duhamel et al., 2019). However, it is unclear if these fluctuations have affected food web dynamics. Other observational studies in this region suggest no major directional change over the time period considered in this model (e.g., Authier et al., 2011; Weimerskirch et al., 2018). Based on this information, the aims of our study were to investigate patterns of variability between the environment and the food web.

We used time-series data that were available and of sufficient length to calibrate the model. We used population trends for southern right whales (Bannister et al., 2015), southern elephant seals (Authier et al., 2011), black-browed albatrosses (Weimerskirch et al., 2018), and Patagonian toothfish and mackerel icefish fisheries data to parameterize the model. A full description of these data is presented in **Table A3**.

In the model, juvenile and adult Patagonian toothfish were partitioned as having a length less than or greater than 75 cm based on previous studies (Pruvost et al., 2005; Collins et al., 2007). Although juveniles may actually mature later in life on the Kerguelen Plateau (Yates et al., 2018), we have chosen to remain consistent with the commonly-used size separation for juveniles. Length-frequency analysis in fishery reports (CCAMLR, 2018a,b) and minimum legal catch limits (60 cm) indicate that toothfish under 75 cm are caught during the fishing season but it is unclear how much of the catch is less than 75 cm. Consultation with fisheries scientists was used to inform an estimated allocation of catch to juveniles.

Trawl fishing for Patagonian toothfish catches mostly immature fish while longline fishing catches mostly mature fish. To account for this difference in selection, time-series of nominal

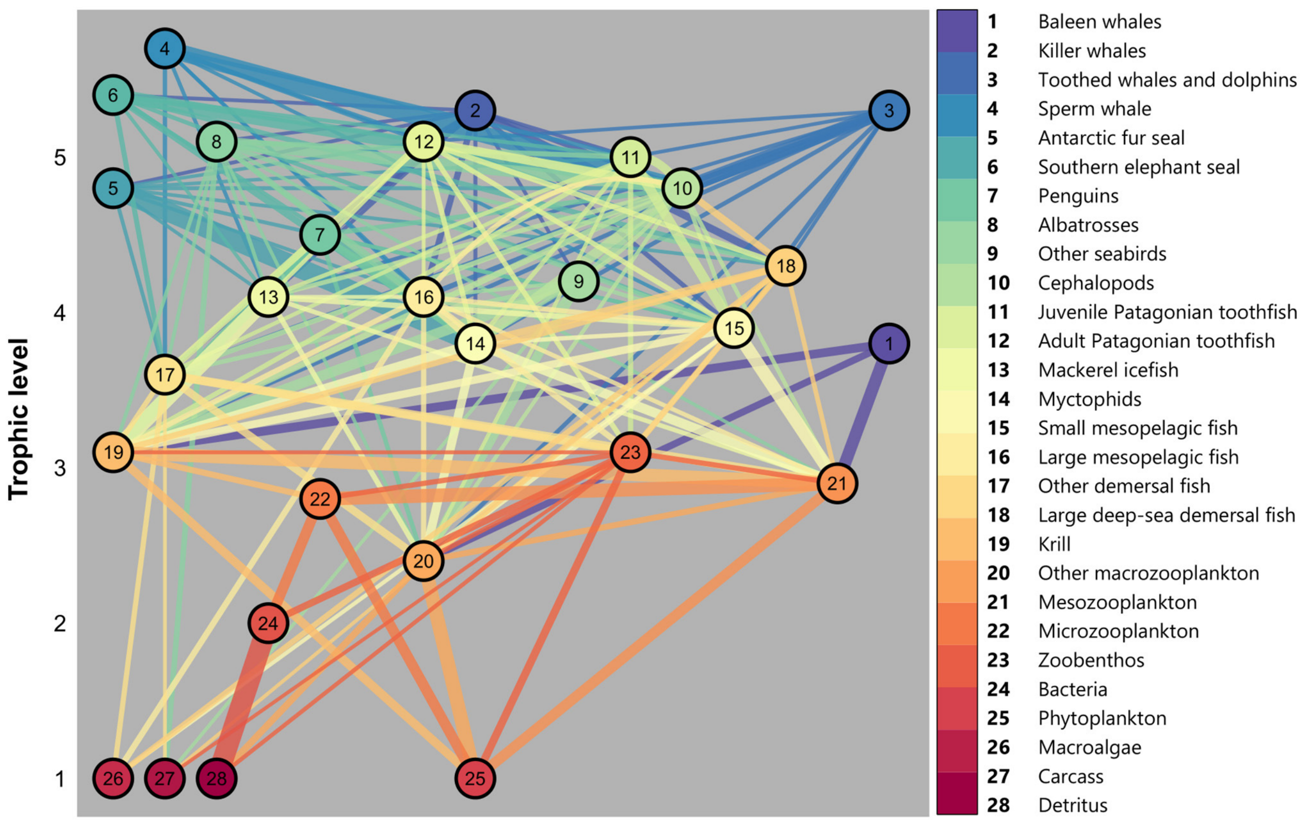

FIGURE 2 | Energy flow through each trophic level on the Kerguelen Plateau. Node number represents functional groups listed on the right, linkages between groups represent diet of each group (colored from predator to prey) and width of linkage indicates proportion of diet (see Subramaniam et al., 2020 for details).

catch per unit effort (CPUE, kg per hook) and total catch for each season was allocated 28% to juveniles and the remainder to adults for longlines and trawl CPUE and catch was allocated to juveniles (Philippe Ziegler, Australian Antarctic Division, pers. comm). Fishing mortality was used to drive fishing activity in Ecosim using model estimated biomass for Patagonian toothfish (**Table A3**), this was calculated as:

$$\text{Fishing mortality} = \frac{\text{Catch}}{\text{Biomass}}$$

Calibration of the model with time-series data was performed using the step-wise fitting procedure described in the EwE best practices guideline (Heymans et al., 2016). Previously, step-wise fitting was done manually however, an automated plug-in of this procedure was developed and recently implemented into the EwE software (Scott et al., 2016). We opted to use the automated plug-in to calibrate the model. The step-wise fitting procedure adjusts vulnerabilities and a primary production anomaly (PP anomaly) for a set of scenarios (see **Figure 3**).

The vulnerability parameter describes interactions between predators and prey in the model. A value in the range 1–100 is attributed to each interaction to dictate how consumption is influenced by changes in predator and prey biomass. Values close to 1 indicate bottom-up control while values close to 100 indicate that top-down influences dominate (Christensen et al., 2008). The PP anomaly parameter represents (non-modeled) bottom-up control on the ecosystem (Scott et al., 2016), and typically represents some environmental influence on phytoplankton. For each version of the model there were a possible 172 trophic interactions that could be tuned to calibrate the model. We found that the maximum number of interactions that would elicit a noticeable change in the sum of squares was 30 interactions (or vulnerabilities). Therefore, we restricted our scenarios to a maximum of 30 vulnerabilities. Model fit using step-wise fitting is evaluated by calculating the Akaike information criterion (AIC) and penalizing for fitting too many parameters based on the number of time-series available resulting in a weighted AIC value (AICc) (Scott et al., 2016). We used a two-step approach to select the best-fitting model by first selecting the models that were statistically the best fit (had the lowest AICc values) then plotting and using a pattern oriented approach (Kramer-Schadt et al., 2007; Heymans et al., 2016).

Our data compilation resulted in biomass trends and fishing data for different periods of time. Biomass data were mostly available for the entire time period, however, fishing data were only available for shorter periods (**Table A3**). Additionally, due to the evolving preferences for different types of fishing gear when targeting Patagonian toothfish, there were three CPUE inputs that could be used as a proxy for toothfish biomass trends in the

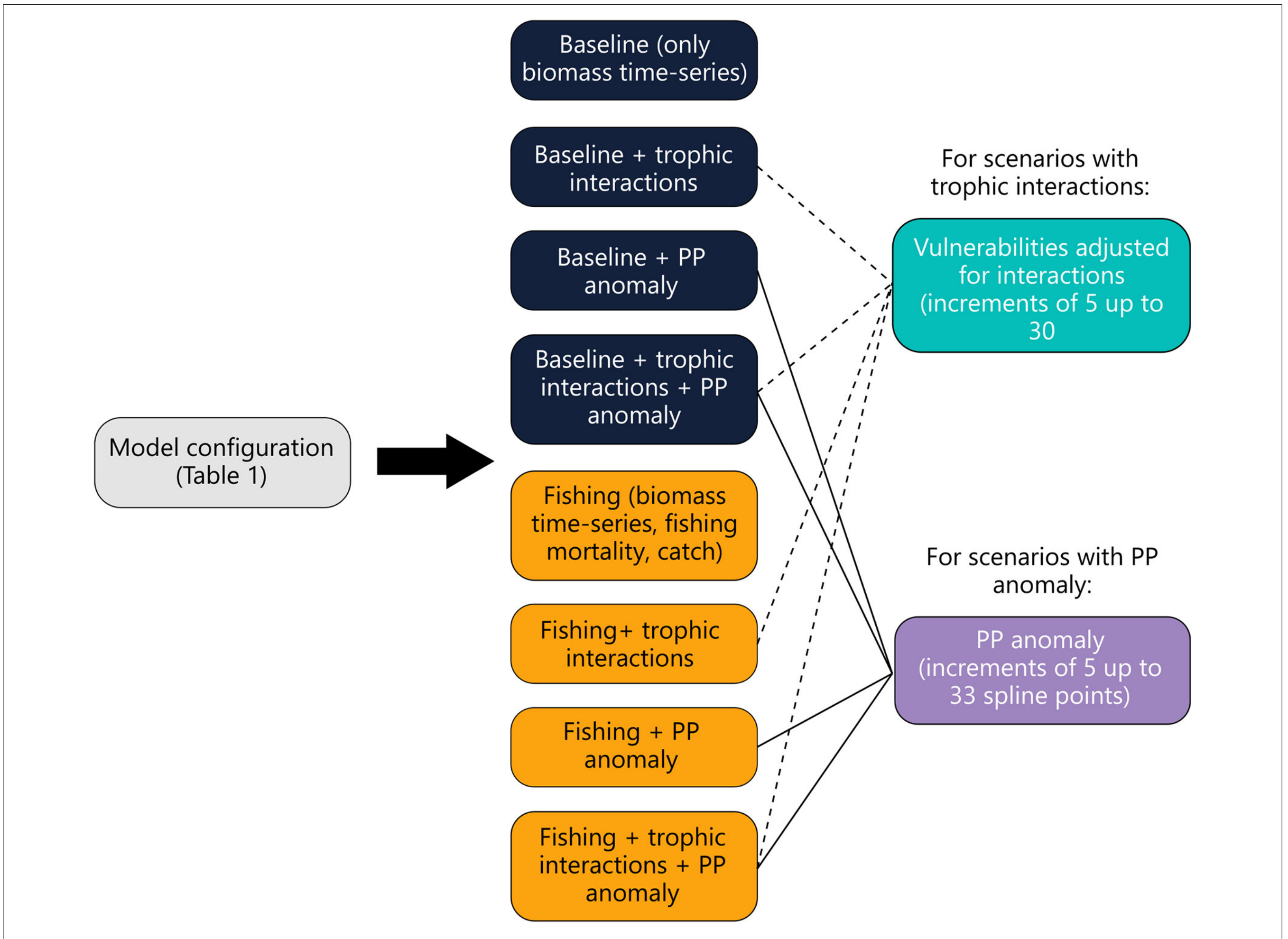

FIGURE 3 | Diagram showing how Ecosim was used to calibrate the model. Eight scenarios were run (dark blue and yellow) for each model configuration in **Table 1**. Baseline scenarios (dark blue) do not include fisheries data. For scenarios including trophic interactions (blue) and PP anomalies (purple), each scenario was run by increasing the number of vulnerabilities estimated for trophic interactions and PP anomaly spline points by 5 until the maximum was reached (5, 10, 15...etc).

model. To cover potential biases resulting from data gaps, the step-wise fitting procedure was performed using four different configurations of the model (shown in **Table 1**). All four model configurations were very similar, only differing in the length of time calibrated or CPUE and fisheries data input.

For scenarios where CPUE inputs were averaged across French and Australian EEZs, only the trawl CPUE was used to approximate the trend for juveniles and 72% of longline CPUE was used for the adults. Juvenile catch and fishing mortality were averaged over gears (trawl and 28% of the longline catch for the French and Australian EEZ) and adult longline catch (72% of the longline catch for the French and Australian EEZ) and fishing mortality were averaged for these scenarios (Models 2 and 4, **Table 1**).

For the best fitting model scenario, Monte Carlo simulations were run within EwE to test the sensitivity of the Ecosim model to the base Ecopath model input as an additional measure to validate our approach. The Monte Carlo routine randomly selects starting biomass values for functional groups based on the coefficient of variation (CV) and calculates a new sum of squares based on the new initial values. The default CV in Ecosim is ±10% however, we tested ±20% Patagonian toothfish biomass as the starting condition for our Ecosim model. We varied toothfish biomass as there is particular uncertainty about the biomass of this group in the late 1980s (Duhamel and Hautecoeur, 2009; Duhamel et al., 2019).

We correlated the PP anomaly trend from the best fitting model with chlorophyll *a*, wind, sea surface temperature (SST) and the Southern Annular Mode index (SAM) taken from satellite data (sources provided in **Table A4**). Estimated PP anomaly and biomass trends from the model were given as monthly averages. To match the model output, climate variables were also derived from satellite data as monthly averages using the white bounding box in **Figure 1**. We examined correlations between the model output from the best-fitting scenario, both monthly and annual averages, and anomalies of remotely sensed data. Environmental variables were also correlated with each other to test the strength of each correlation.

TABLE 1 | Model configurations used to calibrate Ecosim.

Model configuration and description	
Model 1	Time period 2006-2018 where there was most data coverage and each of the three CPUE inputs were used to fit the model to juvenile and adult toothfish biomass. Fishing mortality and catch were included for each fishing gear for scenarios including fishing activity as a driver.
Model 2	Time period 2006-2018 where there was most data coverage and mean CPUE was used to fit the model juvenile and adult toothfish biomass (see methods). Mean fishing mortality and catch were used for scenarios including fishing activity as a driver.
Model 3	Time period 1986-2018 where each of the three CPUE inputs were used to fit the model to juvenile and adult toothfish biomass. Fishing mortality and catch were included for each fishing gear for scenarios including fishing activity as a driver.
Model 4	Time period 1986-2018 where an mean CPUE was used to fit the model juvenile and adult toothfish biomass (see methods). Mean fishing mortality and catch were used for scenarios including fishing activity as a driver.

Each model configuration was used in the calibration procedure described in ***Figure 3*** *and fishing gears used in the study are listed in* ***Table A3****.*

TABLE 2 | Vulnerabilities estimated in the best-fitting scenario for model 1 that were used in model 3.

	Cephalopods	Juvenile Patagonian toothfish
Cephalopods		1
Juvenile Patagonian toothfish	1	
Mackerel icefish		1
Krill		1
Zoobenthos		1

Seasonal anomalies were calculated for summer (December to May of the following year) and winter (June to November of the same year) by calculating the average over the time series then subtracting this value from the seasonal (summer or winter) average for each year. Seasonal anomalies were compared to the summer and winter average biomass for each group. For each set of anomalies (monthly, annual and seasonal), a moving average was calculated in R using the "forecast" package with a 5-step moving window (Hyndman and Khandakar, 2008).

A Spearman's rank correlation was used to test for significance between model output and climate anomalies. *P*-values were adjusted in R using the "p.test" function and the false discovery rate method (Jafari and Ansari-Pour, 2019). We tested environmental correlations against the PP anomaly trend, phytoplankton, juvenile and adult Patagonian toothfish, other macrozooplankton and krill biomass. Due to the size and value of the Patagonian toothfish fishery, and the large-scale removal of Patagonian toothfish by fisheries on both regions of the Kerguelen Plateau, we focus on evaluating climate impacts on Patagonian toothfish in this study.

Recruitment of Patagonian toothfish is variable from year to year and most likely indirectly related to SST (Mintenbeck, 2017; Yates et al., 2018). While there have been no observational studies examining recruitment variability on the Kerguelen Plateau, studies from other regions of the Southern Ocean suggest this could be important for predicting changes to toothfish populations (e.g., Laptikhovsky and Brickle, 2005). The Patagonian toothfish displays a long life cycle: adults spawn during austral winter (May-August), eggs incubate for 3 months and hatch in pelagic waters. Juveniles inhabit pelagic waters until 13–15 months of age where they start to settle in benthic habitats (< 500 m) (Péron et al., 2016). Adults are usually found at depths greater than 600 m (Mintenbeck, 2017). Due to this long life cycle, climate impacts on recruitment may be lagged.

Successful spawning during austral winter may only be observed in the juvenile population once they start to become benthopelagic at 1+ years old (Belchier and Collins, 2008). Belchier and Collins (2008) found a 2 year lag between summer SST and successful recruitment of juvenile Patagonian toothfish. Based on this finding we tested for lagged effects up to 2 years between toothfish groups and climate variables that did not show a significant correlation in the above analysis. We moved climate variables forward (equivalent to lagging toothfish biomass) by two, three and four seasons, corresponding to a 1, 1.5 and 2 year lag, respectively. We performed a correlation analysis between the moved climate variables and toothfish biomass trends.

3. RESULTS

Model configuration 3 demonstrated the best fit of the four model configurations under consideration (model 3, **Table 1**). This was unsurprising as model 3 covered the longer time period, allowing for more data points to fit to. This model covered the entire time period and incorporated all three CPUE inputs for Patagonian toothfish. The best-fitting scenarios from this model involved adjusting vulnerabilities and estimating PP anomalies. All model fits are presented in **Table A5**.

Model 3 was improved when trophic effects and PP anomalies were included in the model. The best-fitting scenario set vulnerabilities for 5 trophic interactions (**Table A6**) and 7 PP anomaly spline points (**Figure A2**). Importantly, the best-fitting model did not include fishing as a driver of food web dynamics. The model reproduced the general trends for toothfish groups, however, observed trends for baleen whales, southern elephant seals, albatrosses and mackerel icefish were not well-represented (**Figure A1**). Therefore, we sought alternative vulnerabilities for use in the model.

We chose to use alternative vulnerabilities from model 1, which had the most comprehensive data coverage. The best-fitting scenario for model 1 was achieved when only trophic effects were included (see **Table A5**). Similarly to model 3, the best fitting scenario for model 1 estimated vulnerabilities for 5 interactions. We replaced the vulnerabilities shown in **Table A6** with those in **Table 2** and ran the scenario again to calibrate the model.

The replacement vulnerabilities produced improved estimates for Patagonian toothfish groups and mackerel icefish compared to observations (**Figure 4**). We also compared both model fits

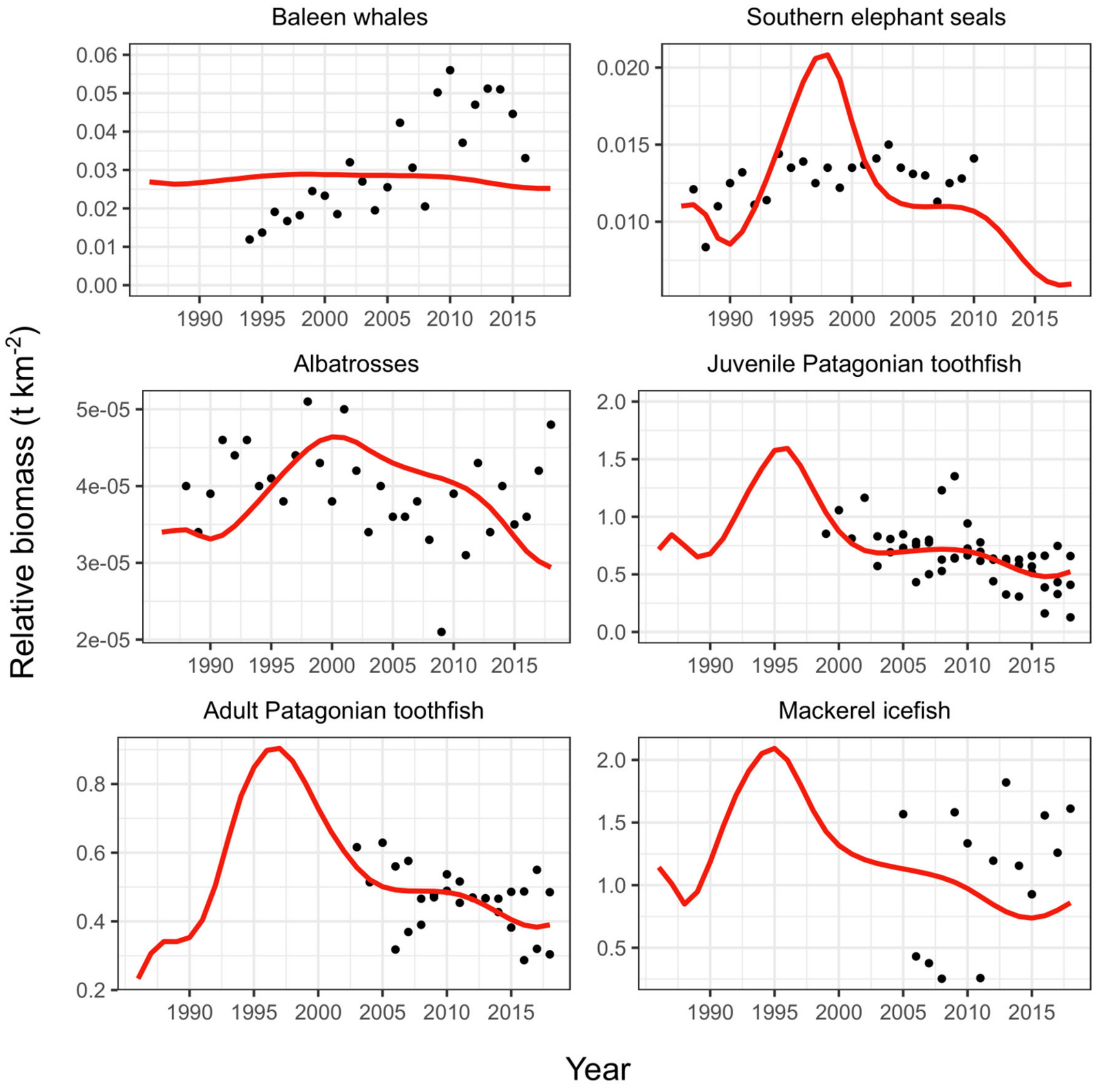

FIGURE 4 | Fit of model to observations with replaced vulnerabilities **(Table 2)**. Red line shows model fit, black points show observations. Toothfish observations are three CPUE inputs as described in **Table 1**.

to a study representing population trends for predators (killer whales, toothed whales and dolphins, sperm whales, other seabirds and Antarctic fur seals) using data collected by fishery-observers (Gasco et al., 2019). Our comparison showed that replacing the vulnerabilities provided a better representation of the observer data presented in Gasco et al. (2019) (see **Table A7** in Appendix).

Results from our sensitivity analysis indicated that while changing the initial conditions did result in increased or decreased biomass throughout the time series, this occurred in a consistent manner (i.e., more biomass at the start of the time series led to more biomass at the end of the time series). The pattern of biomass trends for both toothfish and other functional groups from this analysis show that our model was not sensitive to initial conditions (**Figure 5**).

3.1. Correlation With Environmental Variables

Correlations between environmental variables showed that SST significantly correlated with the SAM at the annual timescale and summer season while zonal wind only significantly correlated with the SAM during summer. SST and zonal were not significantly correlated with each other at any timescale (**Table 3**). These differing correlations support our investigation of individual variables with modeled biomass trends.

SST, zonal wind and SAM were correlated with zooplankton and toothfish biomass trends estimated by the best-fitting model. Correlations between estimated biomass and monthly anomalies for climate variables were lower than those with annual and seasonal anomalies. Annual and seasonal anomalies are more likely to be drivers of biological response

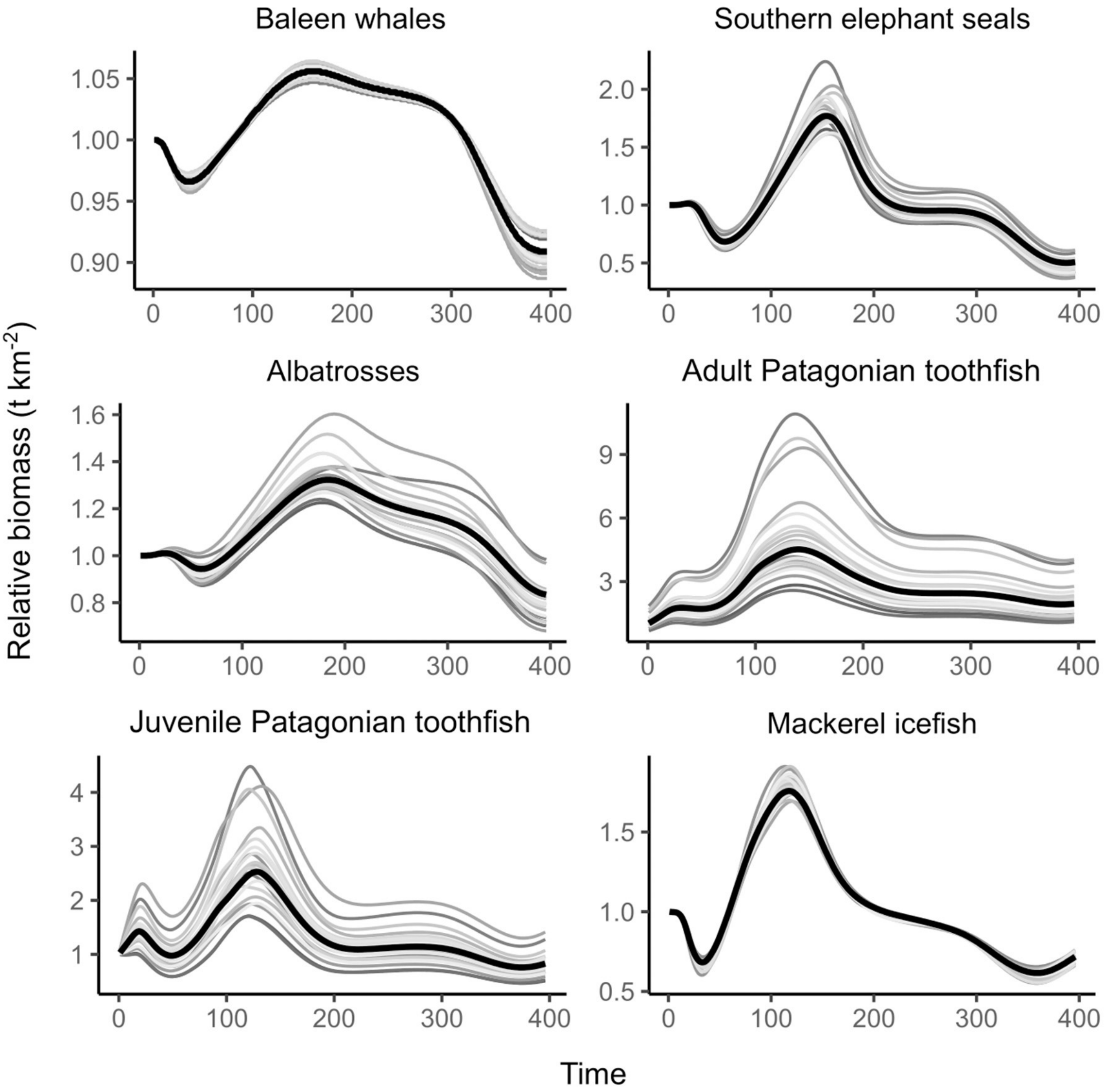

FIGURE 5 | Results from the Monte Carlo simulations for the best-fitting model. Gray lines represent the biomass trend for each of the 20 simulations and the black lines overlay the biomass trend from the best-fitting model. Time is provided in months where January 1986 = 1.

over time than monthly anomalies, therefore we focus on these results for the remainder of this study. Results from correlations with monthly anomalies are presented in the Appendix (**Table A8**).

PP anomaly and zooplankton biomass trends correlated negatively with annual SST and SAM, and positively with annual zonal wind anomalies. Biomass increased during periods when SST was cooler than average (1990–1994 and 2005–2007, **Figure 6**) and declined during periods when SST was warmer than average (e.g., 1994–1999, **Figure 6**). SST did not appear to correlate with juvenile and adult Patagonian toothfish, however there may be a lagged effect (discussed below). Zonal wind correlated with all functional groups: estimated biomass trends increased during periods where surface wind speed was faster than average, and decreased during periods where surface wind speed was slower than average (**Figure 7**). PP anomaly and estimated biomass trends for phytoplankton, macrozooplankton, and krill increased during periods of negative SAM anomaly, indicating that westerly winds were expanding further north than average (**Figure 8**).

Summer SST correlated better with PP anomaly, phytoplankton, macrozooplankton and krill biomass trends (**Table 4**). Similar to annual SST, summer SST demonstrated a negative correlation with model variables. Biomass peaked during periods when summer SST was cooler than average and declined during periods when summer SST was warmer than

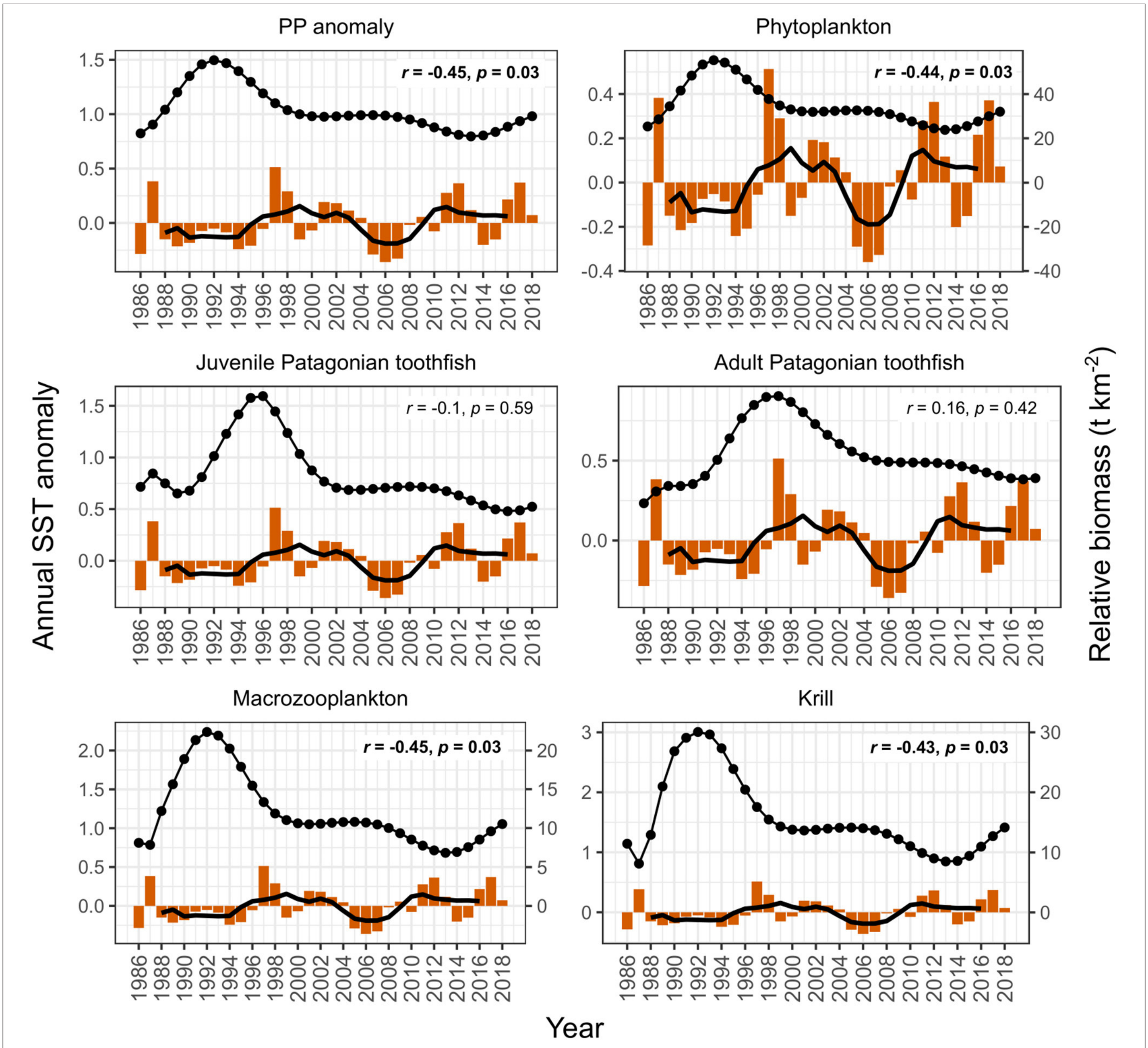

FIGURE 6 | Comparison of model output with annual sea surface temperature (SST) anomalies (orange bars). Black points are the estimated annual biomass values for each year of the model period and black line indicates moving average used to perform correlations (relative biomass in t km^{-2}, right axis for phytoplankton, macrozooplankton, and krill). Strength of correlations are shown by the *r* and *p* values in each plot, with significant correlations in bold.

average. Again, we found no correlation between summer SST and toothfish groups, which may be because of a lagged effect (discussed below). Estimated biomass trends were uncorrelated with winter SST (**Table 4**). Summer zonal wind correlated positively with biomass trends: biomass increased during periods when summer surface wind speed was faster than average and decreased during periods when summer surface wind was slower than average (**Table 4**). Winter wind positively correlated with only adult Patagonian toothfish (**Table 4**). Both summer and winter SAM exhibited a negative correlation with PP anomaly, phytoplankton, macrozooplankton and krill. In contrast, summer SAM correlated positively with adult Patagonian toothfish (**Table 4**).

We tested for lagged effects between juvenile Patagonian toothfish and summer SST, winter SST, winter zonal wind, summer SAM and winter SAM as they did not show a significant correlation in the above analysis. We also tested for lagged effects of adult Patagonian toothfish with summer SST, winter

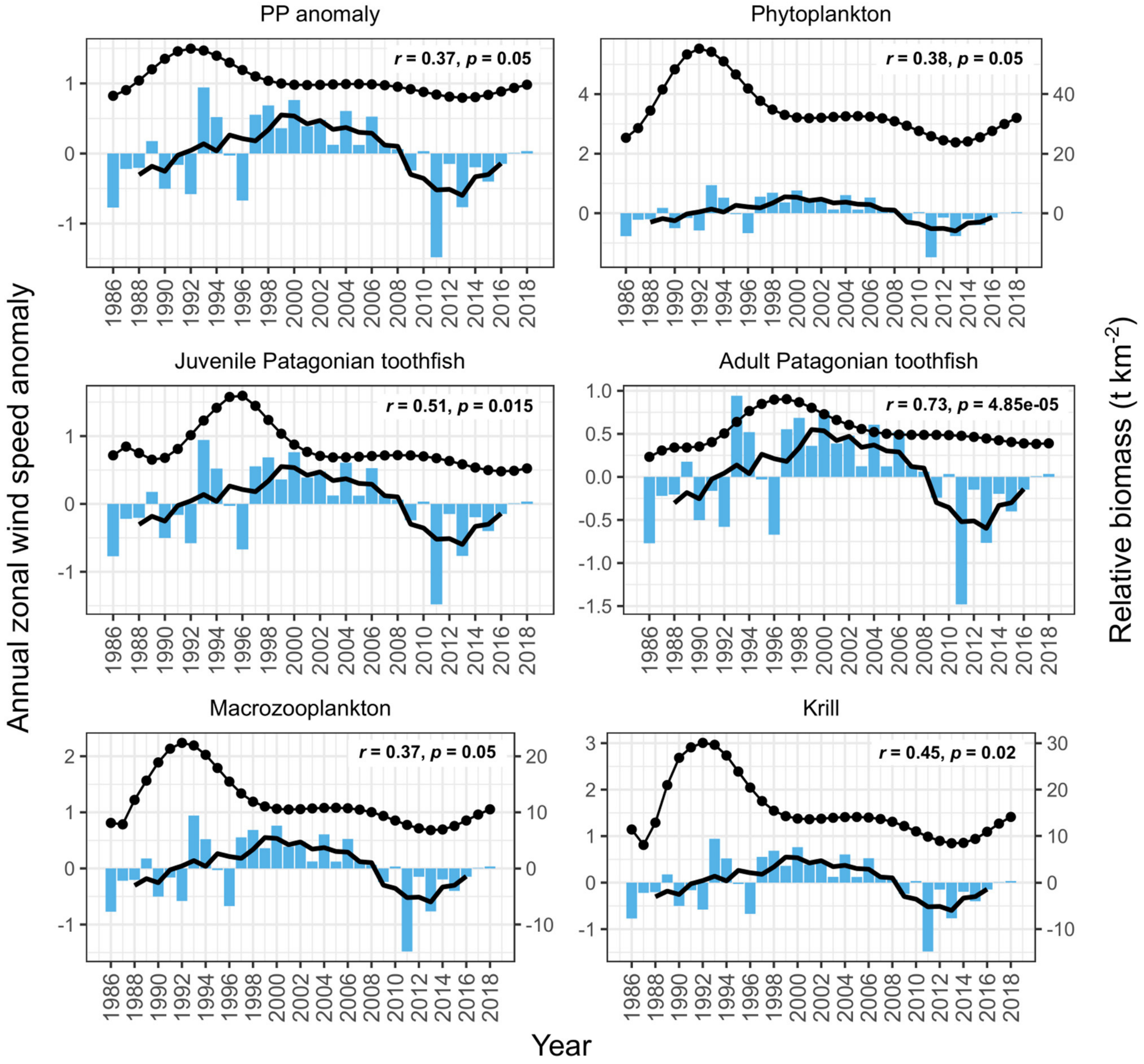

FIGURE 7 | Comparison of model output with annual zonal wind anomalies (blue bars). Black points are the estimated annual biomass values for each year of the model period and black line indicates moving average used to perform correlations (relative biomass in t km^{-2}, right axis for phytoplankton, macrozooplankton and krill). Strength of correlations are shown by the *r* and *p* values in each plot, with significant correlations in bold.

SST and winter SAM. We present only significant correlations in our results. Correlations appeared to be strongest at the three season and four season lag. Our results show a negative correlation between lagged juvenile Patagonian toothfish biomass and summer SST at all three seasonal lags, with the strongest correlation at the four season lag (**Figure 9**). Lagged juvenile biomass also correlated negatively with summer and winter SAM with strongest correlations at the three and four season lag. Lagged adult Patagonian toothfish biomass correlated negatively with summer SST at the four season lag and winter SAM at all three seasonal lags with the strongest at the three season lag (**Figure 9**).

4. DISCUSSION

4.1. Model Evaluation

Our analysis presents the first attempt at calibrating food web dynamics on the Kerguelen Plateau with trends in observed time-series. We acknowledge that this approach to model fitting is not standard practice in the EwE community. We used this

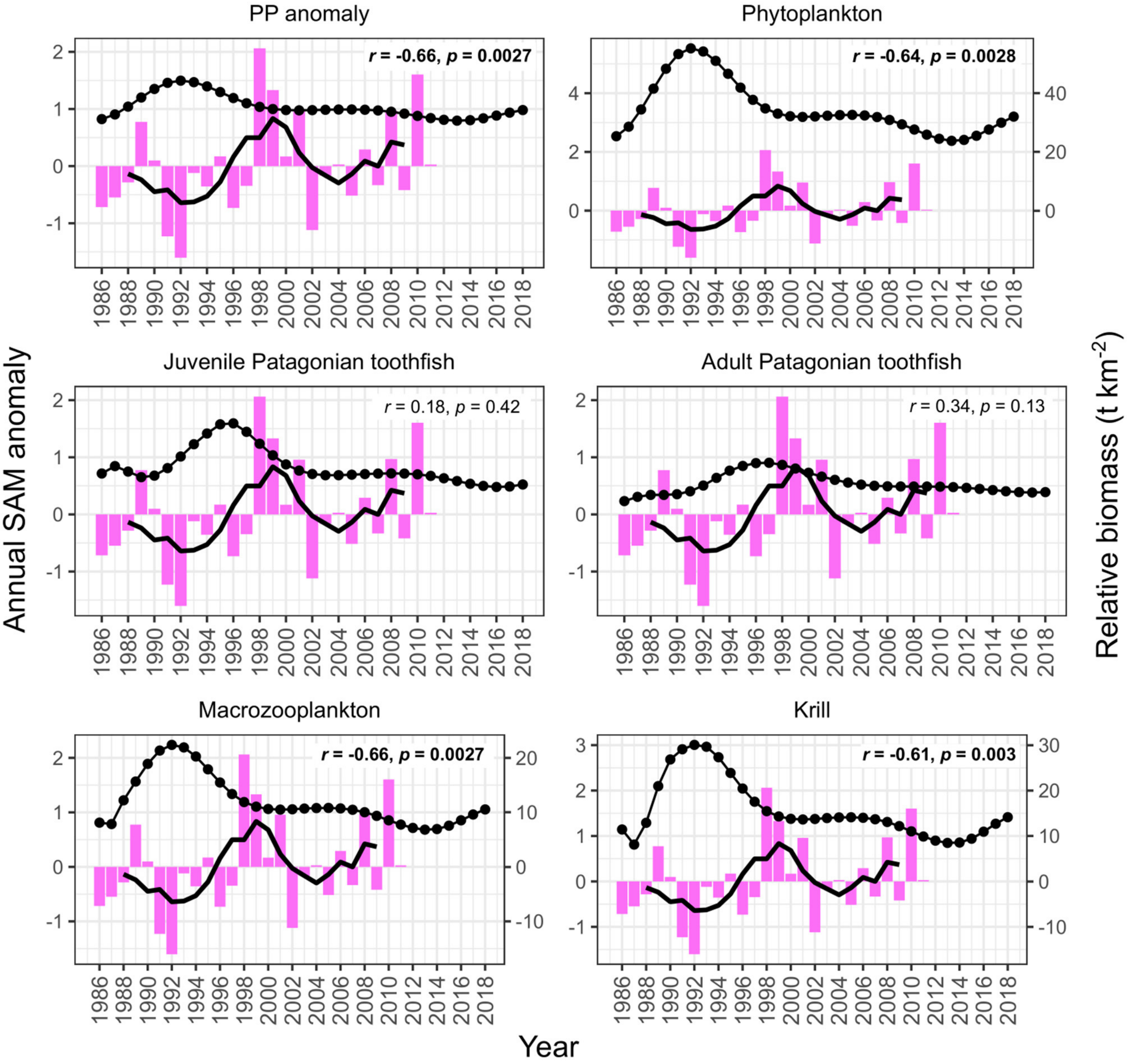

FIGURE 8 | Model output correlations to the Southern Annular Mode (SAM) (pink bars). Black points are the estimated annual biomass values for each year of the model period and black line indicates moving average used to perform correlations (relative biomass in t km^{-2}, right axis for phytoplankton, macrozooplankton, and krill). Strength of correlations are shown by the *r* and *p* values in each plot, with significant correlations in bold.

approach to cover biases in data availability and focus our interpretations on patterns of interannual variability instead of directional change. We implemented several models which reproduced the observed data with varying success. The best-fitting model reproduced observed biomass trends for juvenile Patagonian toothfish, adult Patagonian toothfish and mackerel icefish better than other model versions and reproduced observed trends for groups with no input data (see **Appendix**). The model also partially recreated trends for southern elephant seals and albatrosses although it could not recreate the trend for baleen whales.

Ecosim models are fitted to the data by tuning parameters (vulnerabilities and PP anomaly trends) to show which values could explain observed historical trends (Alexander et al., 2014). Consequently, the ability of the model to fit to observed data is improved with good quality data sets. In situations where data quality is poor, the model may struggle to converge on an accurate solution. The inability of the preferred model to completely represent observed trends for marine predators could be a result of data quality and the inability to incorporate all possible drivers of change. Data on population trends for baleen whales on the Kerguelen Plateau are lacking (Dréo et al., 2019).

The data used to represent baleen whales was taken from an aerial survey of Australian southern right whale population. Aerial surveys are known to have large biases therefore, not much confidence was placed in the data (Marsh and Sinclair, 1989). Additionally, this trend contributed very little to the overall fit of the model. Population trends of southern elephant seals may be related to their life history and may be too complex to capture in aggregated models (Goedegebuure et al., 2018). Southern elephant seals also forage outside of the Kerguelen Plateau (Delord et al., 2014). Declines in albatrosses have been linked to demersal longline fisheries, and particularly illegal, unregulated and unreported (IUU) fisheries by-catch (Michael et al., 2019), especially during the 1990s and early 2000s (Weimerskirch et al., 2018). However, estimates of seabird mortality due to IUU are unavailable. Climatic conditions outside of the Kerguelen Plateau during winter may further contribute to observed population trends for albatrosses as they winter away from the Kerguelen Plateau (Weimerskirch et al., 2018).

TABLE 3 | Correlation analysis between environmental anomalies (as moving averages).

Annual	**Wind**	**SAM**
SST	$r = -0.07$, $p = 0.88$	**$r = 0.52$, $p = 0.042$**
Wind		$r = 0.43$, $p = 0.1$
Summer	**Wind**	**SAM**
SST	$r = 0.05$, $p = 0.88$	**$r = 0.84$, $p = 8.6\text{e}{-06}$**
Wind		**$r = 0.72$, $p = 8.1\text{e}{-03}$**
Winter	**Wind**	**SAM**
SST	$r = -0.1$, $p = 0.88$	$r = -0.03$, $p = 0.89$
Wind		$r = 0.26$, $p = 0.43$

Bold text indicates significant correlations. P-values have been adjusted as described in methods.

Fishing was not identified as a driver of food web dynamics over this time period, indicating that in our model representation, fishing activity is currently sustainable. This is consistent with conclusions of sustainable fishing from a recent assessment of management of marine protected areas in the southern region of the Kerguelen Plateau (Brooks et al., 2019). In addition to fishing activity occurring much later into the time series, more than one gear has operated during this time. Therefore, it is possible that either the direct impacts of fishing are too subtle for the model to capture or the effects have not yet traveled through the food web. Moreover, we were unable to incorporate any fishing activity (trawl and longline) in the French EEZ prior to 2005, nor were we able to include IUU fishing activity due to data quality and/or data unavailability. Despite these limitations, the model was useful for evaluating large-scale environmental drivers of food web dynamics.

4.2. Environmental Drivers of Food Web Dynamics

Our results highlight environmental (or bottom-up control) as an important driver of food web dynamics on the Kerguelen Plateau. Peaks in phytoplankton and zooplankton biomass correlated with negative annual SST anomalies, increasing annual zonal wind speed and a negative SAM index. When seasonality was considered, phytoplankton and zooplankton biomass positively correlated with summers that exhibited cooler temperatures and higher wind speeds. Their biomasses generally correlated with negative SAM anomalies during summer and winter.

Cool surface waters combined with high wind speeds may enhance vertical mixing on the Kerguelen Plateau as strong winds can increase the depth of the mixed layer and bring cold, nutrient-rich water into the euphotic zone (Blain et al., 2007; Gille et al., 2014). This is not typical of negative SAM anomalies in the Southern Ocean (see discussion below). Observations

TABLE 4 | Model output correlations to seasonal environmental anomalies.

Environmental parameter	**PP anomaly**	**Phytoplankton**	**Juvenile Patagonian toothfish**
Summer SST	**$r = -0.55$, $p = 0.003$**	**$r = -0.55$, $p = 0.003$**	$r = -0.13$, $p = 0.48$
Summer wind	**$r = 0.38$, $p = 0.043$**	**$r = 0.41$, $p = 0.036$**	**$r = 0.54$, $p = 0.006$**
Summer SAM	**$r = -0.53$, $p = 0.024$**	**$r = -0.5$, $p = 0.026$**	$r = 0.32$, $p = 0.15$
Winter SST	$r = -0.3$, $p = 0.21$	$r = -0.3$, $p = 0.21$	$r = -0.08$, $p = 0.66$
Winter wind	$r = 0.36$, $p = 0.06$	$r = 0.36$, $p = 0.06$	$r = 0.42$, $p = 0.06$
Winter SAM	**$r = -0.54$, $p = 0.014$**	**$r = -0.54$, $p = 0.013$**	$r = -0.12$, $p = 0.6$
	Adult Patagonian toothfish	**Macrozooplankton**	**Krill**
Summer SST	$r = 0.22$, $p = 0.24$	**$r = -0.55$, $p = 0.003$**	**$r = -0.53$, $p = 0.004$**
Summer wind	**$r = 0.8$, $p = 6.12\text{E}{-07}$**	**$r = 0.37$, $p = 0.04$**	**$r = 0.45$, $p = 0.026$**
Summer SAM	**$r = 0.69$, $p = 0.002$**	**$r = -0.53$, $p = 0.024$**	**$r = -0.44$, $p = 0.047$**
Winter SST	$r = 0.25$, $p = 0.2$	$r = -0.3$, $p = 0.12$	$r = -0.3$, $p = 0.14$
Winter wind	**$r = 0.55$, $p = 0.001$**	$r = 0.36$, $p = 0.06$	$r = 0.39$, $p = 0.06$
Winter SAM	$r = -0.2$, $p = 0.37$	**$p = -0.56$, $p = 0.014$**	**$r = -0.58$, $p = 0.0138$**

Bold text indicates significant correlations.

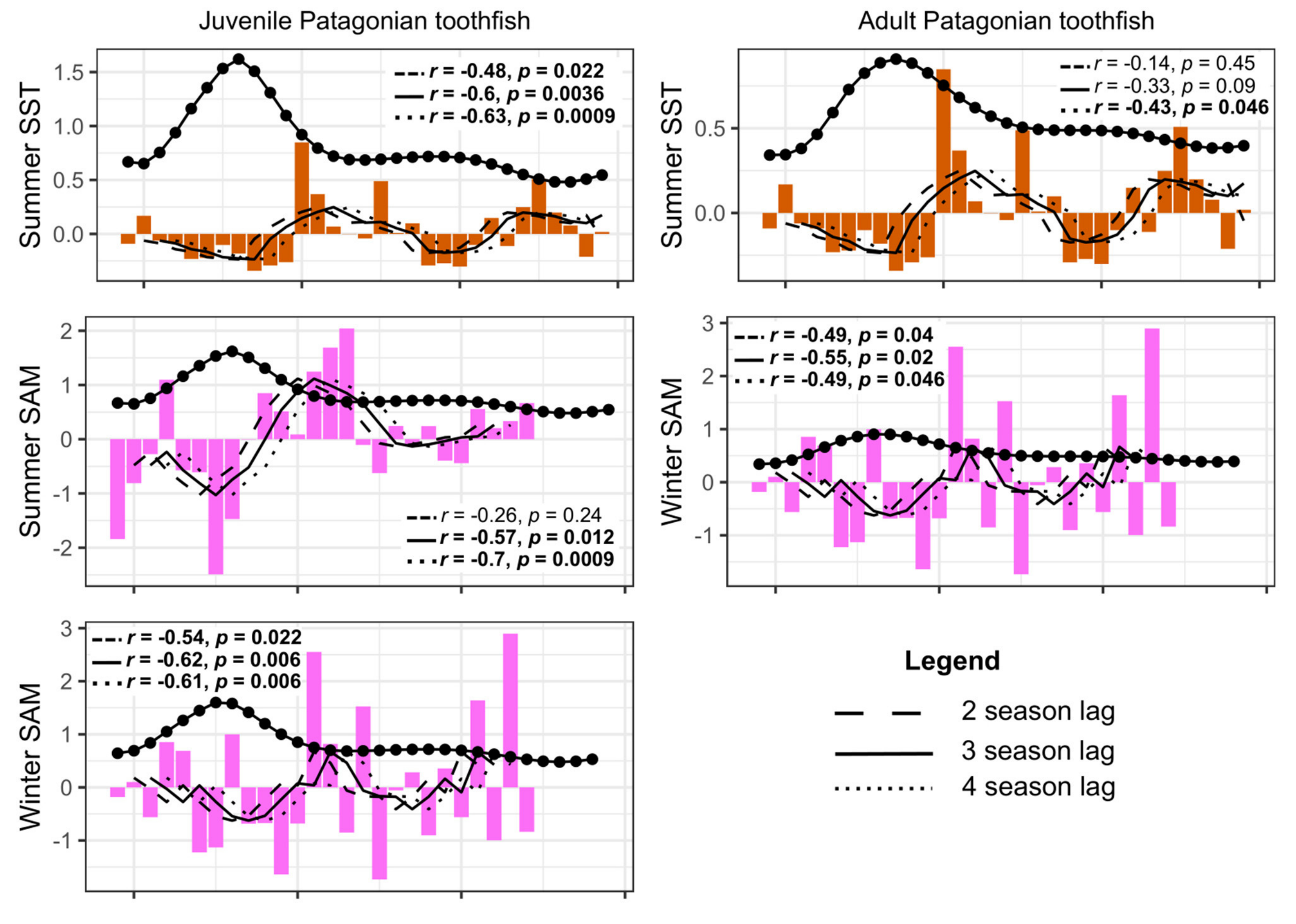

FIGURE 9 | Lagged toothfish biomass correlations to summer SST, summer SAM and winter SAM. Biomass was lagged at two (dashed line), three (solid line), and four time-steps (dotted line), equivalent to 1, 1.5, and 2 year lags, respectively. *R* and *p* values are shown in plots with associated lagged time-step, significant correlations are shown in bold.

indicate that during austral summer, cold and well-mixed waters are dominated by large phytoplankton on the Kerguelen Plateau (Quéguiner, 2013). The resulting zooplankton composition is dominated by large copepods, leading to a short, energy-efficient pathway for predators (Quéguiner, 2013; Venkataramana et al., 2019). Results from our comparison between model output and environmental variables are consistent with these observations.

Other factors such as negative wind stress curl can influence Ekman pumping and further enhance upwelling (Gille et al., 2014; Panassa et al., 2018). However, wind stress curl and Ekman pumping behave differently depending on location. South of 50°S, Ekman pumping drives upwelling while north of 50°S, Ekman pumping can induce downwelling (Gille et al., 2014). Nevertheless, wind stress curl on the Kerguelen Plateau has been useful for investigating marine heatwaves, an important climate extreme that may become more frequent in the future (Oliver et al., 2018). Wind stress curl and Ekman pumping during the winter following a marine heatwave led to downwelling, allowing warmer water to penetrate further down the water column and for the heatwave to persist longer (Su et al., 2020). Wind stress curl was not included in our study, but may be considered in future analyses with the model.

Local environmental conditions are closely linked to large-scale climate drivers (Jones et al., 2016). In our study, cold SST and periods of higher than average wind speed were related to negative SAM phases. This contrasts with other climate studies correlating negative SST anomalies with positive SAM phases across the Southern Ocean (Lovenduski and Gruber, 2005). As indicated above, the oceanography of the Kerguelen Plateau is complex and spatially heterogenous. Lovenduski and Gruber (2005) suggested that positive SAM phases in the southern Indian Ocean lead to cold upwelling in the Antarctic Zone (south of the Polar Front) and downwelling in the sub-Antarctic zone (40–50°S). Other spatial investigations of these trends found that ocean temperature on the Kerguelen Plateau was significantly correlated with the El Niño Southern Oscillation in the north and the SAM index over the whole plateau (Su et al., 2020). Future analyses may need to incorporate spatial variation in order to identify the areas where the food web will be most affected by these changes.

Food web dynamics significantly correlated with summer environmental trends and this is consistent with other studies showing strong summer environmental trends (Lovenduski and Gruber, 2005; Swart and Fyfe, 2012; Panassa et al., 2018; Fonseca and Martín-Torres, 2019; Meredith et al., 2019). Stronger correlations during summer between our model output and environmental data could be a result of the trends used to calibrate the model. Some of the observed annual trends were derived from animal counts during the breeding season in summer (e.g., Weimerskirch et al., 2018). However, other trends used in this study were not derived from counts during the breeding season (e.g., the CPUE data) and outputs from the preferred model reproduced annual trends from other studies (Gasco et al., 2019, see Appendix). Therefore, if there was any bias toward summer from the trend data, it may not be strong. Summer is an important season for the Kerguelen Plateau food web; seabirds and seals breed and forage during this time of year (Delord et al., 2014). A positive summer SAM trend has occurred over the last decade (Panassa et al., 2018; Meredith et al., 2019) and our model output suggests that continued positive SAM events could reduce the productivity of the food web, especially with regards to the Patagonian toothfish.

4.3. Environmental Impacts on the Patagonian Toothfish

Peaks in juvenile biomass correlated positively with annual and summer zonal wind. Peaks in adult biomass correlated positively with winter zonal wind anomalies and positively with summer SAM. Mixing induced by zonal wind could increase prey availability for toothfish, leading to increased biomass. The positive correlation seen with summer SAM could be indicative of downwelling on the Kerguelen Plateau, increasing prey availability for adult Patagonian toothfish located deeper into the water column. This result could be related to the catchability of toothfish rather than biomass itself as CPUE was used as a proxy for biomass. Increased prey availability can affect fish behavior and make toothfish more vulnerable to being caught (Arreguín-Sánchez, 1996; Parkes et al., 1996).

When we investigated time-lagged correlations, we found stronger correlations when we introduced a three and four season lag (equivalent to 1.5 and 2 year lag, respectively). Lagged juvenile biomass correlated negatively with summer SST and summer and winter SAM anomalies. Lagged adult biomass correlated negatively with summer SST and winter SAM at the four season lag.

Our model output produced the strongest correlation between juvenile toothfish and summer SST at the four season lag (2 year lag). This is consistent with results reported by Belchier and Collins (2008) who identified summer SST impacts on juveniles. Juvenile toothfish abundance (older than one year) in South Georgia was inversely correlated with summer SST experienced by adults prior to spawning. Belchier and Collins (2008) suggested that prey availability linked to large-scale climatic processes could be driving this variability. This is consistent with our study as lagged juvenile biomass correlated with the SAM, which has been identified as the underlying driver of prey biomass in our model.

There is no clear reason for the lagged correlations seen between adult toothfish biomass, summer SST and winter SAM. This could be related to catchability in the model. However, studies have reported toothfish showing strong year classes every 4–5 years (Laptikhovsky and Brickle, 2005) and perhaps further separation of toothfish into specific age classes may clarify these correlations. Untangling these relationships will help provide reliable estimates of life history traits that are required for effective management of the fishery (Yates et al., 2018).

5. CONCLUSION

Our study found that fishing was not a driver of food web dynamics and supports other recent findings of sustainable current fishing of Patagonian toothfish on the Kerguelen Plateau, with respect to effects on both toothfish biomass and food web dynamics. Our findings also highlight the importance of bottom-up processes driving the food web for the last 40 years. Cold and well-mixed waters lead to productive food web dynamics on the Kerguelen Plateau and these conditions appear to be linked to negative SAM phases, based on our model results. A continued positive SAM trend, as has been observed over the last decade, could lead to reduced prey availability and reduced predator populations. However, due to the spatial heterogeneity in oceanographic processes on the Kerguelen Plateau, more work is needed to clarify these effects. Our results also suggest that Patagonian toothfish recruitment is influenced by the environment, which is an important consideration for fisheries management, particularly if patterns of variability change under future climate change.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: All data that were not provided under a confidentiality agreement are provided in the article. The fisheries data (CPUE, catch and model estimated biomass) were provided under a confidentiality agreement and therefore cannot be made publicly available. The data are available upon request and the fishing bodies that provided the data are cited in the article. Requests to access these datasets should be directed to Clara Péron, clara.peron@mnhn.fr, Philippe Ziegler, Philippe.Ziegler@awe.gov.au.

AUTHOR CONTRIBUTIONS

RS was responsible for conceptualization, methodology, writing, editing, data visualization, and project administration. JM-T was responsible for conceptualization, methodology, reviewing, editing, and supervision. SC was responsible for conceptualization, reviewing, editing, and supervision. CP provided the data. PZ provided data and advice on methodology. KS was responsible for conceptualization, reviewing, editing, and supervision. All authors contributed to the article and approved the submitted version.

FUNDING

This study was supported by Australian Government's Cooperative Research Centres Programme through the Antarctic Climate and Ecosystems Cooperative Research Centre, the Institute for Marine and Antarctic Studies (IMAS) through the Australian Antarctic Science Programme (AAS 4347) and through the IMAS and University of Tasmania (UTAS) Tasmanian Graduate Research Scholarship.

ACKNOWLEDGMENTS

The authors would like to thank the Muséum national d'Histoire naturelle for providing the fisheries data for the French EEZ and the Australian Fisheries Management Association for providing fisheries data for the Australian EEZ. We would also like to thank the reviewers for their helpful comments on the development of this manuscript and Ben Raymond for his help with R. The following packages were used to generate the figures presented in this paper: ggplot2 (Wickham, 2016), RColorBrewer (Neuwirth, 2014), and gridExtra (Auguie, 2017). This study was supported by Australian Government's Cooperative Research Centres Programme through the Antarctic Climate and Ecosystems Cooperative Research Centre, the Institute for Marine and Antarctic Studies (IMAS) through the Australian Antarctic Science Programme (AAS 4347) and through the IMAS and University of Tasmania (UTAS) Tasmanian Graduate Research Scholarship.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00641/full#supplementary-material

REFERENCES

Alexander, K. A., Heymans, J. J., Magill, S., Tomczak, M. T., Holmes, S. J., and Wilding, T. A. (2014). Investigating the recent decline in gadoid stocks in the west of Scotland shelf ecosystem using a foodweb model. *ICES J. Mar. Sci.* 72, 436–449. doi: 10.1093/icesjms/fsu149

Arreguín-Sánchez, F. (1996). Catchability: a key parameter for fish stock assessment. *Rev. Fish Biol. Fish.* 6, 221–242. doi: 10.1007/BF00182344

Auguie, B. (2017). *gridExtra: Miscellaneous Functions for "Grid" Graphics*. R package version 2.3. Available online at: https://CRAN.R-project.org/package=gridExtra

Authier, M., Delord, K., and Guinet, C. (2011). Population trends of female elephant seals breeding on the Courbet Peninsula, îles kerguelen. *Polar Biol.* 34, 319–328. doi: 10.1007/s00300-010-0881-1

Bannister, J. L., Hammond, P. S., and Double, M. C. (2015). *Population Trend in Right Whales Off Southern Australia 1993-2015*. International Whaling Commission, SC/66b/BRG/09.

Belchier, M., and Collins, M. A. (2008). Recruitment and body size in relation to temperature in juvenile Patagonian toothfish (*Dissostichus eleginoides*) at south Georgia. *Mar. Biol.* 155, 493–503. doi: 10.1007/s00227-008-1047-3

Blain, S., Queguiner, B., Armand, L., Belviso, S., Bombled, B., Bopp, L., et al. (2007). Effect of natural iron fertilization on carbon sequestration in the southern ocean. *Nature* 446, 1070–1074. doi: 10.1038/nature05700

Bost, C. A., Cotté, C., Terray, P., Barbraud, C., Bon, C., Delord, K., et al. (2015). Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nat. Commun.* 6:8220. doi: 10.1038/ncomms9220

Brooks, C. M., Crowder, L. B., Curran, L. M., Dunbar, R. B., Ainley, D. G., Dodds, K. J., et al. (2016). Science-based management in decline in the southern ocean. *Science* 354:185. doi: 10.1126/science.aah4119

Brooks, C. M., Epstein, G., and Ban, N. C. (2019). Managing marine protected areas in remote areas: the case of the Subantarctic heard and Mcdonald islands. *Front. Mar. Sci.* 6:631. doi: 10.3389/fmars.2019.00631

CCAMLR (2018a). *Fishery Report 2018: Dissotichus eleginoides Kerguelen islands, French EEZ (division 58.5.1)*. Report, Commission for the Conservation of Antarctic Marine Living Resources.

CCAMLR (2018b). *Fishery Report 2018: Dissotichus eleginoides Heard island, Australian EEZ (division 58.5.2)*. Report, Commission for the Conservation of Antarctic Marine Living Resources.

Christensen, V., and Walters, C. J. (2004). Ecopath with Ecosim: Methods, capabilities and limitations. *Ecol. Modell.* 172, 109–139. doi: 10.1016/j.ecolmodel.2003.09.003

Christensen, V., Walters, C. J., Pauly, D., and Forrest, R. (2008). *Ecopath with Ecosim Version 6 User Guide*. Lenfest Ocean Futures Project, 1–235.

Collins, M. A., Ross, K. A., Belchier, M., and Reid, K. (2007). Distribution and diet of juvenile Patagonian toothfish on the south Georgia and shag rocks shelves (southern ocean). *Mar. Biol.* 152, 135–147. doi: 10.1007/s00227-007-0667-3

Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes, D. K. A., et al. (2014). Climate change and southern ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Glob. Change Biol.* 20, 3004–3025. doi: 10.1111/gcb.12623

Cristofari, R., Liu, X., Bonadonna, F., Cherel, Y., Pistorius, P., Le Maho, Y., et al. (2018). Climate-driven range shifts of the king penguin in a fragmented ecosystem. *Nat. Clim. Change* 8, 245–251. doi: 10.1038/s41558-018-0084-2

Dahood, A., Watters, G. M., and de Mutsert, K. (2019). Using sea-ice to calibrate a dynamic trophic model for the western Antarctic peninsula. *PLoS ONE* 14:e0214814. doi: 10.1371/journal.pone.0214814

Delord, K., Barbraud, C., Bost, C., Cherel, Y., Guinet, C., and Weimerskirch, H. (2014). *Atlas of Top Predators From French Southern Territories in the Southern Indian Ocean*. CEBC-CNRS.

Dréo, R., Bouffaut, L., Leroy, E., Barruol, G., and Samaran, F. (2019). Baleen whale distribution and seasonal occurrence revealed by an ocean bottom seismometer network in the western Indian ocean. *Deep Sea Res. II Top. Stud. Oceanogr.* 161, 132–144. doi: 10.1016/j.dsr2.2018.04.005

Duhamel, G., and Hautecoeur, M. (2009). Biomass, abundance and distribution of fish in the Kerguelen islands EEZ (CCAMLR statistical division 58.5.1). *CCAMLR Sci.* 16, 1–32. Available online at: https://www.ccamlr.org/en/publications/science_journal/ccamlr-science-volume-16/ccamlr-science-volume-161-32

Duhamel, G., Péron, C., Sinègre, R., Chazeau, C., and Gasco, N. (2019). "Important readjustments in the biomass and distribution of groundfish species in the northern part of the Kerguelen plateau and skiff bank," in *The Kerguelen Plateau: Marine Ecosystem and Fisheries. Proceedings of the Second Symposium, Proceedings of the Second Symposium*, eds D. Welsford, J. Dell, and G. Duhamel (Hobart, TAS), 135–184.

Duhamel, G., Pruvost, P., Bertignac, M., Gasco, N., and Hautecoeur, M. (2011). "Major fishery events in Kerguelen islands: *Notothenia rossi, Champsocephalus gunnari, Dissostichus eleginoides*-current distribution and status of stocks," in *The Kerguelen Plateau: Marine Ecosystem and Fisheries*, eds G. Duhamel and D. C. Welsford (Hobart, TAS: Société française d'ichtyologie), 275–286.

Fonseca, R., and Martín-Torres, J. (2019). High-resolution dynamical downscaling of re-analysis data over the Kerguelen islands using the WRF model. *Theoret. Appl. Climatol.* 135, 1259–1277. doi: 10.1007/s00704-018-2438-0

Fulton, E. A., Blanchard, J. L., Melbourne-Thomas, J., Plagányi, E. E., and Tulloch, V. J. D. (2019). Where the ecological gaps remain, a modelers' perspective. *Front. Ecol. Evol.* 7:424. doi: 10.3389/fevo.2019.00424

Gasco, N., Tixier, P., Delord, K., Guinet, C., and Duhamel, G. (2019). "Scientific observation program around Kerguelen island, a ship-of-opportunity for bird and mammal data collection," in *The Kerguelen Plateau: Marine Ecosystem and Fisheries. Proceedings of the Second Symposium, Proceedings of the Second Symposium*, eds D. Welsford, J. Dell, and G. Duhamel (Hobart, TAS), 365–379.

Gille, S. T., Carranza, M. M., Cambra, R., and Morrow, R. (2014). Wind-induced upwelling in the Kerguelen plateau region. *Biogeosciences* 11, 6389–6400. doi: 10.5194/bg-11-6389-2014

Goedegebuure, M., Melbourne-Thomas, J., Corney, S. P., Hindell, M. A., and Constable, A. J. (2017). Beyond big fish: the case for more detailed representations of top predators in marine ecosystem models. *Ecol. Modell*. 359, 182–192. doi: 10.1016/j.ecolmodel.2017.04.004

Goedegebuure, M., Melbourne-Thomas, J., Corney, S. P., McMahon, C. R., and Hindell, M. A. (2018). Modelling southern elephant seals mirounga leonina using an individual-based model coupled with a dynamic energy budget. *PLoS ONE* 13:e0194950. doi: 10.1371/journal.pone.0194950

Guinet, C., Chastel, O., Koudil, M., Durbec Jean, P., and Jouventin, P. (1998). Effects of warm sea-surface temperature anomalies on the blue petrel at the Kerguelen islands. *Proc. R. Soc. Lond. Ser. B Biol. Sci*. 265, 1001–1006. doi: 10.1098/rspb.1998.0390

Heymans, J. J., Coll, M., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., and Christensen, V. (2016). Best practice in ecopath with ecosim food-web models for ecosystem-based management. *Ecol. Modell*. 331, 173–184. doi: 10.1016/j.ecolmodel.2015.12.007

Hyndman, R. J., and Khandakar, Y. (2008). Automatic time series forecasting: the forecast package for R. *J. Stat. Softw*. 26, 1–22. doi: 10.18637/jss.v027.i03

Jafari, M., and Ansari-Pour, N. (2019). Why, when and how to adjust your p values? *Cell J*. 20, 604–607. doi: 10.22074/cellj.2019.5992

Jones, J. M., Gille, S. T., Goosse, H., Abram, N. J., Canziani, P. O., Charman, D. J., et al. (2016). Assessing recent trends in high-latitude southern hemisphere surface climate. *Nat. Clim. Change* 6, 917–926. doi: 10.1038/nclimate3103

Kramer-Schadt, S., Revilla, E., Wiegand, T., and Grimm, V. (2007). Patterns for parameters in simulation models. *Ecol. Modell*. 204, 553–556. doi: 10.1016/j.ecolmodel.2007.01.018

Laptikhovsky, V., and Brickle, P. (2005). The Patagonian toothfish fishery in Falkland islands' waters. *Fish. Res*. 74, 11–23. doi: 10.1016/j.fishres.2005.04.006

Lescroël, A., and Bost, C.-A. (2006). Recent decrease in gentoo penguin populations at Iles Kerguelen. *Antarct. Sci*. 18, 171–174. doi: 10.1017/S0954102006000198

Lovenduski, N. S., and Gruber, N. (2005). Impact of the southern annular mode on southern ocean circulation and biology. *Geophys. Res. Lett*. 32:L11603. doi: 10.1029/2005GL022727

Marsh, H., and Sinclair, D. F. (1989). Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *J. Wildlife Manage*. 53, 1017–1024. doi: 10.2307/3809604

Meredith, M., Sommerkorn, M., Cassotta, S., Derksen, C., Ekaykin, A., Hollowed, A., et al. (2019). "Polar Regions," in *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*, eds H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, and N. M. Weyer (The Intergovernmental Panel on Climate Change), 203–320.

Michael, P., Wilcox, C., Barbraud, C., Delord, K., de Grissac, S., and Weimerskirch, H. (2019). "Future resilience scaled by surveillance: high sensitivity of albatross to regional illegal, unreported and unregulated fishing effort," in *The Kerguelen Plateau: Marine Ecosystem and Fisheries. Proceedings of the Second Symposium, Proceedings of the Second Symposium*, eds D. Welsford, J. Dell, and G. Duhamel (Hobart, TAS), 341–353.

Mintenbeck, K. (2017). *Impacts of Climate Change on the Southern Ocean*. John Wiley & Sons Ltd. doi: 10.1002/9781119154051.ch20

Neuwirth, E. (2014). *RColorBrewer: ColorBrewer Palettes*. R package version 1.1-2. Available online at: https://CRAN.R-project.org/package=RColorBrewer

Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., et al. (2018). Longer and more frequent marine heatwaves over the past century. *Nat. Commun*. 9:1324. doi: 10.1038/s41467-018-03732-9

Panassa, E., Völker, C., Wolf-Gladrow, D., and Hauck, J. (2018). Drivers of interannual variability of summer mixed layer depth in the southern ocean between 2002 and 2011. *J. Geophys. Res. Oceans* 123, 5077–5090. doi: 10.1029/2018JC013901

Pardo, D., Jenouvrier, S., Weimerskirch, H., and Barbraud, C. (2017). Effect of extreme sea surface temperature events on the demography of an age-structured albatross population. *Philos. Trans. R. Soc. B Biol. Sci*. 372:1723. doi: 10.1098/rstb.2016.0143

Park, Y.-H., Durand, I., Kestenare, E., Rougier, G., Zhou, M., d'Ovidio, F., et al. (2014). Polar front around the Kerguelen islands: an up-to-date determination and associated circulation of surface/subsurface waters. *J. Geophys. Res. Oceans* 119, 6575–6592. doi: 10.1002/2014JC010061

Parkes, G., Moreno, C., Pilling, G., and Young, Z. (1996). Use of the Leslie stock depletion model for the assessment of local abundance of Patagonian toothfish (*Dissostichus eleginoides*). *CCAMLR Sci*. 3, 55–77.

Péron, C., Welsford, D. C., Ziegler, P., Lamb, T. D., Gasco, N., Chazeau, C., et al. (2016). Modelling spatial distribution of Patagonian toothfish through life-stages and sex and its implications for the fishery on the Kerguelen plateau. *Prog. Oceanogr*. 141, 81–95. doi: 10.1016/j.pocean.2015.12.003

Pruvost, P., Duhamel, G., and Palomares, M. L. D. (2005). "An ecosystem model of the Kerguelen islands' EEZ," in *Modeling Antarctic Marine Ecosystems. Fisheries Centre Research Reports*, eds M. L. D. Palomares, P. Pruvost, T. J. Pitcher, and D. Pauly (Vancouver, BC: The Fisheries Centre, University of British Columbia), 40–64.

Quéguiner, B. (2013). Iron fertilization and the structure of planktonic communities in high nutrient regions of the southern ocean. *Deep Sea Res. II Top. Stud. Oceanogr*. 90, 43–54. doi: 10.1016/j.dsr2.2012.07.024

Rayfuse, R. (2018). Climate change and Antarctic fisheries: ecosystem management in CCAMLR. *Ecol. Law Q*. 45:53. doi: 10.15779/Z381834271

Rogers, A., Frinault, B., Barnes, D., Bindoff, N., Downie, R., Ducklow, H., et al. (2020). Antarctic futures: An assessment of climate-driven changes in ecosystem structure, function, and service provisioning in the southern ocean. *Annu. Rev. Mar. Sci*. 12, 87–120. doi: 10.1146/annurev-marine-010419-011028

Scott, E., Serpetti, N., Steenbeek, J., and Heymans, J. J. (2016). A stepwise fitting procedure for automated fitting of ecopath with ecosim models. *SoftwareX* 5, 25–30. doi: 10.1016/j.softx.2016.02.002

Su, Z., Pilo, G. S., Corney, S. P., Holbrook, N. J., Mori, M., and Ziegler, P. (2020). Characterising marine heatwaves in the Kerguelen plateau region. *Front. Mar. Sci*. [Epub ahead of print].

Subramaniam, R. C., Corney, S. P., Swadling, K. M., and Melbourne-Thomas, J. (2020). Exploring ecosystem structure and function of the northern Kerguelen plateau using a mass-balanced food web model. *Deep Sea Res. II Top. Stud. Oceanogr*. 174:104787. doi: 10.1016/j.dsr2.2020.104787

Swart, N. C., and Fyfe, J. C. (2012). Observed and simulated changes in the southern hemisphere surface westerly wind-stress. *Geophys. Res. Lett*. 39:L16711. doi: 10.1029/2012GL052810

Thiers, L., Delord, K., Bost, C.-A., Guinet, C., and Weimerskirch, H. (2017). Important marine sectors for the top predator community around Kerguelen archipelago. *Polar Biol*. 40, 365–378. doi: 10.1007/s00300-016-1964-4

Venkataramana, V., Anilkumar, N., Naik, R. K., Mishra, R. K., and Sabu, P. (2019). Temperature and phytoplankton size class biomass drives the zooplankton food web dynamics in the Indian ocean sector of the southern ocean. *Polar Biol*. 42, 823–829. doi: 10.1007/s00300-019-02472-w

Weimerskirch, H., Delord, K., Barbraud, C., Le Bouard, F., Ryan, P. G., Fretwell, P., et al. (2018). Status and trends of albatrosses in the French southern territories, western Indian ocean. *Polar Biol*. 41, 1963–1972. doi: 10.1007/s00300-018-2335-0

Weimerskirch, H., Louzao, M., de Grissac, S., and Delord, K. (2012). Changes in wind pattern alter albatross distribution and life-history traits. *Science* 335:211. doi: 10.1126/science.1210270

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York, NY: Springer-Verlag. doi: 10.1007/978-3-319-24277-4_9

Yates, P., Ziegler, P., Welsford, D., McIvor, J., Farmer, B., and Woodcock, E. (2018). Spatio-temporal dynamics in maturation and spawning of Patagonian toothfish *Dissostichus eleginoides* on the sub-Antarctic Kerguelen plateau. *J. Fish Biol*. 92, 34–54. doi: 10.1111/jfb.13479

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 15 September 2020
doi: 10.3389/fmars.2020.567445

Changing Physical Conditions and Lower and Upper Trophic Level Responses on the US Northeast Shelf

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Sea surface temperature (SST), salinity, and chlorophyll concentration (CHL) have changed in the US Northeast Shelf ecosystem over recent decades. The changes in these parameters were distinctly marked by change points around the year 2012 resulting in a 0.83°C increase in SST, a 0.3 PSU increase in salinity, and decrease in CHL in excess of 0.4 mg m^{-3}. Where temperature and salinity shifted in mean level around their respective change points, CHL declined in a more monotonic fashion. Modeled data suggest that the shift in CHL resulted in a greater contribution of pico- and nanophytoplankton and a decreased contribution of microphytoplankton to overall CHL. Complementary estimates of the contribution of different phytoplankton functional types suggest a diminished contribution of diatoms to the phytoplankton community. Hence, not only is there evidence of a decline in the overall primary production capacity of the ecosystem, but also evidence of a fundamental change in the size and quality of phytoplankton supporting food webs. Two ecosystem responses to the observed changes in SST, salinity, and CHL were analyzed. Both length and weight at age have declined for a number of species, and both measures of growth appear to be negatively associated with temperature and positively associated with CHL. Biomass of fish and macroinvertebrates has declined in recent years, with a decrease in pelagic species associated with a decrease in CHL, while the decline in demersal species was associated with an increase in temperature. Collectively, these ecosystem changes appear to be the result of the complex interactions of both thermal effects and changes at the base of the food web.

Keywords: temperature, chlorophyll, biomass, growth, production, regimes

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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: *29 May 2020*
Accepted: *24 August 2020*
Published: *15 September 2020*

Citation:
Friedland KD, Morse RE, Shackell N, Tam JC, Morano JL, Moisan JR and Brady DC (2020) Changing Physical Conditions and Lower and Upper Trophic Level Responses on the US Northeast Shelf. Front. Mar. Sci. 7:567445. doi: 10.3389/fmars.2020.567445

INTRODUCTION

Changing climate conditions are expected to impact the base of marine food webs by changing the seasonal timing and intensity of phytoplankton blooms (Lotze et al., 2019). The main mechanism governing this anticipated change is the shoaling of mixed layer depths due to increasing temperature, which in turn restricts vertical mixing (Somavilla et al., 2017) and inhibits the redistribution of dissolved nutrients leading to lower overall chlorophyll biomass (Henson et al., 2013). However, projections that incorporate physical mechanisms such as stratification and biogeochemical interactions require validation. Examination of changes in phytoplankton production in marine ecosystems subject to recent, rapid warming can provide the context to improve the modeled response of lower trophic levels to projected change in climate. Rapid climate change is already occurring and the associated warming is arguably the most evident change observed thus far (Cheng et al., 2019). Therefore, it is prudent to examine the response of both lower and upper trophic levels as proxies for the impacts of longer-term climate change effects.

Remote sensing data sources make it possible to consider contemporary change in the upper water column thermal dynamics and phytoplankton biomass in marine ecosystems. These data sources have matured to time series in excess of two decades (Groom et al., 2019) and now provide the ability to evaluate trends and shifts in ecosystem conditions (Friedland et al., 2018). Temperature can influence marine ecosystem function at both the system and individual levels. Increasing temperature can cause the metabolism in individuals to increase (Dantas et al., 2019), alter the population structure and phenology of phytoplankton communities (Moisan et al., 2002; Conversi et al., 2010), and result in changes in trait variation within populations (Salo et al., 2020). Consequently, marine ecosystems are reorganizing as temperature influences both range size and species richness (Batt et al., 2017). Increasingly, we see that where once fishing had the greatest influence on marine ecosystem structure and productivity (Shackell et al., 2012), climate effects are exacerbating forcing factors (Mérillet et al., 2020). The observational and remote sensing time series of temperature data predates estimates of chlorophyll biomass; hence, our thinking and investigations have tended to be skewed toward long-standing hypotheses of thermal control of marine ecosystem function. However, the base of the food web has not been static in response to climate factors resulting in changes in productivity (Roxy et al., 2016), phytoplankton community structure (Dutkiewicz et al., 2019), and bloom phenology (Friedland et al., 2018). While it is anticipated that climate change will alter the vertical structure of the water column, it is worth emphasizing that stratification has already undergone substantial change (Yamaguchi and Suga, 2019).

Change in the productivity of lower trophic levels can affect the stability and function of ecosystems and the production of surplus biomass to support fisheries. Ecosystem stability has been described as a function of energy flow (Huxel and McCann, 1998). For example, Ullah et al. (2018) described scenarios where trophic transfer is inhibited by thermally related factors and new equilibrium among phytoplankton functional groups are established. This can be particularly problematic when groups like cyanobacteria begin to dominate since they often tend to be refractory foods (Friedland et al., 2005) and some species pose a toxicity threat (Paerl, 2018). Perhaps of greater fundamental importance is how food web function changes if energy flow is modified in magnitude, timing, or becomes highly event driven. Terrestrial and aquatic species time their reproductive cycles to benefit from relatively constant seasonal production cycles. For example, cohort recruitment of fish species is affected by the timing and/or size of blooms (Asch et al., 2019). In much the same vein, subsequent growth and reproduction of cohorts will be impacted by the changing energy content and availability of forage species (Durant et al., 2019). The consequences of a loss of system stability and diversity all too often results in a concentration of fishing on lower trophic level target species, which tends to exacerbate the problem (Howarth et al., 2014). These perturbed ecosystems are often continental shelf large marine ecosystems, which play the dominant role in providing national and global food security compared to the relatively negligible role of high seas fisheries (Schiller et al., 2018). Hence, instability in production in marine systems can translate to instability in economic systems.

Climate change is expected to increase the frequency of extreme events, both transient and transformative in nature, that affect multiple aspects of marine ecosystems. Heatwaves have occurred worldwide and they are characterized as anomalously warm temperatures that persist and produce a myriad of follow-on effects (Holbrook et al., 2019; Pershing et al., 2019). Heatwaves can actuate change in community structure by stimulating emigration and causing regionalized mortality (Sanford et al., 2019). They have been associated with phytoplankton blooms and the development of hazardous blooms species that can cause fish mortality in other species (Roberts et al., 2019). Heatwaves can also impact fishery populations as they have been observed to play a role in the recruitment of both invertebrate (Chandrapavan et al., 2019) and vertebrate species (Smith et al., 2019).

The US Northeast Continental Shelf is a well-studied ecosystem that is already displaying warming induced changes in physical forcing and ecosystem response. It is a system that has experienced rapid temperature change (Pershing et al., 2015), has seen two prominent heatwaves in as many decades (Mills et al., 2013; Gawarkiewicz et al., 2019), and has experienced progressive warming in large measure due to change in basin scale circulation (Chen et al., 2020). Fish and macroinvertebrate species have undergone significant shifts in their distribution (Friedland et al., 2019), which is already impacting human populations (Rogers et al., 2019). Rising temperatures appears to have increased the available occupancy habitat for most species and concomitant with this expansion of habitat, there has been an increase in upper trophic level biomass across a range of functional groups (Friedland et al., 2020). The principal multi-species fisheries in the region were greatly reduced by over-fishing in the 1990s, and much of the economic space is now occupied by single species fisheries on invertebrate taxa (Goode et al., 2019; Wiedenmann and Jensen, 2019).

The aim of this study was to examine contemporary trends in sea surface temperature and chlorophyll concentration from remote sensing data sources, and salinity from observational data for the US Continental Shelf ecosystem. Furthermore, these trends are scrutinized for time series change points as an indication of potential regime change. The phytoplankton community was characterized by its size fraction composition, functional type contributions, and seasonal bloom patterns. Ecosystem response to both trend and events in the physical

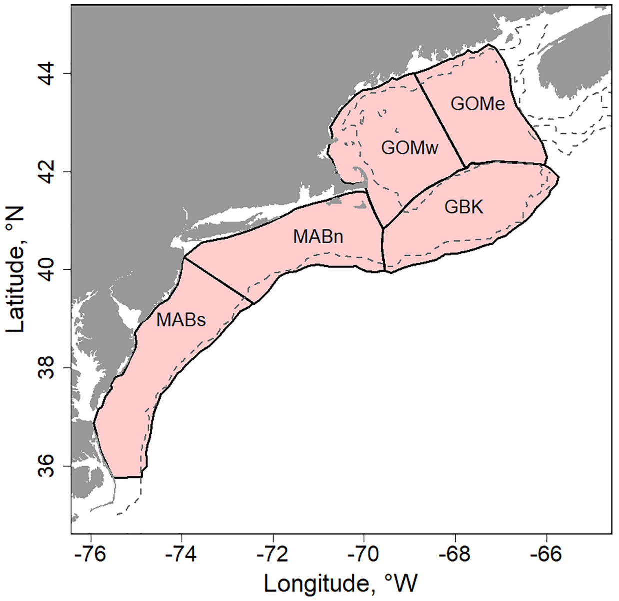

FIGURE 1 | US Northeast Shelf study area (NES) highlighted with shading and delimited to five subareas including: Georges Bank (GBK); Gulf of Maine east and west (GOMe and GOMw, respectively); and, Middle Atlantic Bight north and south (MABn and MABs, respectively), dashed line is the 100 m depth contour.

forcing and phytoplankton change was evaluated using growth and abundance data for fish and macroinvertebrates from a concomitant fisheries independent trawl survey.

MATERIALS AND METHODS

Study Site

We studied physical and biological changes occurring in the Northeast US Continental Shelf ecosystem (NES). The shaded portion of the continental shelf shown in **Figure 1** denotes the study area. We characterized conditions and responses of the ecosystem based on five subdivisions as described in Friedland et al. (2015a). The five subareas were Georges Bank (GBK), Gulf of Maine east and west (GOMe and GOMw, respectively), and Middle Atlantic Bight north and south (MABn and MABs, respectively). These five areas capture much of the variability of the system, especially as related to the distribution and dynamics of primary producers and the fish populations that rely on them.

Sea Surface Temperature

High resolution sea surface temperature (SST) data for the ecosystem and subdivisions were sourced from the NOAA Optimum Interpolation (OISTT) 0.25 Degree Daily Sea Surface Temperature Analysis dataset (Reynolds et al., 2007). For the purposes of this study, we calculated monthly means from the daily data while retaining its spatial resolution (see "Data Availability Statement").

Salinity

Salinity in practical salinity units (PSU) for the NES was sourced from shipboard data and estimated using an interpolation method described in Friedland et al. (2019). The main source of the data was ongoing resource and ecosystem surveys of the NES conducted by the Northeast Fisheries Science Center (NEFSC) of the National Marine Fisheries Service (see "Data Availability Statement"). Water column temperature and salinity have been collected contemporaneously with tows associated with the fall seasonal bottom trawl survey beginning in 1963 with the spring survey starting 5 years later (Desprespatanjo et al., 1988). In addition, data was also collected in two comprehensive ecosystem surveys over the study period including the Marine Resources Monitoring Assessment and Prediction program or MARMAP (1977–1987) and the Ecosystem Monitoring program or EcoMon (1992-present), both providing shelf-wide observations (Sherman et al., 1998; Kane, 2007). These data provide time series of spring and fall salinity in all the subareas. The spring and fall salinity time series were correlated (Spearman rank order correlation, $p < 0.05$); hence, we combined the seasonal time series to produce an annual PSU time series by taking the mean.

Chlorophyll Concentration

Chlorophyll concentration (CHL) data were extracted from a merged multi-sensor ocean color data product from the Hermes GlobColour (see "Data Availability Statement"). This product includes measurements made with the Sea-viewing Wide Field of View Sensor (SeaWiFS), Moderate Resolution Imaging Spectroradiometer on the Aqua satellite (MODIS), Medium Resolution Imaging Spectrometer (MERIS), and Visible and Infrared Imaging/Radiometer Suite (VIIRS) sensors during the period 1998–2019. The data were merged using the Garver, Siegel, Maritorena Model (GSM) algorithm (Maritorena et al., 2010). CHL was summarized as annual and seasonal means; the spring or first half of year seasonal was the average CHL from January through June; and, fall or second half of the year was the average CHL from July through December. The two halves of the year reflect the bloom patterns found in the NES that includes both spring and fall blooms (Friedland et al., 2016). Seasonal CHL time series were plotted as Z-scores (observation minus the mean and divided by the standard deviation) as were the phytoplankton size fraction and phytoplankton functional type data described below.

Time Series Change Points and Trend

We identified change in study time series as both discreet change points and trends, both of which may potentially indicate underlying processes such as a regime shift. We applied two parametric modeling approaches to identify potential change points in the annual means of SST, salinity, and CHL data. First, discrete change points or a change in signal level within a single time step were identified with the sequential averaging algorithm called STARS or "sequential *t*-test analysis of regime shifts" (Rodionov, 2004, 2006; Thomson and Emery, 2014). The STARS algorithm parameters were specified *a priori* to detect change in thermal, salinity, and chlorophyll regimes (alpha level $\alpha = 0.05$;

the length criteria was set to 10; and, the Huber weight was set to 1). To be consistent with the terminology associated with the STARS algorithm, the change in a parameter level before and after a change point is referred to as the change in regime means, which may have the units of°C, PSU, or mg m^{-3}. Second, we fit piecewise linear relationships using the R package "segmented" (version 1.1-0), which fits the data as segmented linear models while identifying time series break-points (Muggeo, 2003, 2017). The performance of these approaches was compared for an individual time series with Akaike information criterion (AIC) using the simplified form intended for model comparison.

$$AIC = 2k + nln(RSS)$$

Where *RSS* is the residual sum of squares, n is the number of observations, and k is the number of independent parameters (Burnham and Anderson, 2004). To evaluate trends in the data, we applied a non-parametric test of time series trend using the R package "zyp" (version 0.10–1.1). We used the Yue and Pilon method to estimate Theil-Sen slopes and performs an auto-correlation corrected Mann-Kendall test of trend (Yue et al., 2002).

Phytoplankton Size Fractions

Estimates of phytoplankton size fraction contribution to total CHL were based on the three-component model of phytoplankton size classes (Lamont et al., 2019) using the global parameters from Brewin et al. (2015). The model provides estimates of the contribution of microphytoplankton (> 20 μm), nanophytoplankton (2–20 μm), and picophytoplankton (< 2 μm) to total CHL. Model equations provide an estimate of the CHL fraction that is associated with combined contribution of pico- and nanoplankton:

$$C_{p,n} = C_{p,n}^{m}\left[1 - exp\left(-\frac{D_p}{C_p^m}\right)CHL\right]$$

and picoplankton only:

$$C_{p} = C_{p}^{m}\left[1 - exp\left(-\frac{D_p}{C_p^m}\right)CHL\right]$$

Which by difference yield the nano- and the microplankton fractions, Cn and Cm, respectively. The model was parameterized using the following global model estimates.

$$C_{p,n}^{m} = 0.77;\ C_{p}^{m} = 0.13;\ D_{p,n} = 0.94;\ D_{p} = 0.80$$

These parameters are similar to the average across regional and other global study estimates.

Phytoplankton Functional Types

Three complimentary approaches are considered for estimating Phytoplankton Functional Types (PFTs) to evaluate change in the quality of phytoplankton entering the food web of the NES. First, we used the method presented in Moisan et al. (2017) for studying spatial distributions of PFTs, their phenology, and ecotones along the U.S. east coast. That study utilized a total of 172 independent measurements of phytoplankton absorption spectra and High-Performance Liquid Chromatography (HPLC) pigment measurements to develop a satellite-based model for PFTs. Pigment-specific absorption spectra for 18 phytoplankton pigments were obtained by inverting the observed pigment concentrations and the total phytoplankton absorption at each wavelength using Singular Value Decomposition, SVD (Press et al., 1987). The resulting pigment-specific absorption spectra were then used with individual phytoplankton absorption spectra with the Non-Negative Least Squares, NNLS (Lawson and Hanson, 1995) inversion method to estimate the pigment concentrations. The individual phytoplankton absorption spectra values at each wavelength were modeled as a second order function with chlorophyll *a* as the independent variable.

In this study, the resulting SVD-derived pigment-specific absorption spectra and the wavelength-dependent, second order model coefficients for absorption spectra from Moisan et al. (2011) are used with the annual mean 1998–2019 chlorophyll *a* estimates for each of the five subareas to estimate the PFT time series. The chlorophyll *a* values are used with the second-order linear model to estimate the phytoplankton absorption spectra. These spectra are then used with the SVD-derived pigment-specific absorption spectra in the NNLS inverse process to estimate the 18 different phytoplankton pigments.

Once maps of the 18 phytoplankton pigments were derived, they were used to generate estimates of the various PFTs by using the estimation formulas outlined in Table 1 of Hirata et al. (2011) for diatoms, dinoflagellates, prymnesiophytes, prokaryotes, and green algae. The pigments necessary as inputs for these algorithms included: fucoxanthin, peridinin, chlorophyll-b, 19-butanoyloxyfucoxanthin, 19-hexanoyloxyfucoxanthin, alloxanthin, and zeaxanthin. A time series of these functional types were calculated for all five subareas.

The second approach used was an algorithm designed to estimate the dominant PFTs at a location. The method is called PHYSTWO and is described in Correa-Ramirez et al. (2018). The approach uses Empirical Orthogonal Function (EOF) decomposition to relate pigment signatures to water-leaving radiances. It applies normalized radiances at seven wavelengths including 412, 443, 469, 488, 531, 547, and 555 nm. The analysis was based on the monthly 25 km merged reflectance data retrieved from the same source as the CHL data. The PFT estimates were made for the period 2003 through 2019, which corresponds to the sensor collections for these wavelengths. Reflectance at 488 nm was estimated based on an interpolation of reflectance data for 469 and 490 nm. The PFT identified Nanoeucaryotes (typically chlorophytes and cryptophytes), Diatoms, Coccolithophorids, Phaeocystis-like (typically haptophytes), and two cyanobacteria, Prochloroccocus and Synechococcus. Following the approach used in Alvain et al. (2008), the percent contribution of a PFT was estimated as the ratio of the area of NES with each PFT to the total. Monthly means of the percent contributions of PFT were calculated over the course of each year.

Finally, as verification of modeled PFT data, we queried the abundance of total diatoms and dinoflagellates from the Continuous Plankton Recorder (CPR) Survey dataset. The CPR collects continuous measurements of zooplankton and phytoplankton taxa retained on the CPR mesh, hence it includes a partial sampling of the microphytoplankton (Batten et al., 2003). Monthly samples were collected in the NES during the period of 1998–2018, however, not all NES subareas were sampled over the entire period. The GBK and MABn subareas were sampled in all 21 years the time series and GOMe was sample in 20 years, however, GOMw and MABs were sampled in less than 7 years each. The average number of annual sample units was 138; a sample consisted of a total number of diatoms and dinoflagellates from 68 to 35 taxa, respectively (see “Data Availability Statement”).

Survey Growth Trends

Change in the size at age of fish in the NES was assessed using biological data collected during the Northeast Fisheries Science Center (NEFSC) bottom trawl survey (Desprespatanjo et al., 1988). Catch weight was collected during the full duration of the survey, however, individual weight measurements began in 1992 (see “Data Availability Statement”). From these data, changes in length and weight at age were examined. The size at age metrics were computed for a subset of survey species having sufficient age samples. Annual growth indices were computed using a general linear model (GLM) following the approaches applied to estimate catch per unit effort (Forrestal et al., 2019). The general form of the size at age GLM was:

$$GLM\ (Length/Weight) \sim factor\ (Species)\ +\ factor\ (Age)\ +\ factor\ (Year)$$

Moreover, it was also partitioned by season and sex. Year factor coefficients were used to represent the rate of change over time. The change in size at age was assessed with canonical correlation with temperature, salinity, and chlorophyll concentration as environmental covariates. The canonical correlation was fit using the CCA package in R (version 1.2).

Survey Biomass by Functional Groups

Seasonal time series trends in biota were represented by the CPUE for biomass of all taxa from the bottom trawl survey (see “Data Availability Statement”), and by assignment to functional groups based on their adult prey preferences and vertical distribution (Friedland et al., 2020). The functional groupings included benthivores, demersal piscivores, pelagic piscivores, and planktivores. Catches were standardized for various correction factors related to vessels and gears used in the time series (Miller et al., 2010). The spring and fall CPUE time series were correlated with Spearman rank order correlation reasoning that since many taxa are known to undertake seasonal migrations, correlated spring and fall signals could be considered an indication of more reliable abundance data. Similar to the change in size at age analysis, the change in biomass was assessed with canonical correlation with temperature, salinity, and chlorophyll concentration as environmental covariates.

RESULTS

Trends in SST, PSU, and CHL

The main result of the trend analysis is that CHL declined in the Northeast Shelf as both SST and salinity increased, with change points in these data around the year 2012. We found that SST in the NES increased from ∼12 to 13°C in a stepwise fashion with a change point in 2012 (**Figure 2A**), which was also the highest SST in the time series. Salinity also increased in a stepwise fashion by ∼0.3 PSU, albeit in the year after the SST shift, noting there were no local maxima in salinity around the year 2012 (**Figure 2B**). The non-parametric trend test for NES SST yielded a significant positive Theil–Sen slope, however, the positive slope for salinity was non-significant at $p = 0.1$ (**Table 1**). In contrast, CHL decreased from ∼1.5 to 1.1 mg m^{-3} in a segmented linear fashion, with a change point in 2012 (**Figure 2C**); and, the highest system-wide CHL level occurred in 2011. The Theil–Sen slope for NES CHL was negative and significant.

Similar patterns were found in the NES subareas time series of SST, salinity, and CHL. The pattern found for the NES as a whole was reflected in Georges Bank (**Figures 2D–F**) and MABn (**Figures 2M–O**). The SST change points in Gulf of Maine east (**Figures 2G–I**), and Gulf of Maine west (**Figures 2J–L**) subareas initiated earlier than the NES as a whole or in the neighboring Georges Bank area. In addition, the GOMe and GOMw salinity time series were modeled marginally better with a segment regression suggesting a less distinct transition in salinity. The segmented regression depiction of change in CHL in these areas was similar to the other parts of the ecosystem. The SST time series in the MABs was modeled best with segmented regression, and though 2012 was the warmest year in the time series, there was no evidence of a change in SST level as seen in the more northerly subareas (**Figures 2P–R**). The Theil–Sen slopes for the subareas follow the NES trend with the exception of Georges Bank SST, which had a positive trend that was non-significant. To summarize, the NES and its regional subareas experienced a shift in SST, salinity, and CHL around 2012. Both SST and salinity started increasing around this change point while CHL decreased, noting that the change in SST and salinity were generally more stepwise whereas the change in CHL was gradual.

Seasonal CHL

Seasonal CHL generally followed the patterns established in the annual means suggesting that spring and fall blooms have been affected by a similar set of factors. CHL for the first half of the year followed a coherent pattern of decline after 2012, similar to the CHL annual trend for the NES (**Figure 3A**). The Theil–Sen slopes for the first half of the year CHL were all negative and significant (**Table 1**). The CHL for the second half of the year were also coherent among the subareas, but had features that varied from the first half of the year (**Figure 3B**). In particular, localized minima around 2004 and maxima around 2011 varied between the data series. The Theil–Sen slopes for the second half of the year CHL were all negative and significant with exception of the data for Gulf of Maine east.

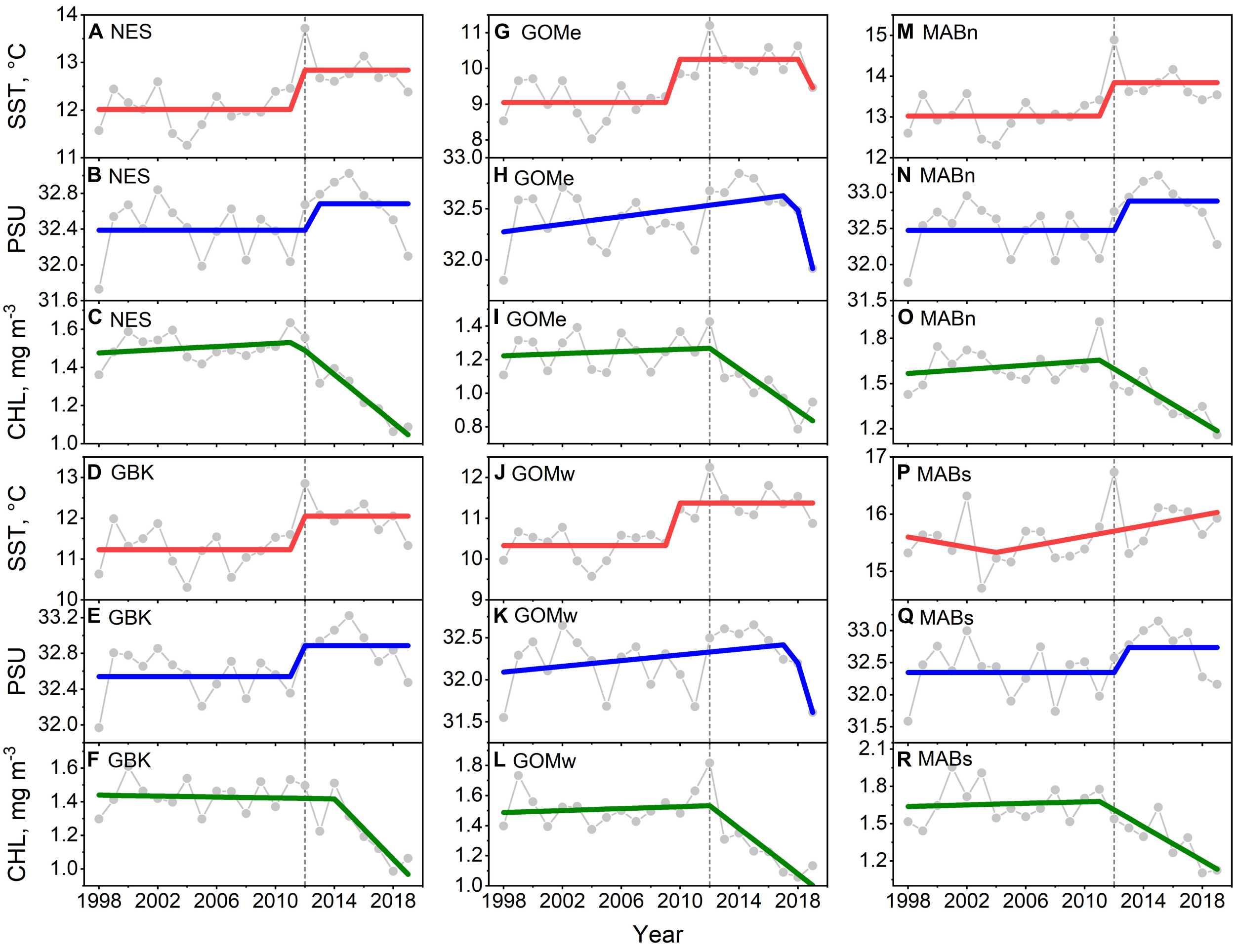

FIGURE 2 | Mean annual SST **(A,D,G,J,M,P)** for the Northeast Shelf (NES) and NES subareas (NES, GBK, GOMe, GOMw, MABn, and MABs, respectively), mean annual PSU **(B,E,H,K,N,Q)** and mean annual CHL **(C,F,I,L,O,R)** for the same areas, respectively. Lines are either STARS or segmented regression model fits; 2012 is highlighted with vertical dotted line.

Phytoplankton Size Classes

The decrease in CHL throughout the ecosystem after 2012 was associated with a change in the size-class composition of the phytoplankton community. The estimates of the percent contribution to total CHL by picophytoplankton shifted from ~10 to 14% after 2012, or a 40% increase in the contribution (**Figure 4A**). Similarly, nanophytoplankton exhibited a shift in composition from ~23 to 28%, or a 22% increase in the contribution (**Figure 4B**). The increase in the contribution of smaller phytoplankton appears to come at the expense of microphytoplankton, which shifted from a contribution of 67 to 58%, or a 13% decline in contribution (**Figure 4C**). The Theil–Sen slopes for the trends in pico- and nanophytoplankton were all positive and significant; whereas, the trends for microphytoplankton were negative and significant (**Table 1**). In summary, the shift in NES CHL likely also represents a shift in the size class composition of the phytoplankton community driven by the increasing availability of smaller cells vs. larger cell taxa.

Phytoplankton Functional Types

Analysis of the PFT time series using the Moisan method suggests phytoplankton populations were relatively stable from 1998 to 2012. In the NES region, diatoms, dinoflagellates, green algae, prymnesiophytes and prokaryotes comprised nearly 63, 11, 13, 2, and 12 percent of the phytoplankton biomass in terms of chlorophyll *a*, respectively (**Figures 5A–E**). In 2012, all of these populations of phytoplankton show a dramatic linear trend away from the prior relatively stable levels. Specifically, the diatom population shows a decrease while all of the other functional types show increases in their relative percent biomass. These changes were consistent with a shift away from high production coastal phytoplankton populations to a more open ocean, less productive domain. These estimated changes were supported by the observed nearly 50% decrease in the chlorophyll *a* levels. These changes in phytoplankton composition were further corroborated by the phytoplankton size class estimates which show stable size class population levels prior to 2012 and decreasing microplankton with increasing nanoplankton

TABLE 1 | Theil–Sen slope estimates expressed in decadal rate of change for environmental variables by NES and NES subareas (NES, GBK, GOMe, GOMw, MABn, and MABs).

Data type	Variable	NES	GBK	GOMe	GOMw	MABn	MABs
Temperature, Salinity, and Chlorophyll	SST	**0.52**	0.52	**0.75**	**0.70**	**0.50**	**0.28**
	PSU	0.21	0.11	0.16	0.06	0.04	0.17
	CHL	**−0.21**	**−0.17**	**−0.16**	**−0.14**	**−0.20**	**−0.17**
	CHL–first	**−0.23**	**−0.16**	**−0.24**	**−0.18**	**−0.22**	**−0.21**
	CHL-second	**−0.15**	**−0.20**	−0.20	**−0.21**	**−0.27**	**−0.21**
Phytoplankton size classes	Pico	**0.01**	**0.01**	**0.02**	**0.02**	**0.01**	**0.01**
	Nano	**0.02**	**0.02**	**0.02**	**0.02**	**0.02**	**0.02**
	Micro	**−0.03**	**−0.03**	**−0.03**	**−0.04**	**−0.03**	**−0.04**
Phytoplankton Functional Types Moisan	Diatoms	**−2.08**	**−2.39**	**−2.88**	**−2.61**	**−1.96**	**−2.20**
	Dinoflagellates	**0.20**	**0.22**	**0.23**	**0.25**	**0.20**	**0.24**
	Green algae	**0.78**	**0.89**	**1.07**	**0.98**	**0.73**	**0.83**
	Prymnesiophytes	**0.11**	**0.13**	**0.16**	**0.14**	**0.11**	**0.11**
	Prokaryotes	**0.98**	**1.13**	**1.41**	**1.23**	**0.92**	**1.01**
Phytoplankton Functional Types PHYSTWO	Nanoeucaryotes	2.03	6.35	**5.28**	5.65	−3.34	**−3.06**
	Prochloroccocus	0.17	0.57	0.00	0.00	0.20	0.00
	Synechococcus	−0.15	0.52	0.00	0.00	−0.61	**−1.20**
	Diatoms	**−3.86**	−5.12	**−7.21**	**−5.52**	−1.38	−3.48
	Phaeocystis-like	1.24	−3.60	0.27	−0.35	**3.39**	**4.95**
	Coccolithophorids	0.29	0.00	−0.23	0.00	−0.60	**2.09**
CPR	Diatoms	**−40619**	**−39731**	−49373		−6465	
	Dinoflagellates	745	610	0		−1403	

Estimates with associated $p < 0.1$ highlighted in bold.

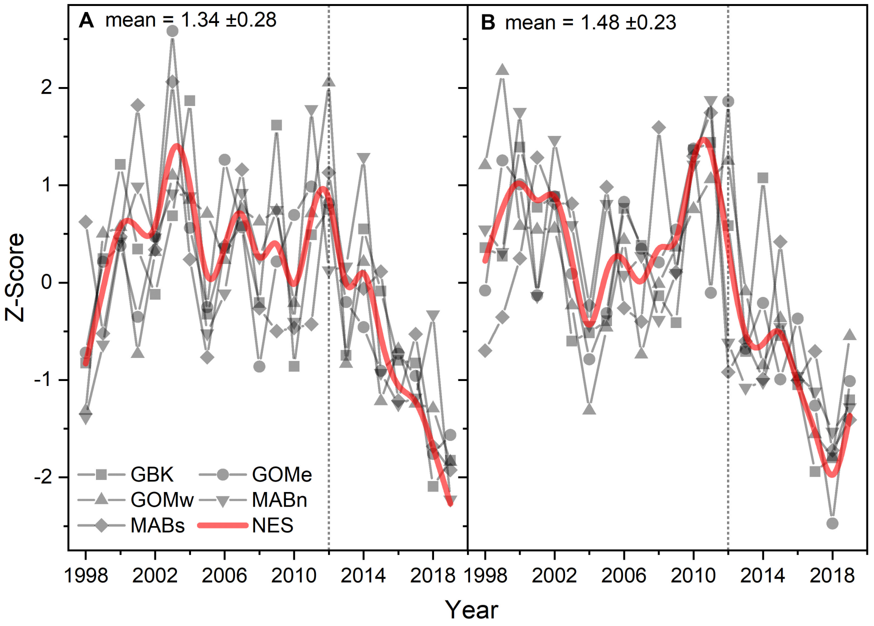

FIGURE 3 | Z-score of CHL for the first **(A)** and second **(B)** half of the year for the Northeast Shelf (NES) and NES subareas (NES, GBK, GOMe, GOMw, MABn, and MABs). The mean for each size class shown in the panel title with ± 1 SD; the NES time series is shown as a b-spline; 2012 is highlighted with vertical dotted line.

and picoplankton levels after 2012, indicating a population shift away from a eutrophic coastal productive population to a more oligotrophic and less productive population. The Theil–Sen slopes for PFT in the analysis were significant and were positive trends except for diatoms, which had negative trends (**Table 1**).

Analysis of Phytoplankton Functional Types using the PHYSTWO method largely corroborated the changes identified

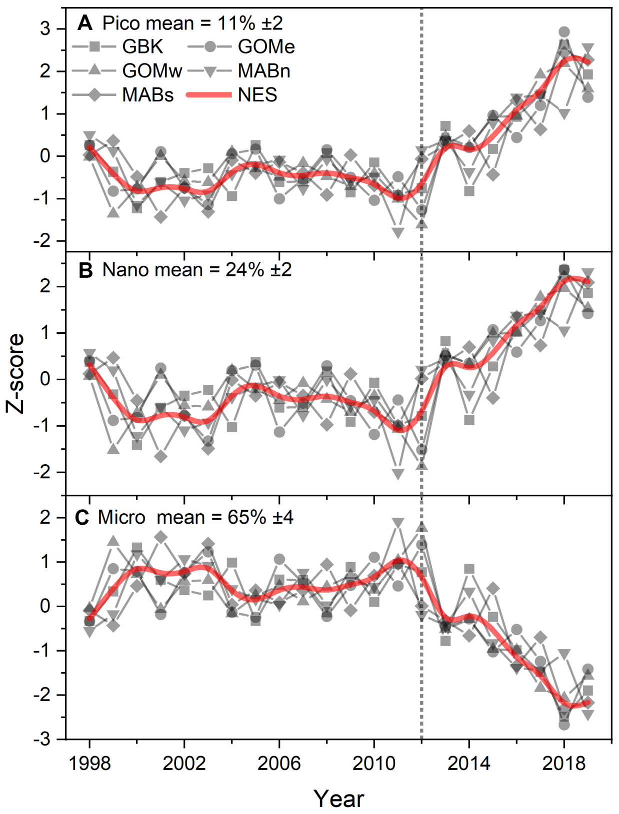

FIGURE 4 | Z-score of estimated phytoplankton size fractional contribution percentage of pico **(A)**, nano **(B)**, and micro **(C)** plankton to total chlorophyll for the Northeast Shelf (NES) and NES subareas (NES, GBK, GOMe, GOMw, MABn, and MABs). The mean percentage for each size class shown in the panel title with ± 1 SD; the NES time series is shown as a b-spline; 2012 is highlighted with vertical dotted line.

by the Moisan method and had the advantage of identifying changes in the dominant PFT by subarea. For the NES, Nanoeucaryotes and Diatoms were the most important functional types with average percentages of 43% in all areas (**Figures 6A,B**). Phaeocystis-like forms, Coccolithophorids, and cyanobacteria were low contributors with mean percentages of only 8, 3, and > 1–2%, respectively (**Figures 6C–F**). The only consistent trend observed was a decrease in the contribution of diatoms, however, this trend was only significant in the NES and the Gulf of Maine subareas (**Table 1**). The other dominant group, Nanoeucaryotes, had a significant positive trend in the Gulf of Mine east and a negative trend in the Middle Atlantic Bight south.

The time series CPR abundances support the conclusion that there was a change in diatom populations, but were inconclusive in respect to any change in dinoflagellates. Diatom abundances on a CPR sample unit averaged over 89,000 cells and in all the time series with sufficient data trended downward over the study period (**Figure 7A**). The Theil–Sen slopes were all negative for diatom trends and significant for the GBK and NES areas (**Table 1**). There were no apparent trends in the dinoflagellate time series (**Figure 7B**) and Theil–Sen slopes for these time series were of mixed sign and all non-significant. In summary, using two model-based methods to characterize Phytoplankton Functional Types, a shift was observed in functional types associated with the change in CHL in 2012 and most notably evidence to suggest a decline in diatoms in the plankton community. The conclusion of a change in diatom population based on the model-based data is in part supported by *in situ* sampling data.

Change in Fish Growth

Size at age has declined for a number of fish species in the NES. GLM coefficients indicate that length at age for males declined during spring (**Figure 8A**), however, the decline in female length at age was not significant (**Table 2**). Spring weight at age declined for both sexes (**Figure 8B**). Similar to spring, fall length at age for males showed a decline, whereas females did not decline significantly (**Figure 8C**). Fall weight at age declined for both sexes (**Figure 8D**). These GLM results are a composite trend of a number of important groundfish species. Two change points emerge from these data, one in the spring male length at age data in 2009 and in the fall male weight at age data in 2005. When we decomposed the analysis to the species level, we found that not all species had declining trends in growth. For example, two species, silver hake *Merluccius bilinearis* and butterfish *Peprilus triacanthus*, were consistently increasing in length and weight at age for both sexes and seasonal categories (**Table 2**). The canonical correlation analysis between environmental and growth variables for the composite fish sizes yielded two significant dimensions at $p < 0.1$ (**Table 3**). The growth variables were positively correlated with CHL and negatively related to temperature (**Figure 9A**); salinity produced weaker correlative relationships.

Change in Survey Biomass by Functional Groups

Time series of biomass constructed from scientific surveys are difficult to interpret since they are shaped by a number of different factors and often dependent upon the catch of migratory species. It would appear the total biomass for the system has increased over time (**Figure 10E**). The biomass of the functional groups, benthivores, pelagic piscivores, and planktivores, seem to suggest a recent decline in biomass (**Figures 10A,C,D**). In contrast, the biomass of demersal piscivores appears to have remained high, although the level of biomass has been highly variable from year to year (**Figure 10B**); this variability may be due to the influence of migratory species. Two functional groups, benthivores and planktivores, had spring and fall signals that were correlated suggesting the same populations were sampled between seasons. These time series show similar patterns, namely that biomass increased to high levels within the last decade and has been declining since around 2015. The benthivore time series was the only CPUE time series with the suggestion of a change point, which occurred in 2012. The analysis of overall trend suggests the increase in CPUE has been higher in the spring and that the increase in total biomass may be driven by changes

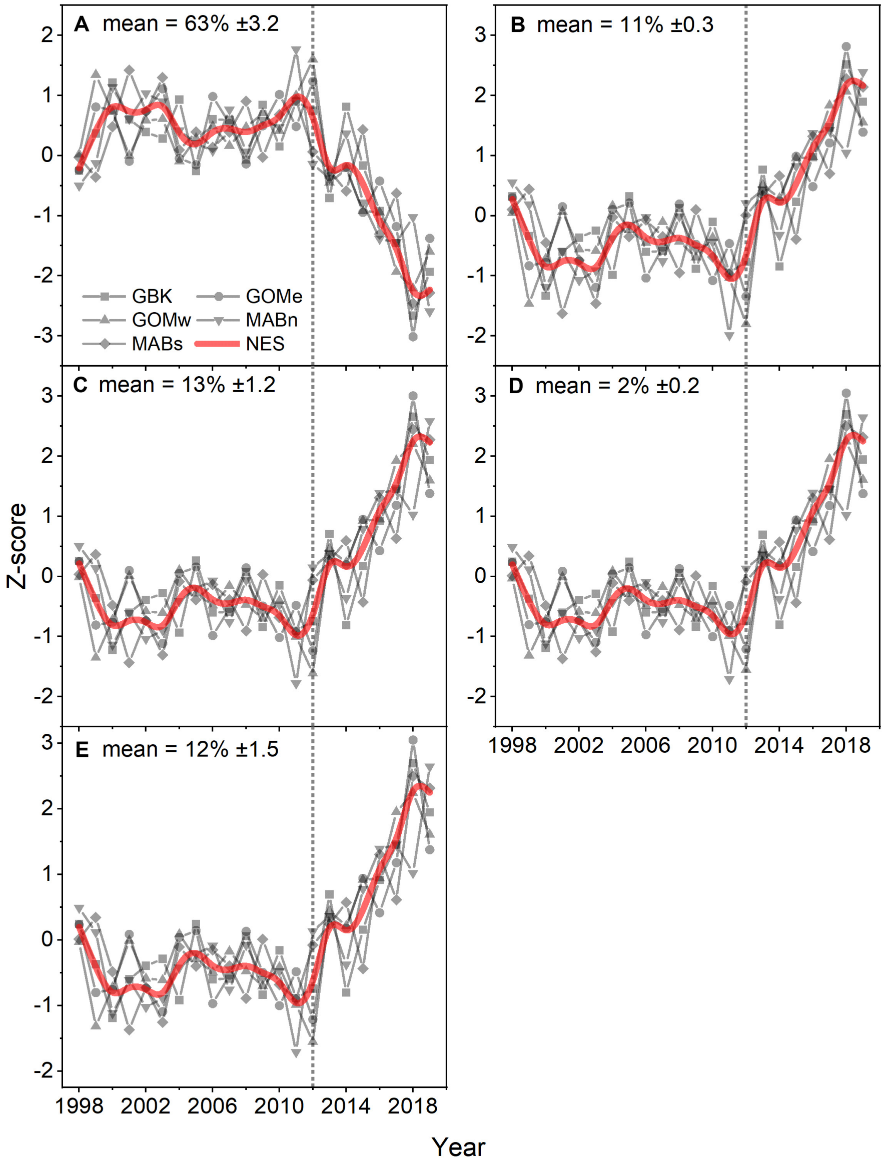

FIGURE 5 | Z-score of estimated percent contribution of PFT diatoms **(A)**, dinoflagellates **(B)**, green algae **(C)**, prymnesiophytes **(D)**, and prokaryotes **(E)** for the Northeast Shelf (NES) and NES subareas (NES, GBK, GOMe, GOMw, MABn, and MABs). The mean percentage for each PFT shown in the panel title with ± 1 SD; the NES time series is shown as a b-spline; 2012 is highlighted with vertical dotted line.

in benthivore and demersal piscivore populations (**Table 4**). The canonical correlation analysis between environmental and biomass variables yielded two significant dimensions at $p < 0.1$ (**Table 3**). The biomass of benthivores and demersal piscivores were positively related to temperature whereas pelagic piscivores were correlated with CHL (**Figure 9B**); planktivores appear to be uncorrelated with these factors.

DISCUSSION

The US Northeast Shelf ecosystem has gone through a transformational change in thermal state, primary producer biomass levels, and functional group assemblages over the past two decades. The upper part of the water column increased in temperature around the year 2012 and has since remained at a temperature level nearly 1°C higher than prior to 2012. The year 2012 was an exceptionally warm year and is recognized as the warmest year in the historical record of SST measurements for the ecosystem (Chen et al., 2014). Salinity has also increased on the order of 0.3 PSU, indicating a change in advective source water in the upper water column and photic zone of the ecosystem (Austin et al., 2019). Coincident with this transition in temperature and salinity, chlorophyll biomass peaked in 2011, and then declined from a relatively stable pre-2011 level in excess of 1.5 mg m^{-3} progressively to a low value of ~1.0 mg m^{-3}. These broad

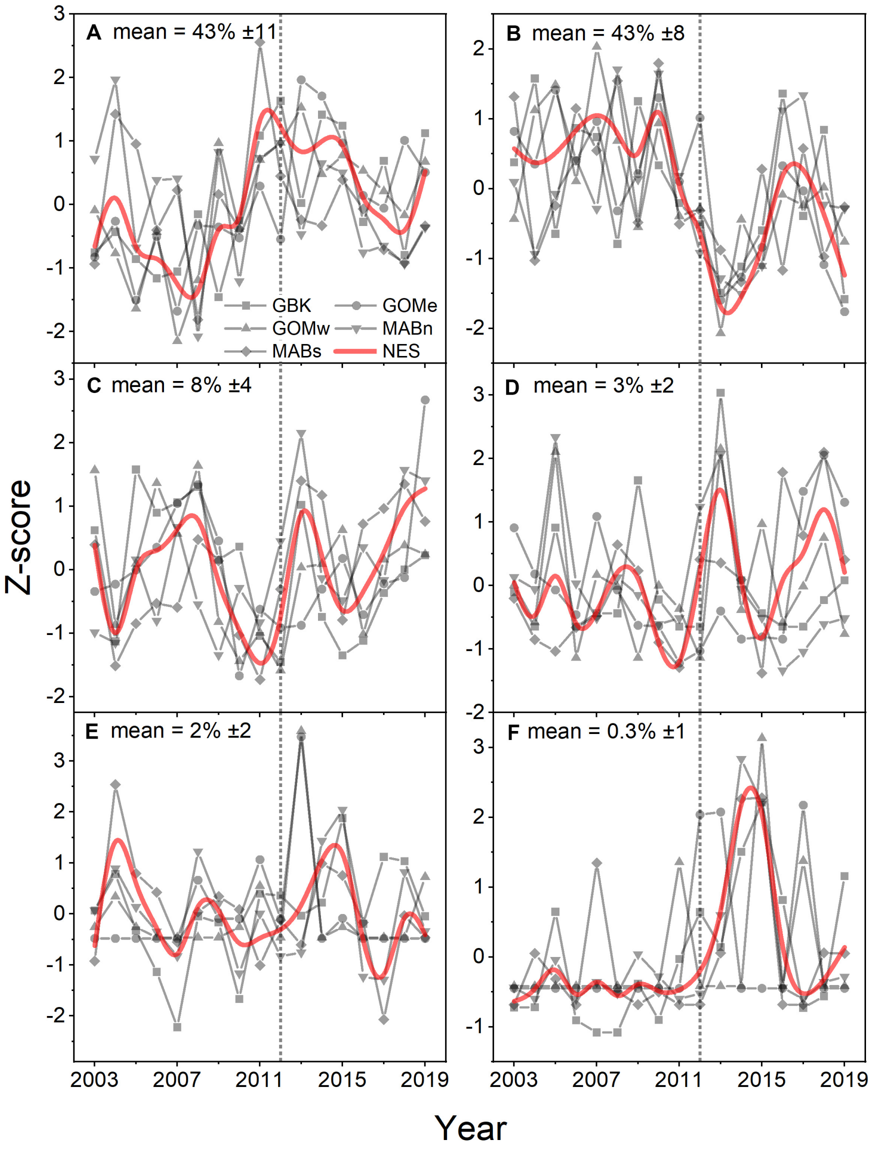

FIGURE 6 | Z-score of percentage area where Nanoeucaryotes **(A)**, Diatoms **(B)**, Phaeocystis-like **(C)**, Coccolithophorids **(D)**, Synechococcus **(E)**, Prochloroccocus **(F)** were the dominant PFT for the Northeast Shelf (NES) and NES subareas (NES, GBK, GOMe, GOMw, MABn, and MABs). The mean percentage for each PFT shown in the panel title with ± 1 SD; the NES time series is shown as a b-spline; 2012 is highlighted with vertical dotted line.

scale ecosystem level changes were most evident in the northern segments of the ecosystem, specifically in the Gulf of Maine and on Georges Bank.

The link between climate-induced warming and CHL is extremely complex. If warming was primarily driven by internal heating processes, then we might expect that phytoplankton communities will shift to a warm tolerant assemblage over time (Barton et al., 2016). However, warming in the NES is often the result of changing offshore water masses entering the system and these water masses can have significantly different nutrient concentrations and ratios. For example, Townsend et al. (2015) documented more frequent incursions of low-nutrient Scotian shelf waters into the Gulf of Maine and Georges Bank over a ten year period. Shifts in the nature of incoming water masses may exert strong and unpredictable controls on NES productivity. However, stratification, another important driver of phytoplankton production, is generally expected to increase due to increases in freshwater inflow from the Arctic and associated warming (Greene, 2012; Li et al., 2015). Enhanced stratification can potentially reduce the depth of the photic zone, thereby increasing the light exposure of phytoplankton in the surface mixed layer, however, it can also disconnect surface phytoplankton from bottom waters limiting the availability of nutrients, particularly nitrate. The importance of vertical mixing for the delivery of bottom water nitrate for phytoplankton production is well documented in the NES (Townsend, 1998) and

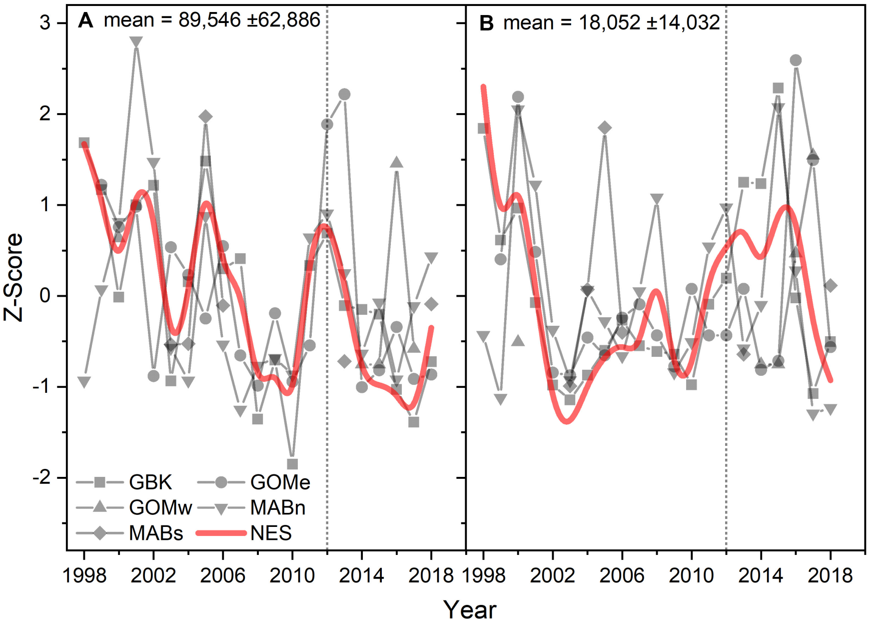

FIGURE 7 | Z-score of the abundance of diatoms **(A)** and dinoflagellates **(B)** in a CPR sample unit for the Northeast Shelf (NES) and NES subareas (NES, GBK, GOMe, GOMw, MABn, and MABs). The mean for each abundance shown in the panel title with ± 1 SD; the NES time series is shown as a b-spline; 2012 is highlighted with vertical dotted line.

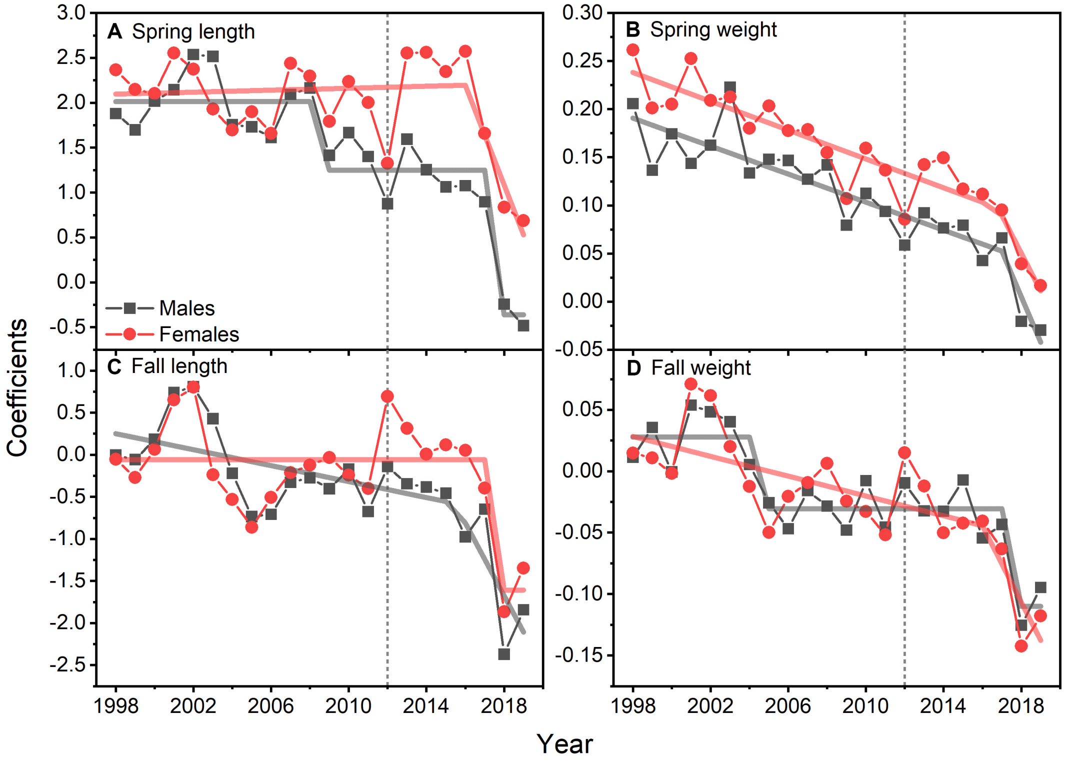

FIGURE 8 | GLM model coefficients of length **(A)** and weight **(B)** for males and females of 15 species of fish during spring. GLM model coefficients of length **(C)** and weight **(D)** for males and females of 15 species of fish during fall. Lines are either STARS or segmented regression model fits; vertical dotted line marks 2012.

TABLE 2 | Theil–Sen slope estimates expressed in decadal rates of change for growth variables by season and sex for the results of GLM models and by species.

	Spring				Fall			
	Male		Female		Male		Female	
Species	**Length**	**Weight**	**Length**	**Weight**	**Length**	**Weight**	**Length**	**Weight**
All	**−0.791**	**−0.078**	−0.260	**−0.084**	**−0.719**	**−0.053**	−0.179	**−0.051**
Centropristis striata	−0.143	**−0.894**	**−0.054**	**−0.041**	−0.828	**−0.980**	**−0.080**	**−0.044**
Clupea harengus	−0.160	−0.033	0.001	0.004	**−0.225**	−0.165	−0.003	−0.005
Gadus morhua	−0.934	−1.187	−0.173	−0.209	0.002	0.091	−0.075	−0.076
Glyptocephalus cynoglossus	−0.154	**0.314**	−0.005	0.006	**0.894**	**1.041**	**0.013**	**0.019**
Hippoglossoides platessoides	0.059	−0.125	−0.006	−0.022	−0.124	0.461	−0.011	−0.001
Limanda ferruginea	**−2.319**	**−2.288**	**−0.058**	**−0.117**	**−1.055**	**−1.109**	**−0.035**	**−0.057**
Melanogrammus aeglefinus	**−4.218**	**−3.514**	**−0.284**	**−0.287**	**−3.621**	**−3.389**	**−0.233**	**−0.244**
Merluccius bilinearis	**2.713**	**4.125**	**0.025**	**0.069**	**0.950**	**2.540**	**0.010**	**0.074**
Paralichthys dentatus	**−2.452**	**−2.131**	**−0.128**	**−0.137**	**−2.567**	**−2.525**	**−0.123**	−0.183
Peprilus triacanthus	**0.498**	**0.454**	**0.005**	0.003	**0.641**	**0.654**	**0.007**	**0.009**
Pollachius virens	**−2.876**	**−3.090**	**−0.411**	**−0.410**	**−1.344**	**−1.344**	**−0.183**	**−0.181**
Pseudopleuronectes americanus	**−1.075**	−0.849	**−0.045**	**−0.046**	−0.193	−0.261	−0.013	−0.021
Scomber scombrus	−0.315	−0.338	−0.010	−0.010	0.071	0.053	0.000	0.002
Stenotomus chrysops	−0.006	**−0.458**	**−0.014**	**−0.018**	−0.387	−0.463	−0.015,	−0.017
Urophycis tenuis	**−1.548**	**−2.488**	**−0.113**	**−0.226**	0.580	0.712	0.030	0.023

Estimates with associated $p < 0.1$ highlighted in bold.

enhanced stratification induced uncoupling of the water column may be a reason for the 0.4 mg m^{-3} reduction in CHL observed in this analysis since 2011. However, Li et al. (2015) points out that stratification dynamics in the Northwest Atlantic shelf systems can vary considerably with more haline control of stratification in the Gulf of Maine and thermal control in the Mid-Atlantic bight. A recent model analysis by Shin and Alexander (2019) using downscaled Global Climate Models contends that the rate of bottom water warming may outstrip surface water warming. Ultimately, a comprehensive analysis of stratification in recent high resolution downscaled models of the region coupled to the biogeochemical processes controlled by vertical mixing will be necessary step in projecting future climate induced changes in the productivity of the NES.

In addition to the change in chlorophyll biomass observed in recent years, evidence suggest there has been a dramatic change in the phytoplankton structure of the NES that portends ecosystem impacts (Flombaum et al., 2020). The size structure of the NES phytoplankton community has shifted to smaller sized cells, which due to functional trait-environment interactions and the saturation of productivity of these smaller cells would be expected to have a negative effect on primary production (Chen et al., 2019). The shift in cell size may be related to the pulsed uptake of resources during winter months just prior to the development of the spring bloom that favor small cells relative to larger celled phytoplankton (Lin et al., 2020). As systems become more oligotrophic there tends to be a shift to dominance by picophytoplankton that produces a size-dependent change in food quality associated with low grazing pressure (Branco et al., 2020). For example, it is well known that important secondary producers in the NES, such as *Calanus finmarchicus* and other large copepods, do not graze on cells less than 10 μm (Marshall and Orr, 1955; Frost, 1972; Bundy et al., 1998). In addition to *Calanus finmarchicus* (a keystone species in the Gulf of Maine), the filter feeding by commercially harvested bivalves in the NES declines when feeding on particle sizes below 10 microns as seen in blue mussels *Mytilus edulis* (Strohmeier et al., 2012), bay scallops *Argopecten irradians* and eastern oyster *Crassostrea virginica* (Palmer and Williams, 1980), and sea scallops *Placopecten magellanicus* (Brillant and MacDonald, 2000). The opposite occurs in nutrient-rich waters that favor larger phytoplankton species and higher grazing pressure. In the Southern Ocean, warm, stratified conditions in the surface waters are dominated by picophytoplankton and a zooplankton community dominated by small bodied crustaceans (Venkataramana et al., 2019). Aquatic food webs utilize greater than 50% of their primary production owning to the higher

TABLE 3 | Tests of Canonical Dimensions for environmental and growth and biomass data.

	Canonical				
Dimension	**Corr.**	***Mult. F***	***df1***	***df2***	***p***
Growth Variables					
1	0.923	3.017	24	33	0.002
2	0.840	1.895	14	24	0.082
3	0.485	0.666	6	13	0.679
Biomass Variables					
1	0.883	5.499	15	39	0.000
2	0.837	4.687	8	30	0.001
3	0.583	2.741	3	16	0.077

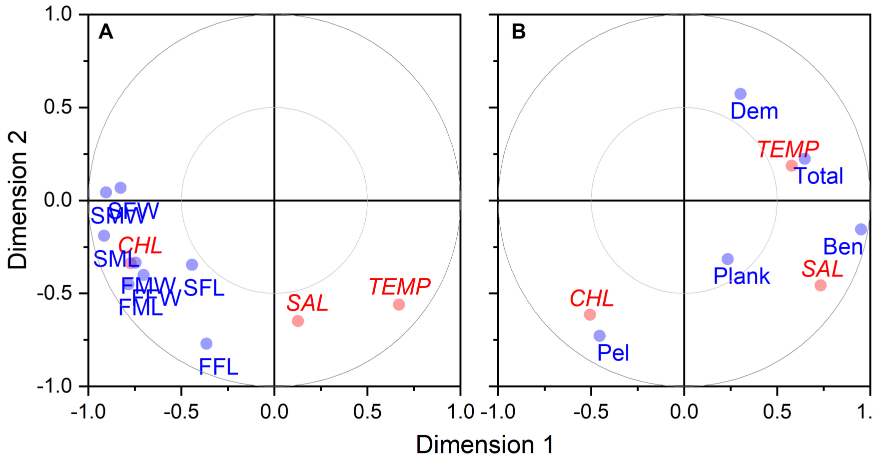

FIGURE 9 | Canonical correlation two-dimensional plot of environmental factors vs. growth **(A)** and biomass **(B)** variables. Environmental variable (shown in red) include temperature (TEMP), salinity (SAL), and CHL. Growth variables (shown in blue) are coded with first position as S for spring and F for fall, second position as M for males and F for females, and third positons as W for weight and L for length. Biomass variables (shown in blue) include benthivores (BEN), demersal piscivores (DEM), pelagic piscivores (PEL), planktivores (PLANK), and total biomass (TOTAL).

turnover rates associated with phytoplankton, making variation in phytoplankton production that much more critical to the production of secondary consumers and higher trophic level organisms (Barbier and Loreau, 2019).

In addition to an apparent shift in cell size fractions of phytoplankton, the dominant functional types of phytoplankton appear to have shifted, most notably a putative decline in diatoms. Diatoms play a pivotal role in marine food-webs shaping the productivity of ecosystems and are an important link in biogeochemical cycling (Harvey et al., 2019). Since diatoms are often chain forming and large-celled, a decline in diatoms may be synonymous with the size fraction shifts posited for the NES. And as with the factors associated with the development of size fraction patterns, vertical mixing is associated with the presence of larger phytoplankton like diatoms (Fragoso et al., 2019). The source phytoplankton that generates the flux of organic matter to the benthos is typically reflective of the dominant functional types in a given area on a global basis (Durkin et al., 2016), but since the NES phytoplankton community consists largely of diatoms, the contribution of diatoms to the POC is that much more critical. And since diatoms are passively buoyant, unlike other actively mobile flagellated phytoplankton, diatom blooms represent active transport of fixed carbon to the benthos (Gemmell et al., 2016). This effect is most pronounced with the fall bloom, which is known to produce enhanced rates of particulate organic carbon flux. Zooplankton grazing communities are in a transitional state in fall and can leave portions of aggressive blooms underutilized (Fujiwara et al., 2018). The fall period is also associated with changeover in the phytoplankton community leading to functional types that more readily tend to settle to the benthos (Kemp et al., 2000). We would expect that the Gulf of Maine and Georges Bank would be most impacted by the change in diatom populations since they more reliably have fall bloom activity (Friedland et al., 2015b). As with any set of modeling results, it is critical be circumspect about the reliability of the model fits and data output; hence, we also stress that the model results are at lease consistent with the observational counts of diatoms from the CPR samples.

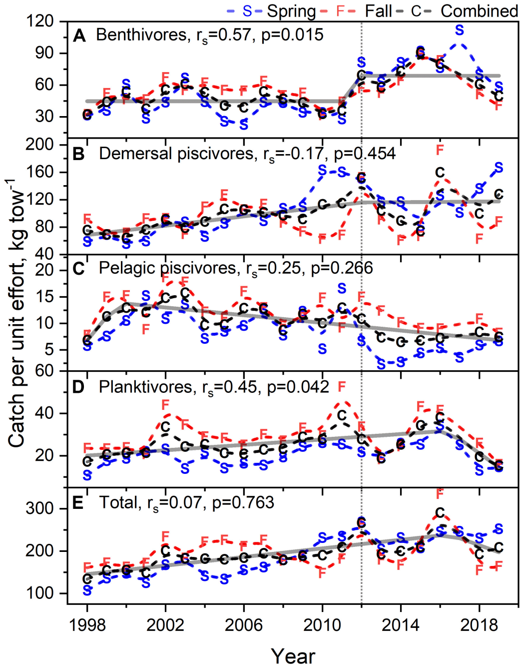

FIGURE 10 | Biomass as catch per unit effort for benthivores **(A)**, demersal piscivores **(B)**, pelagic piscivores **(C)**, planktivores **(D)**, and total biomass **(E)** during spring and fall time frames. Dashed black line is mean of spring and fall curves. In each caption, r_S is the Spearman correlation with associated *p*-value. Dashed line are b-splines; solid line either STARS or segmented regression models; vertical dotted line marks 2012.

TABLE 4 | Theil–Sen slope estimates expressed in decadal rates of change for CPUE variables by functional groups.

Functional group	Spring	Fall	Combined
Benthivores	**20.9**	3.9	12.6
Demersal piscivores	**39.0**	-2.7	**24.3**
Pelagic piscivores	**-2.7**	**-2.6**	**-2.8**
Planktivores	4.1	2.2	3.3
Total biomass	**64.8**	3.7	**32.0**

Estimates with associated $p < 0.1$ highlighted in bold.

The new levels of CHL and the associated potential decline in POC deposition in the NES may represent a stressor or critical production limitation for this ecosystem, and in particular, ecosystem services related to resource species. Though not well studied, it would appear large marine ecosystems may have a threshold of CHL associated with fishery yields. In LMEs with an average annual CHL over 1.0 mg m^{-3}, fishery total catch or fisheries production on an areal basis tend to be over twice the level of ecosystems with annual CHL less than 1.0 mg m^{-3} (Friedland et al., 2012). Much of the NES is now at or below this threshold, which we would anticipate would result in lower productivity of higher trophic level organisms. In contemporary research, the most demonstrative effects of phytoplankton biomass and production relate to the feeding and condition of larval fish and its effect on year class strength. Over many decades in the North Sea, primary production measurements suggest a gradual decline in the base of the food chain and is implicated in the decline of secondary producers, notably small copepods including the genera *Temora*, *Acartia*, *Pseudocalanus*, and *Paracalanus* (Capuzzo et al., 2018). Small copepods often play a pivotal role in the first feeding of larval fish (Buckley and Durbin, 2006), hence the concern that recruitment levels have eroded as a consequence. Over shorter time series and with the benefit of remote sensing datasets, interannual variation in blooms and primary production levels have been associated with recruitment success of Pacific herring, *Clupea pallasi*, which seem to benefit from the proximity of the spring bloom to adult spawning (Boldt et al., 2019) and pre-metamorphic growth of rockfish (*Sebastes* spp.) larvae (Wheeler et al., 2017). Finally, in walleye pollock (*Gadus chalcogrammus*), whose recruitment is governed by thermally mediated predation effects (Uchiyama et al., 2020), bloom activity can serve as an event level forcing factor affecting year class strength (Gann et al., 2016).

It is difficult to predict the specific ecological response to any change in habitat (Friedland et al., 2020) due to the complexity of interactions and pressures in the region. Our observations indicate that there is an expansion of fish biomass in the NES, but at the same time, growth is slowing for many species. There are clear examples of the inverse relationship between fish growth and temperature, particularly at range edges (von Biela et al., 2015). Thus, while expanded thermal habitat is associated with higher recruitment, under the same temperature regime there is an expectation of a loss of larger fish as oxygen supply restricts increases in body size (Neuheimer et al., 2011). Long-term impacts of declining growth rates are also likely to reduce fecundity and egg quality, which varies with female fish size, and increases the risk of predation and starvation. For species such as silver hake *Merluccius bilinearis* that has shown a steady increase in growth over time in the NES, there is some evidence that they are able to supplement their diet with invertebrates such as Northern shrimp (*Pandalus borealis*) and avoid starvation (Link and Idoine, 2009). Thus, defining winners and losers under a thermal habitat regime shift, especially those coupled to changes in primary production, depends on more than just an individual species' thermal tolerance; other ecological considerations need to be considered to fully understand and manage species under such changes to the habitat.

While the concept of regime change or shift in marine ecosystems has been extensively reviewed (Collie et al., 2004; Jiao, 2009), the definition of what constitutes a regime change varies by the ecosystem function under investigation. Regime change has been used in both formal and informal contexts. In the informal context, many practitioners simply associate a step change in conditions to be a regime change; and in many cases, the change in conditions is represented by a shift in a single factor (van Putten et al., 2019). However, in a more formal application of the term, a change of regime is considered a demonstration of a change in not only a suite of environmental indicators, but also evidence of a change in ecosystem function and productivity (Mollmann et al., 2015). In exploring the notion of high magnitude regime shifts, Scheffer and Carpenter (2003) considered what might cause a catastrophic shift in ecosystem state and conditions. They made the observation that a large change, or one with hysteresis, may be the result of accumulated gradual change that arrives at a threshold level and then the shift occurs. Another important distinction can be made between consumer and producer effects on transformative change (Connell et al., 2011). The producer level effects on the NES ecosystem state would appear to be dominant since the physical forcing and production level biology are associated with concomitant change points. Consumer effects would appear to be moderated by multiyear time lags in the sense the impacts of a change in growth and recruitment persists over the life cycle of the organism. This sharpens our focus on the shifts in temperature and salinity. The proximity of change on the NES to basin scale circulation (Kwon et al., 2019) would suggest the accumulated effects of climate perturbation resulted in a change point in ocean dynamics, which will likely be seen elsewhere beyond the confines of the NES. What should not be lost in the detail of the proximate response to change in physical and biological factors is that this climate change event on the NES simultaneously impacted the niche space of many species. What we do not know as of yet is whether the extent of niche change has or will actuate a change in biodiversity and fisheries productivity (Trisos et al., 2020).

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: The data used in this analysis is available from the following sources: Sea surface temperature is available from the OISST website https://www.ncdc.noaa.gov/oisst; NEFSC survey salinity data is available from the National Center for Environmental Information https://www.nodc.noaa.gov/oads/stewardship/data_assets.html; CHL and water leaving radiance data is available from the Hermes GlobColour website http://hermes.acri.fr/index.php; NEFSC Survey length and weight at age and biomass is from the InPort NMFS Data Management Program https://inport.nmfs.noaa.gov/inport/; CPR data is from the Marine Biological survey site https://www.cprsurvey.org/

AUTHOR CONTRIBUTIONS

KF led the analysis and drafting of the manuscript. RM and JRM assisted with data analysis and along with NS, JT, DB, and JLM contributed to the drafting of the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

Funding for JM's effort was provided by the NASA Ecosystem Forecasting Program, The Gordon and Betty Moore Foundation under Grant No. 3292, and the NASA Applied Information Systems Technology Program under NNH18ZDA001N-AIST.

ACKNOWLEDGMENTS

We thank M. Correa-Ramirez and C. Melrose for help in estimating phytoplankton functional type data. J. Langan for comments on an early draft of the manuscript. P. Kostovick for assistance with data.

REFERENCES

Alvain, S., Moulin, C., Dandonneau, Y., and Loisel, H. (2008). Seasonal distribution and succession of dominant phytoplankton groups in the global ocean: a satellite view. *Glob. Biogeochem. Cycles* 22:GB3001. doi: 10.1029/2007GB003154

Asch, R. G., Stock, C. A., and Sarmiento, J. L. (2019). Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. *Glob. Change Biol.* 25, 2544–2559. doi: 10.1111/gcb.14650

Austin, A. M., Bisagni, J. J., and Schmidt, A. (2019). Inter-annual variability of shelf water volume on the northeastern Canadian and United States continental shelf, 1973–2013. *Cont. Shelf Res.* 187:103962. doi: 10.1016/j.csr.2019.103962

Barbier, M., and Loreau, M. (2019). Pyramids and cascades: a synthesis of food chain functioning and stability. *Ecol. Lett.* 22, 405–419. doi: 10.1111/ele.13196

Barton, A. D., Irwin, A. J., Finkel, Z. V., and Stock, C. A. (2016). Anthropogenic climate change drives shift and shuffle in North Atlantic phytoplankton communities. *Proc. Natl. Acad. Sci. U.S.A.* 113, 2964–2969. doi: 10.1073/pnas.1519080113

Batt, R. D., Morley, J. W., Selden, R. L., Tingley, M. W., and Pinsky, M. L. (2017). Gradual changes in range size accompany long-term trends in species richness. *Ecol. Lett.* 20, 1148–1157. doi: 10.1111/ele.12812

Batten, S. D., Clark, R., Flinkman, J., Hays, G., John, E., John, A. W. G., et al. (2003). CPR sampling: the technical background, materials and methods, consistency and comparability. *Prog. Oceanogr.* 58, 193–215. doi: 10.1016/j.pocean.2003.08.004

Boldt, J. L., Thompson, M., Rooper, C. N., Hay, D. E., Schweigert, J. F., Quinn, T. J., et al. (2019). Bottom-up and top-down control of small pelagic forage fish: factors affecting age-0 herring in the strait of Georgia, British Columbia. *Mar. Ecol. Prog. Ser.* 617, 53–66. doi: 10.3354/meps12485

Branco, P., Egas, M., Hall, S. R., and Huisman, J. (2020). Why do phytoplankton evolve large size in response to grazing? *Am. Nat.* 195, E20–E37. doi: 10.1086/706251

Brewin, R. J. W., Sathyendranath, S., Jackson, T., Barlow, R., Brotas, V., Airs, R., et al. (2015). Influence of light in the mixed-layer on the parameters of a three-component model of phytoplankton size class. *Remote Sens. Environ.* 168, 437–450. doi: 10.1016/j.rse.2015.07.004

Brillant, M. G. S., and MacDonald, B. A. (2000). Postingestive selection in the sea scallop, *Placopecten magellanicus* (Gmelin): the role of particle size and density. *J. Exp. Mar. Biol. Ecol.* 253, 211–227. doi: 10.1016/S0022-0981(00)00258-6

Buckley, L. J., and Durbin, E. G. (2006). Seasonal and inter-annual trends in the zooplankton prey and growth rate of Atlantic cod (Gadus morhua) and haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 53, 2758–2770. doi: 10.1016/j.dsr2.2006.08.009

Bundy, M. H., Gross, T. F., Vanderploeg, H. A., and Rudi Strickler, J. (1998). Perception of inert particles by calanoid copepods: behavioral observations and a numerical model. *J. Plankton Res.* 20, 2129–2152. doi: 10.1093/plankt/20.11.2129

Burnham, K. P., and Anderson, D. R. (2004). Multimodel Inference: understanding AIC and BIC in model selection. *Soc. Methods Res.* 33, 261–304. doi: 10.1177/0049124104268644

Capuzzo, E., Lynam, C. P., Barry, J., Stephens, D., Forster, R. M., Greenwood, N., et al. (2018). A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. *Glob. Change Biol.* 24, E352–E364. doi: 10.1111/gcb.13916

Chandrapavan, A., Caputi, N., and Kangas, M. I. (2019). The decline and recovery of a crab population from an extreme marine heatwave and a changing climate. *Front. Mar. Sci.* 6:510. doi: 10.3389/fmars.2019.00510

Chen, B., Smith, S. L., and Wirtz, K. W. (2019). Effect of phytoplankton size diversity on primary productivity in the North Pacific: trait distributions under environmental variability. *Ecol. Lett.* 22, 56–66. doi: 10.1111/ele.13167

Chen, K., Gawarkiewicz, G. G., Lentz, S. J., and Bane, J. M. (2014). Diagnosing the warming of the Northeastern US Coastal Ocean in 2012: a linkage between the atmospheric jet stream variability and ocean response. *J. Geophys. Res.-Oceans* 119, 218–227. doi: 10.1002/2013jc009393

Chen, Z., Kwon, Y.-O., Chen, K., Fratantoni, P., Gawarkiewicz, G., and Joyce, T. M. (2020). Long-term SST variability on the northwest Atlantic Continental shelf and slope. *Geophys. Res. Lett* 47:e2019GL085455. doi: 10.1029/2019GL085455

Cheng, L., Abraham, J., Hausfather, Z., and Trenberth, K. E. (2019). How fast are the oceans warming? *Science* 363:eaax1875. doi: 10.1126/science.aax1875

Collie, J. S., Richardson, K., and Steele, J. H. (2004). Regime shifts: can ecological theory illuminate the mechanisms? *Prog. Oceanogr.* 60, 281–302. doi: 10.1016/j.pocean.2004.02.013

Connell, S. D., Russell, B. D., and Irving, A. D. (2011). Can strong consumer and producer effects be reconciled to better forecast "catastrophic" phase-shifts in marine ecosystems? *J. Exp. Mar. Biol. Ecol.* 400, 296–301. doi: 10.1016/j.jembe.2011.02.031

Conversi, A., Umani, S. F., Peluso, T., Molinero, J. C., Santojanni, A., and Edwards, M. (2010). The mediterranean sea regime shift at the end of the 1980s, and intriguing parallelisms with other European basins. *PLoS One* 5:e10633. doi: 10.1371/journal.pone.0010633

Correa-Ramirez, M., Morales, C. E., Letelier, R., Anabalón, V., and Hormazabal, S. (2018). Improving the remote sensing retrieval of Phytoplankton functional types (PFT) using empirical orthogonal functions: a case study in a coastal upwelling region. *Remote Sens.* 10:498. doi: 10.3390/rs10040498

Dantas, D. D. F., Caliman, A., Guariento, R. D., Angelini, R., Carneiro, L. S., Lima, S. M. Q., et al. (2019). Climate effects on fish body size-trophic position relationship depend on ecosystem type. *Ecography* 42, 1579–1586. doi: 10.1111/ecog.04307

Desprespatanjo, L. I., Azarovitz, T. R., and Byrne, C. J. (1988). 25 years of fish surveys in the Northwest Atlantic - the Nmfs northeast fisheries centers bottom Trawl survey program. *Mar. Fish. Rev.* 50, 69–71.

Durant, J. M., Molinero, J.-C., Ottersen, G., Reygondeau, G., Stige, L. C., and Langangen, Ø. (2019). Contrasting effects of rising temperatures on trophic interactions in marine ecosystems. *Sci. Rep.* 9:15213. doi: 10.1038/s41598-019-51607-w

Durkin, C. A., Mooy, B. A. S. V., Dyhrman, S. T., and Buesseler, K. O. (2016). Sinking phytoplankton associated with carbon flux in the Atlantic Ocean. *Limnol. Oceanogr.* 61, 1172–1187. doi: 10.1002/lno.10253

Dutkiewicz, S., Hickman, A. E., Jahn, O., Henson, S., Beaulieu, C., and Monier, E. (2019). Ocean colour signature of climate change. *Nat. Commun.* 10:578. doi: 10.1038/s41467-019-08457-x

Flombaum, P., Wang, W.-L., Primeau, F. W., and Martiny, A. C. (2020). Global picophytoplankton niche partitioning predicts overall positive response to ocean warming. *Nat. Geosci.* 13, 116–120. doi: 10.1038/s41561-019-0524-2

Forrestal, F. C., Schirripa, M., Goodyear, C. P., Arrizabalaga, H., Babcock, E. A., Coelho, R., et al. (2019). Testing robustness of CPUE standardization and inclusion of environmental variables with simulated longline catch datasets. *Fish. Res.* 210, 1–13. doi: 10.1016/j.fishres.2018.09.025

Fragoso, G. M., Davies, E. J., Ellingsen, I., Chauton, M. S., Fossum, T., Ludvigsen, M., et al. (2019). Physical controls on phytoplankton size structure, photophysiology and suspended particles in a Norwegian biological hotspot. *Prog. Oceanogr.* 175, 284–299. doi: 10.1016/j.pocean.2019.05.001

Friedland, K. D., Ahrenholz, D. W., and Haas, L. W. (2005). Viable gut passage of cyanobacteria through the filter-feeding fish Atlantic menhaden, Brevoortia tyrannus. *J. Plankton Res.* 27, 715–718. doi: 10.1093/plankt/fbi036

Friedland, K. D., Langan, J. A., Large, S. I., Selden, R. L., Link, J. S., Watson, R. A., et al. (2020). Changes in higher trophic level productivity, diversity and niche space in a rapidly warming continental shelf ecosystem. *Sci. Total Environ.* 704:135270. doi: 10.1016/j.scitotenv.2019.135270

Friedland, K. D., Leaf, R. T., Kane, J., Tommasi, D., Asch, R. G., Rebuck, N., et al. (2015a). Spring bloom dynamics and zooplankton biomass response on the US Northeast Continental Shelf. *Cont. Shelf Res.* 102, 47–61. doi: 10.1016/j.csr.2015.04.005

Friedland, K. D., Leaf, R. T., Kristiansen, T., and Large, S. I. (2015b). Layered effects of parental condition and larval survival on the recruitment of neighboring haddock stocks. *Can. J. Fish. Aquat. Sci.* 72, 1672–1681. doi: 10.1139/cjfas-2015-0084

Friedland, K. D., McManus, M. C., Morse, R. E., and Link, J. S. (2019). Event scale and persistent drivers of fish and macroinvertebrate distributions on the Northeast US Shelf. *ICES J. Mar. Sci.* 76, 1316–1334. doi: 10.1093/icesjms/fsy167

Friedland, K. D., Mouw, C. B., Asch, R. G., Ferreira, A. S. A., Henson, S., Hyde, K. J. W., et al. (2018). Phenology and time series trends of the dominant seasonal phytoplankton bloom across global scales. *Glob. Ecol. Biogeogr.* 27, 551–569. doi: 10.1111/geb.12717

Friedland, K. D., Record, N. R., Asch, R. G., Kristiansen, T., Saba, V. S., Drinkwater, K. F., et al. (2016). Seasonal phytoplankton blooms in the North Atlantic linked to the overwintering strategies of copepods. *Elementa* 4:99.

Friedland, K. D., Stock, C., Drinkwater, K. F., Link, J. S., Leaf, R. T., Shank, B. V., et al. (2012). Pathways between primary production and fisheries yields of large marine ecosystems. *Plos One* 7:e28945. doi: 10.1371/journal.pone.0028945

Frost, B. W. (1972). Effects of size and concentration of food particles on the feeding behavior of the marine Planktonic copepod Calanus Pacificus1. *Limnol. Oceanogr.* 17, 805–815. doi: 10.4319/lo.1972.17.6.0805

Fujiwara, A., Nishino, S., Matsuno, K., Onodera, J., Kawaguchi, Y., Hirawake, T., et al. (2018). Changes in phytoplankton community structure during wind-induced fall bloom on the central Chukchi shelf. *Polar Biol.* 41, 1279–1295. doi: 10.1007/s00300-018-2284-7

Gann, J. C., Eisner, L. B., Porter, S., Watson, J. T., Cieciel, K. D., Mordy, C. W., et al. (2016). Possible mechanism linking ocean conditions to low body weight and poor recruitment of age-0 walleye pollock (Gadus chalcogrammus) in the southeast Bering Sea during 2007. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 134, 115–127. doi: 10.1016/j.dsr2.2015.07.010

Gawarkiewicz, G., Chen, K., Forsyth, J., Bahr, F., Mercer, A. M., Ellertson, A., et al. (2019). Characteristics of an advective marine heatwave in the middle atlantic bight in early 2017. *Front. Mar. Sci.* 6:712. doi: 10.3389/fmars.2019.00712

Gemmell, B. J., Oh, G., Buskey, E. J., and Villareal, T. A. (2016). Dynamic sinking behaviour in marine phytoplankton: rapid changes in buoyancy may aid in nutrient uptake. *Proc. R. Soc. B Biol. Sci.* 283:20161126. doi: 10.1098/rspb.2016.1126

Goode, A. G., Brady, D. C., Steneck, R. S., and Wahle, R. A. (2019). The brighter side of climate change: how local oceanography amplified a lobster boom in the Gulf of Maine. *Glob. Change Biol.* 25, 3906–3917. doi: 10.1111/gcb.14778

Greene, C. (2012). Recent arctic climate change and its remote forcing of northwest Atlantic shelf ecosystems. *Oceanography* 25, 208–213. doi: 10.5670/oceanog.2012.64

Groom, S., Sathyendranath, S., Ban, Y., Bernard, S., Brewin, R., Brotas, V., et al. (2019). Satellite ocean color: current status and future perspective. *Front. Mar. Sci.* 6:485. doi: 10.3389/fmars.2019.00485

Harvey, B. P., Agostini, S., Kon, K., Wada, S., and Hall-Spencer, J. M. (2019). Diatoms dominate and alter marine food-webs when CO2 rises. *Diversity* 11:242. doi: 10.3390/d11120242

Henson, S., Cole, H., Beaulieu, C., and Yool, A. (2013). The impact of global warming on seasonality of ocean primary production. *Biogeosciences* 10, 4357–4369. doi: 10.5194/bg-10-4357-2013

Hirata, T., Hardman-Mountford, N. J., Brewin, R. J. W., Aiken, J., Barlow, R., Suzuki, K., et al. (2011). Synoptic relationships between surface Chlorophyll-*a* and diagnostic pigments specific to phytoplankton functional types. *Biogeosciences* 8, 311–327. doi: 10.5194/bg-8-311-2011

Holbrook, N. J., Scannell, H. A., Sen Gupta, A., Benthuysen, J. A., Feng, M., Oliver, E. C. J., et al. (2019). A global assessment of marine heatwaves and their drivers. *Nat. Commun.* 10:2624. doi: 10.1038/s41467-019-10206-z

Howarth, L. M., Roberts, C. M., Thurstan, R. H., and Stewart, B. D. (2014). The unintended consequences of simplifying the sea: making the case for complexity. *Fish Fish.* 15, 690–711. doi: 10.1111/faf.12041

Huxel, G. R., and McCann, K. (1998). Food web stability: the influence of trophic flows across habitats. *Am. Nat.* 152, 460–469. doi: 10.1086/286182

Jiao, Y. (2009). Regime shift in marine ecosystems and implications for fisheries management, a review. *Rev. Fish Biol. Fish.* 19, 177–191. doi: 10.1007/s11160-008-9096-8

Kane, J. (2007). Zooplankton abundance trends on Georges Bank, 1977-2004. *ICES J. Mar. Sci.* 64, 909–919. doi: 10.1093/icesjms/fsm066

Kemp, A. E. S., Pike, J., Pearce, R. B., and Lange, C. B. (2000). The "Fall dump" - a new perspective on the role of a "shade flora" in the annual cycle of diatom production and export flux. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 47, 2129–2154. doi: 10.1016/S0967-0645(00)00019-9

Kwon, Y.-O., Seo, H., Ummenhofer, C. C., and Joyce, T. M. (2019). Impact of multidecadal variability in Atlantic SST on winter atmospheric blocking. *J. Clim.* 33, 867–892. doi: 10.1175/JCLI-D-19-0324.1

Lamont, T., Barlow, R. G., and Brewin, R. J. W. (2019). Long-term trends in Phytoplankton chlorophyll a and size structure in the Benguela upwelling system. *J. Geophys. Res. Oceans* 124, 1170–1195. doi: 10.1029/2018jc014334

Lawson, C. L., and Hanson, R. J. (1995). "Solving least squares problems," in *Society for Industrial and Applied Mathematics* (Philadelphia, PA: SIAM Publications). doi: 10.1137/1.9781611971217

Li, Y., Fratantoni, P. S., Chen, C., Hare, J. A., Sun, Y., Beardsley, R. C., et al. (2015). Spatio-temporal patterns of stratification on the Northwest Atlantic shelf. *Prog. Oceanogr.* 134, 123–137. doi: 10.1016/j.pocean.2015.01.003

Lin, F.-S., Ho, P.-C., Sastri, A. R., Chen, C.-C., Gong, G.-C., Jan, S., et al. (2020). Resource availability affects temporal variation of phytoplankton size structure in the Kuroshio east of Taiwan. *Limnol. Oceanogr.* 65, 236–246. doi: 10.1002/lno.11294

Link, J. S., and Idoine, J. S. (2009). Estimates of predator consumption of the northern shrimp *Pandalus borealis* with implications for estimates of population biomass in the gulf of maine. *North Am. J. Fish. Manag.* 29, 1567–1583. doi: 10.1577/M08-233.1

Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W. L., Galbraith, E. D., et al. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc. Natl. Acad. Sci. U.S.A.* 116, 12907–12912. doi: 10.1073/pnas.1900194116

Maritorena, S., d'Andon, O. H. F., Mangin, A., and Siegel, D. A. (2010). Merged satellite ocean color data products using a bio-optical model: characteristics, benefits and issues. *Remote Sens. Environ.* 114, 1791–1804. doi: 10.1016/j.rse.2010.04.002

Marshall, S. M., and Orr, A. P. (1955). On the biology of Calanus finmarchicus VIII. Food uptake, assimilation and excretion in adult and Stage *V Calanus*. *J. Mar. Biol. Assoc. U.K.* 34, 495–529. doi: 10.1017/S0025315400008778

Mérillet, L., Kopp, D., Robert, M., Mouchet, M., and Pavoine, S. (2020). Environment outweighs the effects of fishing in regulating demersal community structure in an exploited marine ecosystem. *Glob. Change Biol.* 26, 2106–2119. doi: 10.1111/gcb.14969

Miller, T. J., Das, C., Politis, P. J., Miller, A. S., Lucey, S. M., Legault, C. M., et al. (2010). Estimation of albatross IV to henry B. NEFSC Ref. Doc. 10-05, 238.

Mills, K. E., Pershing, A. J., Brown, C. J., Chen, Y., Chiang, F. S., Holland, D. S., et al. (2013). Fisheries management in a changing climate lessons from the 2012 ocean heat wave in the Northwest Atlantic. *Oceanography* 26, 191–195.

Moisan, J. R., Moisan, T. A., and Abbott, M. R. (2002). Modelling the effect of temperature on the maximum growth rates of phytoplankton populations. *Ecol. Model.* 153, 197–215. doi: 10.1016/S0304-3800(02)00008-X

Moisan, J. R., Moisan, T. A. H., and Linkswiler, M. A. (2011). An inverse modeling approach to estimating phytoplankton pigment concentrations from phytoplankton absorption spectra. *J. Geophys. Res. Oceans* 116:C09018. doi: 10.1029/2010JC006786

Moisan, T. A., Rufty, K. M., Moisan, J. R., and Linkswiler, M. A. (2017). Satellite observations of Phytoplankton functional type spatial distributions, phenology, diversity, and ecotones. *Front. Mar. Sci.* 4:189. doi: 10.3389/fmars.2017.00189

Mollmann, C., Folke, C., Edwards, M., and Conversi, A. (2015). Marine regime shifts around the globe: theory, drivers and impacts. *Philos. Trans. R. Soc. B Biol. Sci.* 370, 1–5. doi: 10.1098/rstb.2013.0260

Muggeo, V. M. R. (2003). Estimating regression models with unknown breakpoints. *Stat. Med.* 22, 3055–3071. doi: 10.1002/sim.1545

Muggeo, V. M. R. (2017). Interval estimation for the breakpoint in segmented regression: a smoothed score-based approach. *Aust. N.Z. J. Stat.* 59, 311–322. doi: 10.1111/anzs.12200

Neuheimer, A. B., Thresher, R. E., Lyle, J. M., and Semmens, J. M. (2011). Tolerance limit for fish growth exceeded by warming waters. *Nat. Clim. Change* 1, 110–113. doi: 10.1038/nclimate1084

Paerl, H. W. (2018). Mitigating toxic planktonic cyanobacterial blooms in aquatic ecosystems facing increasing anthropogenic and climatic pressures. *Toxins* 10:76. doi: 10.3390/toxins10020076

Palmer, R. E., and Williams, L. G. (1980). Effect of particle concentration on filtration efficiency of the bay scallop *Argopecten irradians* and the oyster *Crassostrea virginica*. *Ophelia* 19, 163–174. doi: 10.1080/00785326.1980.10425514

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., et al. (2015). Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350, 809–812. doi: 10.1126/science.aac9819

Pershing, A. J., Record, N. R., Franklin, B. S., Kennedy, B. T., McClenachan, L., Mills, K. E., et al. (2019). Challenges to natural and human communities from surprising ocean temperatures. *Proc. Natl. Acad. Sci. U.S.A.* 116, 18378–18383. doi: 10.1073/pnas.1901084116

Press, W. H., Flannery, B. P., Teukolsky, S. A., Vetterling, W. T., and Gould, H. (1987). Numerical recipes, The art of scientific computing. *Am. J. Phys.* 55, 90–91. doi: 10.1119/1.14981

Reynolds, R. W., Smith, T. M., Liu, C., Chelton, D. B., Casey, K. S., and Schlax, M. G. (2007). Daily high-resolution-blended analyses for sea surface temperature. *J. Clim.* 20, 5473–5496. doi: 10.1175/2007jcli1824.1

Roberts, S. D., Van Ruth, P. D., Wilkinson, C., Bastianello, S. S., and Bansemer, M. S. (2019). Marine heatwave, harmful algae blooms and an extensive fish kill event during 2013 in South Australia. *Front. Mar. Sci* 6:610. doi: 10.3389/fmars.2019.00610

Rodionov, S. N. (2004). A sequential algorithm for testing climate regime shifts. *Geophys. Res. Lett.* 31, 1–4. doi: 10.1029/2004gl019448

Rodionov, S. N. (2006). Use of prewhitening in climate regime shift detection. *Geophys. Res. Lett.* 33, 1–4. doi: 10.1029/2006gl025904

Rogers, L. A., Griffin, R., Young, T. L., Fuller, E., St Martin, K., and Pinsky, M. L. (2019). Shifting habitats expose fishing communities to risk under climate change. *Nat. Clim. Change* 9, 512-516. doi: 10.1038/s41558-019-0503-z

Roxy, M. K., Modi, A., Murtugudde, R., Valsala, V., Panickal, S., Kumar, S. P., et al. (2016). A reduction in marine primary productivity driven by rapid warming over the tropical Indian Ocean. *Geophys. Res. Lett.* 43, 826–833. doi: 10.1002/2015gl066979

Salo, T., Mattila, J., and Eklöf, J. (2020). Long-term warming affects ecosystem functioning through species turnover and intraspecific trait variation. *Oikos* 129, 283–295. doi: 10.1111/oik.06698

Sanford, E., Sones, J. L., Garcia-Reyes, M., Goddard, J. H. R., and Largier, J. L. (2019). Widespread shifts in the coastal biota of northern California during the 2014-2016 marine heatwaves. *Sci. Rep.* 9:4126. doi: 10.1038/s41598-019-40784-3

Scheffer, M., and Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* 18, 648–656. doi: 10.1016/j.tree.2003.09.002

Schiller, L., Bailey, M., Jacquet, J., and Sala, E. (2018). High seas fisheries play a negligible role in addressing global food security. *Sci. Adv.* 4:4216. doi: 10.1126/sciadv.aat8351

Shackell, N. L., Bundy, A., Nye, J. A., and Link, J. S. (2012). Common large-scale responses to climate and fishing across Northwest Atlantic ecosystems. *ICES J. Mar. Sci.* 69, 151–162. doi: 10.1093/icesjms/fsr195

Sherman, K., Solow, A., Jossi, J., and Kane, J. (1998). Biodiversity and abundance of the zooplankton of the Northeast Shelf ecosystem. *Ices J. Mar. Sci.* 55, 730–738. doi: 10.1006/jmsc.1998.0377

Shin, S.-I., and Alexander, M. A. (2019). Dynamical downscaling of future hydrographic changes over the Northwest Atlantic Ocean. *J. Clim.* 33, 2871–2890. doi: 10.1175/JCLI-D-19-0483.1

Smith, K. A., Dowling, C. E., and Brown, J. (2019). Simmered then boiled: multi-decadal Poleward shift in distribution by a temperate fish accelerates during marine heatwave. *Front. Mar. Sci* 6:407. doi: 10.3389/fmars.2019.00407

Somavilla, R., Gonzalez-Pola, C., and Fernandez-Diaz, J. (2017). The warmer the ocean surface, the shallower the mixed layer. *How much of this is true?*. *J. Geophys. Res. Oceans* 122, 7698–7716. doi: 10.1002/2017jc013125

Strohmeier, T., Strand, Ø, Alunno-Bruscia, M., Duinker, A., and Cranford, P. J. (2012). Variability in particle retention efficiency by the mussel *Mytilus edulis*. *J. Exp. Mar. Biol. Ecol* 412, 96–102. doi: 10.1016/j.jembe.2011.11.006

Thomson, R. E., and Emery, W. J. (2014). "Chapter 5 - Time Series Analysis Methods," in *Data Analysis Methods in Physical Oceanography*, 3rd Edn, eds R. E. Thomson, and W. J. Emery, (Boston: Elsevier), 425–591. doi: 10.1016/B978-0-12-387782-6.00005-3

Townsend, D. W. (1998). Sources and cycling of nitrogen in the Gulf of Maine. *J. Mar. Syst.* 16, 283–295. doi: 10.1016/S0924-7963(97)00024-9

Townsend, D. W., Pettigrew, N. R., Thomas, M. A., Neary, M. G., McGillicuddy, D. J., and O'Donnell, J. (2015). Water masses and nutrient sources to the Gulf of Maine. *J. Mar. Res.* 73, 93–122. doi: 10.1357/002224015815848811

Trisos, C. H., Merow, C., and Pigot, A. L. (2020). The projected timing of abrupt ecological disruption from climate change. *Nature* 580, 496–501. doi: 10.1038/s41586-020-2189-9

Uchiyama, T., Mueter, F. J., and Kruse, G. H. (2020). Multispecies biomass dynamics models reveal effects of ocean temperature on predation of juvenile pollock in the eastern Bering Sea. *Fish. Oceanogr.* 29, 10–22. doi: 10.1111/fog.12433

Ullah, H., Nagelkerken, I., Goldenberg, S. U., and Fordham, D. A. (2018). Climate change could drive marine food web collapse through altered trophic flows and cyanobacterial proliferation. *Plos Biol* 16:e2003446. doi: 10.1371/journal.pbio.2003446

van Putten, I., Boschetti, F., Ling, S., and Richards, S. A. (2019). Perceptions of system-identity and regime shift for marine ecosystems. *ICES J. Mar. Sci.* 76, 1736–1747. doi: 10.1093/icesjms/fsz058

Venkataramana, V., Anilkumar, N., Naik, R. K., Mishra, R. K., and Sabu, P. (2019). Temperature and phytoplankton size class biomass drives the zooplankton food web dynamics in the Indian Ocean sector of the Southern Ocean. *Polar Biol.* 42, 823–829. doi: 10.1007/s00300-019-02472-w

von Biela, V. R., Kruse, G. H., Mueter, F. J., Black, B. A., Douglas, D. C., Helser, T. E., et al. (2015). Evidence of bottom-up limitations in nearshore marine systems based on otolith proxies of fish growth. *Mar. Biol.* 162, 1019–1031. doi: 10.1007/s00227-015-2645-5

Wheeler, S. G., Anderson, T. W., Bell, T. W., Morgan, S. G., and Hobbs, J. A. (2017). Regional productivity predicts individual growth and recruitment of rockfishes in a northern California upwelling system. *Limnol. Oceanogr.* 62, 754–767. doi: 10.1002/lno.10458

Wiedenmann, J., and Jensen, O. P. (2019). Could recent overfishing of New England groundfish have been prevented? A retrospective evaluation of alternative management strategies. *Can. J. Fish. Aquat. Sci.* 76, 1006–1018. doi: 10.1139/cjfas-2018-0129

Yamaguchi, R., and Suga, T. (2019). Trend and variability in global upper-ocean stratification since the 1960s. *J. Geophys. Res. Oceans* 124, 8933–8948. doi: 10.1029/2019jc015439

Yue, S., Pilon, P., Phinney, B., and Cavadias, G. (2002). The influence of autocorrelation on the ability to detect trend in hydrological series. *Hydrol. Process.* 16, 1807–1829. doi: 10.1002/hyp.1095

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.

frontiers in Marine Science

OPINION
published: 24 September 2020
doi: 10.3389/fmars.2020.554573

The Ocean Decade: A True Ecosystem Modeling Challenge

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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: *22 April 2020*
Accepted: *24 August 2020*
Published: *24 September 2020*

Citation:
Heymans JJ, Bundy A, Christensen V, Coll M, de Mutsert K, Fulton EA, Piroddi C, Shin Y-J, Steenbeek J and Travers-Trolet M (2020) The Ocean Decade: A True Ecosystem Modeling Challenge. Front. Mar. Sci. 7:554573. doi: 10.3389/fmars.2020.554573

Keywords: Ocean Decade, ecosystem modeling, climate change, ecosystem based management (EBM), sustainable development goals (SDG)

INTRODUCTION

The UN declared the 2021–2030 as the Decade of Ocean Science for Sustainable Development (Ocean Decade). The Ocean Decade's vision is to "develop scientific knowledge, build infrastructure and foster relationships for a sustainable and healthy ocean." The Ocean Decade aims to achieve six societal outcomes: (1) A clean ocean, through identifying and removing sources of pollution; (2) A healthy and resilient ocean, with mapped and protected marine ecosystems; (3) A predicted ocean, enabling society to understand current and future ocean conditions; (4) A safe ocean, protecting people from ocean hazards; (5) A sustainably harvested ocean, providing food and resources for the blue economy; and (6) A transparent ocean, giving citizens equitable access to data, information and technologies. It also aims to provide concrete scientific support to coastal management, adaptation and restoration, marine spatial planning, marine protected areas, fisheries management, sustainable expansion of the blue economy, nationally determined contributions to the United Nations Framework Convention on Climate Change (UNFCCC), national ocean policies, development of national Research and Development (R&D), capacity development, and early warning systems.

The Ocean Decade offers the ocean science community a unique opportunity to change the way we support sustainable development and galvanize ocean sciences for the future (Ryabinin et al., 2019). In addition, the UN Decade for Ecosystem Restoration (2021–2030), gives the ocean science community an imperative to work toward a sustainable future for the ocean.

We challenge the marine ecosystem modeling community to address how we: (i) enable ocean managers and decision-makers to use our science, (ii) communicate our science, and most importantly (iii) ensure co-design of our science to achieve sustainable development. For this, we define ecosystem models as those that span physical and human drivers of change in the full ecosystem from plankton to top predators.

WHAT IS NEEDED TO ACHIEVE THE GOALS OF THE OCEAN DECADE?

Ryabinin et al. (2019) suggested seven research and development priority areas for the Ocean Decade. For each of these, we indicate how ecosystem models can benefit from the data products generated and propose how these models can address the Ocean Decade priorities.

1. A full map of the ocean (or georeferenced digital atlas) is needed for ecosystem models to address sustainable ocean use and operational marine spatial planning (MSP). Well-parameterized ecosystem models can contribute by providing estimates of biological and ecosystem variables in areas hard to observe or with low spatio-temporal coverage, and provide non-measurable information (e.g., flow of ecosystem services) consistent with existing knowledge and ecological principles. The work by the MSP Challenge gives direction (Steenbeek et al., 2020), but there is a more comprehensive ecosystem modeling ensemble should support this work (see below).

2. A comprehensive Ocean Observing System (OOS) should include observations of biology at the appropriate temporal and spatial scales (Miloslavich et al., 2018; Claudet et al., 2019; Mackenzie et al., 2019). Currently, OOSs provide some of the essential physical, chemical and biological data to parameterize models, which are combined into databases such as the European Union's Earth Observation Programme "Copernicus," where they are re-analyzed to provide free and open information on the physical and biogeochemical state of the ocean. However, not all regions of the world or types of data are equally represented. Physical and chemical parameters are better represented in the northern hemisphere while in the south the frequency of observations generally is insufficient to achieve well-calibrated physico-chemical models (López-Ballesteros et al., 2018). Biological observations and data are much less prevalent (Miloslavich et al., 2018), since very little R&D or funding has gone into observing biology, and with the lack of taxonomists globally, this priority will be difficult to achieve (Pinheiro et al., 2019). Data collection could be enhanced if more ocean transport undertakes physical, chemical and biological observations, as is done by Ships of Opportunity. In addition, for the OOS to be used in operational models, observations of industrial uses, human behavior, social change and economy should be included (Miloslavich et al., 2018; Bax et al., 2019; Jouffray et al., 2020). This will come with substantial (but surmountable) challenges for how to store, organize, integrate and distribute such data (Guidi et al., 2020).

3. A quantitative understanding of the ocean structure and functioning is imperative for management of ecosystems. This priority encapsulates the need for observations of the full ecosystem, and is important for achieving the societal goal of predicting the ocean (Claudet et al., 2019). This priority is where the ecosystem modeling community can contribute the most through an ensemble of possibly coupled ecosystem models, each with its own properties and uncertainties (Heymans et al., 2018; Lotze et al., 2019). Marine ecosystem models span a highly diverse range of approaches, which between them capture much uncertainty about marine ecosystem structure and function. We must make best use of that diversity. This is happening to some extent through European projects (Piroddi et al., 2017; Serpetti et al., 2017; Spence et al., 2018) and in international initiatives such as Fish-MIP (Lotze et al., 2019) that are already informing management. However, these initiatives should be extended to marine ecosystems globally and at local, regional and global scales. Marine ecosystem modeling has started to embrace new technological data and advances such as eDNA, metabarcoding, Big Data, machine learning and Artificial Intelligence (Guidi et al., 2020)—a trend with great potential. To be fully operational, the models must be validated in real time and should continue the expanding inclusion of diverse modeling approaches (Coll et al., 2019).

4. A fully open data and information system will enable the futuristic vision put forward in the epilogue of Navigating the Future V (EMB, 2019), of a virtual ocean or "digital twin," where citizens can follow the ocean in real time. This will require a much more in-depth understanding of the structure and function of marine ecosystems and their connected human systems. For both, we will need better integrated databases, and for the latter, new data streams. Data richness and accessibility could be improved if all databases were linked to those developed for ocean-related activities such as fisheries, energy industries and shipping. The recovery of data into an open system would provide the information needed to drive an ensemble of ecosystem models and may revolutionize the ability of modelers to make priority 3 a reality. In addition, ecosystem models applied across the world can highlight the data gaps that need to be addressed to sustainably use the ocean. Ecosystem models can identify the parameters with the biggest impact on key management questions, and point to the efficient use of funding for future ocean observations, as has been done with physical models and ARGO floats (Wang et al., 2018).

5. A fully integrated Multi-Hazard Warning System will be enhanced by the ability of the ensemble of ecosystem models to predict possible impacts from a specific hazard and from multiple hazards. For instance, current ecosystem models already address possible impacts of climate change on species' habitats and food web interactions (Spence et al., 2018; Lotze et al., 2019) and are considering evolution and acclimation (Fulton et al., 2019). However, there is significant scope for expansion and refinement of a more comprehensive ensemble of ecosystem models to provide more reliable predictions of future impacts. This is currently being undertaken by the Joint Research Centre of the European Commission under the Blue2 Project and Marine Modeling Framework (Stips et al., 2015), which uses a pan-European ensemble of ecosystem models to assess the impact of selected EU policies (Macias et al., 2019). This approach needs to be undertaken comprehensively across the globe. In addition, possible impacts from storms or high temperature events on coastal ecosystems could be addressed through full end-to-end interdisciplinary models, as is already done by assemblages of models informing Louisiana's Coastal Master Plan, the restoration of the Mississippi River Delta (De Mutsert et al., 2017; Baustian et al., 2018), the Baltic Sea (Niiranen et al.,

2013) and the Great Barrier Reef, making this priority achievable in the Ocean Decade.

6. The Ocean and Earth-System Observation, Research and specifically Prediction of the future state of the ocean will require ecosystem models to include a broader set of industries and human behavior, including social change, requiring social and economic data (Ryabinin et al., 2019). This challenging frontier is being tackled to some extent in ecosystem models that are co-designed for fisheries management (Bentley et al., 2019a,b,c), coastal planning (Fulton et al., 2017) and in initiatives linking ecosystem and economic models (Weatherdon et al., 2016). However, these are rare and currently only a small subset

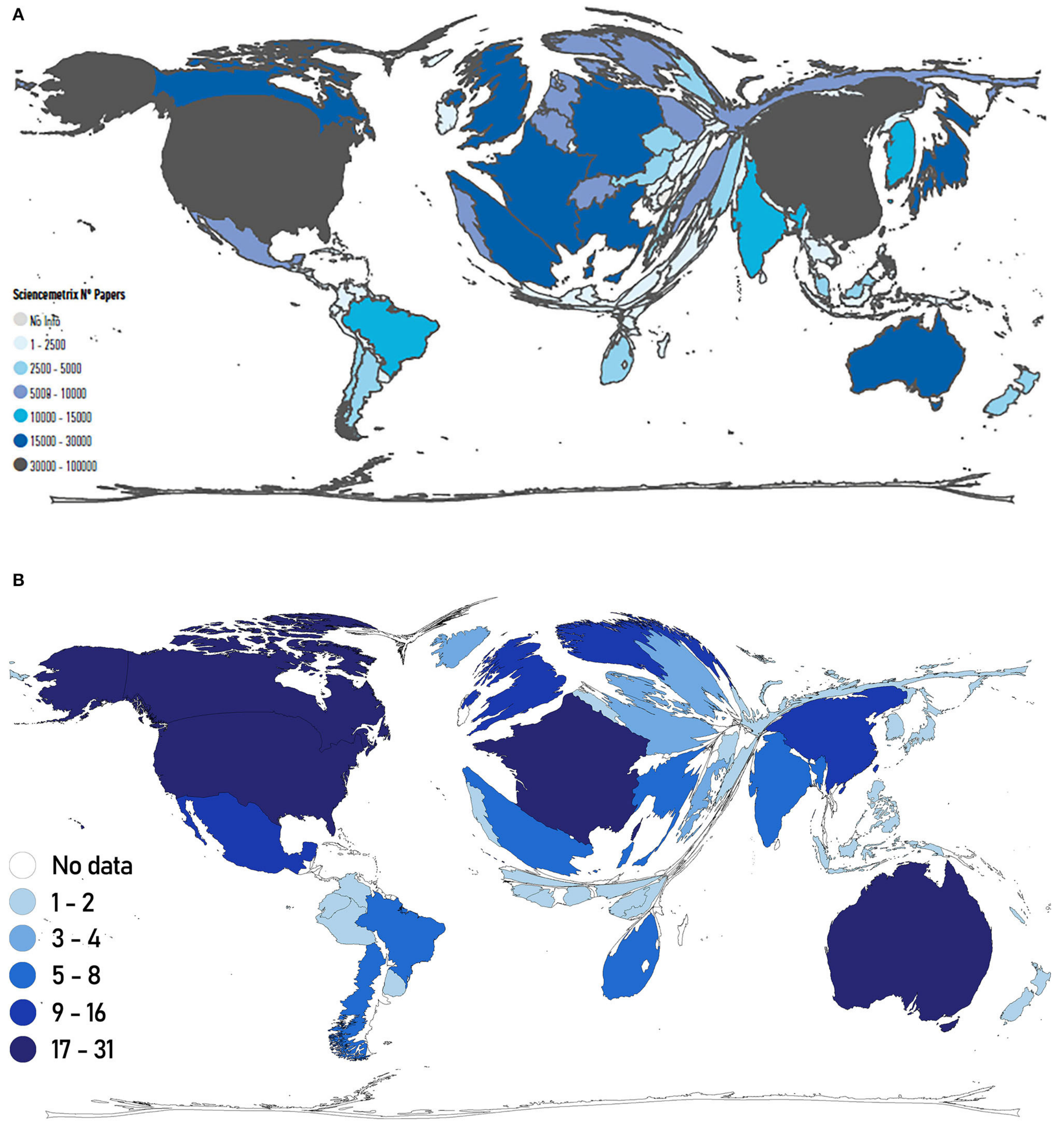

FIGURE 1 | Cartograms* depicting **(A)** Number of ocean science publications by country (from Figure 5.2 in IOC-UNESCO Global Ocean Science Report under the license: CC BY-NC-SA 3.0 IGO) and **(B)** indicative number of ecosystem modelers per country based on the author's networks and knowledge. * In these cartograms the countries are deformed and rescaled in proportion to their relative research production by **(A)** Publication and **(B)** Percentage of ecosystem modelers.

of physical-biogeochemical-ecological-social model assemblages make predictions in two directions; i.e., driven by physical changes but also driven by social changes, with feedback through the assemblage to the physics or chemistry. This important research gap is also highlighted by Claudet et al. (2019).

Ryabinin et al. (2019) suggest that activities in coastal seas are becoming more interdependent, and suggest that they require real-time decision-making and anticipatory planning. Unfortunately, models with sufficient scope (across scales and ecosystem components) cannot currently support this in real time, though near real-time physical-biogeochemical models are now becoming more common. Development versions of models with sufficient scope and resolution do exist, but still require refinement to address constraining computing capacity (which could be addressed by new morphing model approaches Gray and Wotherspoon, 2012 or larger computing infrastructure). Such models are also significantly constrained by the lack of suitable data (especially reliable and instantly accessible data) and other relevant information (see priority 5). Ryabinin et al. (2019) also suggest that the Ocean Decade might engage the unconnected modeling groups and industries to design the multi-scale ocean observation and prediction system of the future. This would be ideal and will be assisted by the ecosystem modeling community's historical openness to working together, embracing a diversity of approaches and not being drawn into unproductive "my model is better than yours" mantras that competitive funding can unintentionally incentivize.

7. Capacity Building, Accelerated Technology Transfer, Training, Education, and Ocean Literacy will be imperative to the success of the Ocean Decade (Claudet et al., 2019). To meet the capacity shortfall already felt globally by bodies attempting to deliver sustainable ocean use, this capacity development requirement needs to be taken on board by the ocean modeling community, supported by funders. To obtain the widespread use of ecosystem models (and its products) to deliver new kinds of modeling and the model ensembles suggested above, we will need many more modeling-literate scientists, managers and users. However, as the cartogram in the IOC/UNESCO Global Ocean Science Report (IOC-UNESCO, 2017) shows, there is a very significant problem with the distribution of general science capacity across the world (**Figure 1A**), which is even more desperate if we look at a cartogram of the ecosystem modeling capacity (**Figure 1B**). Therefore, a concerted effort to train more modelers, and to make models more understandable to all scientists, managers and policy makers is of the utmost importance (Fulton et al., 2015).

DISCUSSION

The Ocean Decade starts in 2021. Its scope is necessarily ambitious and requires cooperation, collaboration and a common vision among researchers from all disciplines, policy, management, stakeholders and the public. This includes ecosystem modelers. As an essential component of the Ocean Decade, how can we do our part to address the priorities to conserve and sustainably use the ocean and its resources to help ensure its success? Questions we need to address include:

i To connect to policy and management, how do we:
- Improve (and explain) our models to enhance policy makers' confidence in the models and their predictions?
- Make models ready-to-use for managers?
- Deal with and communicate uncertainty?

ii To include the technical advances needed, how do we:
- Effectively couple models to better capture reality?
- Deal with multiple spatio-temporal scales, given that some of our drivers are local, while others are regional or even global?

iii To enhance research and modeling capacity, how do we:
- Build the capacity required, and determine where it is needed?
- Better engage with and co-design our models with a broader set of knowledge holders, whether industry, the Ocean Observation community, traditional owners/indigenous communities, and policy and decision makers?
- Work together to achieve the ensemble of well-parameterized, calibrated and validated ecosystem models needed to address the questions asked of us in the Ocean Decade?

We therefore challenge all ecosystem modelers to achieve a fully operational ensemble of ecosystem models for all marine ecosystems and the global ocean by the end of the Ocean Decade. We believe that if we work together, we can.

AUTHOR CONTRIBUTIONS

JH conceived and lead the study. AB, VC, MC, KM, EF, CP, Y-JS, JS, and MT-T contributed to the ideas and discussion. JS created **Figure 1B**. All authors contributed to the article and approved the submitted version.

FUNDING

Y-jS and MT-T have been partially funded by the Biodiversa and Belmont Forum project SOMBEE (BiodivScen programme, ANR contract N°ANR-18-EBI4-0003-01). MC and JS were funded by the European Union's Horizon 2020 research and innovation programme under grant agreement N° 817578 (TRIATLAS project) and MC also received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N° 869300 (FutureMARES project). VC acknowledges support through NSERC Discovery Grant RGPIN-2019-04901.

REFERENCES

Baustian, M. M., Meselhe, E., Jung, H., Sadid, K., Duke-Sylvester, S. M., Visser, J. M., et al. (2018). Development of an Integrated Biophysical Model to represent morphological and ecological processes in a changing deltaic and coastal ecosystem. *Environ. Model. Softw.* 109, 402–419. doi: 10.1016/j.envsoft.2018.05.019

Bax, N. J., Miloslavich, P., Muller-Karger, F. E., Allain, V., Appeltans, W., Batten, S. D., et al. (2019). A response to scientific and societal needs for marine biological observations. *Front. Mar. Sci.* 6:395. doi: 10.3389/fmars.2019.00395

Bentley, J. W., Hines, D., Borrett, S., Serpetti, N., Fox, C., Reid, D. G., et al. (2019b). Diet uncertainty analysis strengthens model-derived indicators of food web structure and function. *Ecol. Indic.* 98, 239–250. doi: 10.1016/j.ecolind.2018.11.008

Bentley, J. W., Hines, D. E., Borrett, S. R., Serpetti, N., Hernandez-Milian, G., Fox, C., et al. (2019a). Combining scientific and fishers' knowledge to co-create indicators of food web structure and function. *ICES J. Mar. Sci.* 76, 2218–2234. doi: 10.1093/icesjms/fsz121

Bentley, J. W., Serpetti, N., Fox, C., Heymans, J. J., and Reid, D. G. (2019c). Fishers' knowledge improves the accuracy of food web model predictions. *ICES J. Mar. Sci.* 76, 897–912. doi: 10.1093/icesjms/fsz003

Claudet, J., Bopp, L., Cheung, W. W. L., Devillers, R., Escobar-Briones, E., Haugan, P., et al. (2019). A roadmap for using the UN decade of ocean science for sustainable development in support of science, policy, and action. *One Earth* 2, 34–42. doi: 10.1016/j.oneear.2019.10.012

Coll, M., Grazia Pennino, M., Steenbeek, J., Sole, J., and Bellido, J. M. (2019). Predicting marine species distributions: complementarity of food-web and Bayesian hierarchical modelling approaches. *Ecol. Modell.* 405, 86–101. doi: 10.1016/j.ecolmodel.2019.05.005

De Mutsert, K., Lewis, K. A., Milroy, S., Buszowski, J., and Steenbeek, J. (2017). Using ecosystem modeling to evaluate trade-offs in coastal management: effects of large-scale river diversions on fish and fisheries. *Ecol. Modell.* 360, 14–26. doi: 10.1016/j.ecolmodel.2017.06.029

EMB (2019). "Navigating the Future V: Marine Science for a Sustainable Future." in *European Marine Board Position Paper No. 24*, ed. J. J. Heymans (Oostende: European Marine Board), 89.

Fulton, E. A., Blanchard, J. L., Melbourne-Thomas, J., Plagányi, É. E., and Tulloch, V. J. D. (2019). Where the ecological gaps remain, a modelers' perspective. *Front. Ecol. Evol.* 7:424. doi: 10.3389/fevo.2019.00424

Fulton, E. A., Boschetti, F., Sporcic, M., Jones, T., Little, L. R., Dambacher, J. M., et al. (2015). A multi-model approach to engaging stakeholder and modellers in complex environmental problems. *Environ. Sci. Policy* 48, 44–56. doi: 10.1016/j.envsci.2014.12.006

Fulton, E. A., T., Hutton, T., van Putten, I. E., Lozano-Montes, H., and Gorton, R. (2017). *Gladstone Atlantis Model – Implementation and Initial Results. Report to the Gladstone Healthy Harbour Partnership.* CSIRO, 167.

Gray, R., and Wotherspoon, S. (2012). Increasing model efficiency by dynamically changing model representations. *Environ. Model. Softw.* 30, 115–122. doi: 10.1016/j.envsoft.2011.08.012

Guidi, L., Fernandez Guerra, A., Canchaya,C., Curry, E., Foglini, F., Irisson, J-O., et al. (2020). "Big Data in Marine Science." In *European Marine Board Future Science Brief No 6*, eds B. Alexander, J. J. Heymans, A. Muñiz Piniella, P. Kellett, and J. Coopman (Oostende: European Marine Board), 1–50.

Heymans, J. J., Skogen, M., Schrum, C., and Solidoro, C. (2018). "Enhancing Europe's capability in marine ecosystem modelling for societal benefit," in *European Marine Board Future Science Brief No 4*, eds K. E. Larkin, J. Coopman, A. Muñiz Piniella, P. Kellett, C. Simon, and C. Rundt (Oostende: European Marine Board), 32.

IOC-UNESCO (2017). *Global Ocean Science Report - the Current Status of Ocean Science Around The World*, eds L. Valdés L, K. Isensee, A. Cembella, A. C. Santimaria, M. Crago, L. Horn (Paris: IOC-UNESCO).

Jouffray, J.-B., Blasiak, R., Norström, A. V., and Österblom, H., and Nyström, M. (2020). The blue acceleration: the trajectory of human expansion into the ocean. *One Earth* 2, 43–54. doi: 10.1016/j.oneear.2019.12.016

López-Ballesteros, A., Beck, J., Bombelli, J., Grieco, E., Lorencová E. K., Merbold, M., et al. (2018). Towards a feasible and representative pan-African research inftrastructure network for GHG observations. *Environ. Res. Lett.* 13:085003. doi: 10.1088/1748-9326/aad66c

Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W. L., Galbraith, E. D., et al. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc. Nat. Acad. Sci. U.S.A.* 16, 12907–12912. doi: 10.1073/pnas.1900194116

Macias, D., Friedland, R., Piroddi, C., Miladinova, S., Parn, O., Garcia-Gorriz, E., et al. (2019). *Report on the Fourth Workshop of the Network of Experts for Redeveloping Models of the European Marine Environment.* Publications Office of the European Union, JRC Reports, Luxembourg.

Mackenzie, B., Celliers, L., de. Freitas Assad, L. P., F., Heymans, J. J., Rome, N., Thomas, J., et al. (2019). The role of stakeholders in creating societal value from coastal and ocean observations. *Front. Mar. Sci.* 6:137. doi: 10.3389/fmars.2019.00137

Miloslavich, P., Nicholas, J. B., Simmons, S. E., Klein, E., Appeltans, W., Aburto-Oropeza, O., et al. (2018). Essential ocean variables for global sustained observations of biodiversity and ecosystem changes. *Glob. Chang. Biol.* 24, 2416–2433. doi: 10.1111/gcb.14108

Niiranen, S., Yletyinen, J., Tomczak, M. T., Blenckner, T., Hjerne, O., MacKenzie, B. R., et al. (2013). Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. *Glob. Chang. Biol.* 19, 3327–3342. doi: 10.1111/gcb.12309

Pinheiro, H. T., Moreau, C. S., Daly, M., and Rocha, L. A. (2019). Will DNA barcoding meet taxonomic needs? *Science* 365:873. doi: 10.1126/science.aay7174

Piroddi, C., Coll, M., Liquete, C., Macias, D., Greer, K., Buszowski, J., et al. (2017). Historical changes of the Mediterranean Sea ecosystem: modelling the role and impact of primary productivity and fisheries changes over time. *Nat. Sci. Rep.* 7:44491. doi: 10.1038/srep44491

Ryabinin, V., Barbière, J., Haugan, P., Kullenberg, G., Smith, N., McLean, C., et al. (2019). The UN decade of ocean science for sustainable development. *Front. Mar. Sci.* 6:470. doi: 10.3389/fmars.2019.00470

Serpetti, N., Baudron, A. R., Burrows, M. T., Payne, B. L., Helaouët, P., Fernandes, P. G., et al. (2017). Impact of ocean warming on sustainable fisheries management informs the ecosystem approach to fisheries. *Nat. Sci. Rep.* 7:13438. doi: 10.1038/s41598-017-13220-7

Spence, M. A., Blanchard, J. L., Rossberg, A. A., Heath, M. R., Heymans, J. J., Mackinson, S., et al. (2018). A general framework for combining ecosystem models. *Fish Fish.* 19, 1031–1042. doi: 10.1111/faf.12310

Steenbeek, J., Romagnoni, G., Bentley, J., Heymans, J. J., Serpetti, N., Gonçalves, M., et al. (2020). Combining ecosystem modelling with serious gaming in support of transboundary maritime spatial planning. *Ecol. Soc.* 25:21. doi: 10.5751/ES-11580-250221

Stips, A., Dowell, M., Somma, F., Coughlan, C., Piroddi, C., Bouraoui, F., et al. (2015). *Towards an Integrated Water Modelling Toolbox.* JRC Technical Reports, JRC. ISPRA.

Wang, T., Gille, S. T., Mazloff, M. R., Zilberman, N. V., and Du, Y. (2018). Numerical simulations to project argo float positions in the middepth and deep southwest pacific. *J. Atmos. Oceanic Technol. Technol.* 35, 1425–1440. doi: 10.1175/JTECH-D-17-0214.1

Weatherdon, L. V., Magnan, A. K., Rogers, A. D., Sumaila, U. R., and Cheung, W. W. L. (2016). Observed and projected impacts of climate change on marine fisheries, aquaculture, coastal tourism, and human health: an update. *Front. Mar. Sci.* 3:48. doi: 10.3389/fmars.2016.00048

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 25 September 2020
doi: 10.3389/fmars.2020.567758

Geographic Variation in Life-History Traits of Black Sea Bass (*Centropristis striata*) During a Rapid Range Expansion

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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: 30 May 2020
Accepted: 02 September 2020
Published: 25 September 2020

Citation:
McMahan MD, Sherwood GD and Grabowski JH (2020) Geographic Variation in Life-History Traits of Black Sea Bass (Centropristis striata) During a Rapid Range Expansion. Front. Mar. Sci. 7:567758. doi: 10.3389/fmars.2020.567758

The warming of the world's oceans has resulted in the redistribution of many marine species globally. As species undergo range shifts, the expanding edge of the population often experiences novel environmental and demographic conditions that may result in the emergence of variation in life-history strategies. The northern stock of black sea bass, *Centropristis striata*, has recently expanded its distribution poleward, into the Gulf of Maine. Management has struggled to keep pace with this rapid range shift, in part, because very little is known about the expanding population. We compared life-history traits of black sea bass collected from 2013 to 2016 from the northern most point of the historic range of the northern stock (southern Massachusetts) to those from two areas in the newly expanded range (northern Massachusetts and Maine). We found significant differences in size, diet, condition, maturity and sex ratio between black sea bass from southern Massachusetts and the Gulf of Maine. Overall, sea bass in the newly expanded range consumed a less diverse diet and their condition was lower, but they reached maturity at a younger age. We also found greater length- and age-at-maturity estimates from all regions combined compared to the most recent black sea bass stock assessment which includes data from Cape Hatteras, NC to southern Massachusetts. This study represents initial observations of life-history traits of sea bass in its newly expanded range in the Gulf of Maine, and suggests that these sea bass exhibit life-history strategies that differ from their southern counterparts within their historic range. Given these findings, the stock assessment for the Northeast U.S. Continental Shelf black sea bass stock may not be adequate for sea bass in the Gulf of Maine. Studies investigating the expanding edge of economically valuable fishery species are needed to aid in ongoing and future efforts to assess and manage their stocks.

Keywords: black sea bass, range expansion, life-history traits, warming water, Gulf of Maine, population dynamics

INTRODUCTION

Climate-induced range shifts have become common in recent decades. Species are altering their distributions to avoid climatic stress, which is modifying the structure and function of ecosystems globally (e.g., Parmesan and Yohe, 2003; Perry et al., 2005; Poloczanska et al., 2013; Pecl et al., 2017). This movement is expected to intensify, and may already be occurring at unprecedented rates

(Lawing and Polly, 2011; Pecl et al., 2017). As species undergo range shifts, they encounter unique selective pressures that may alter life-history traits and lead to increased spatial heterogeneity among populations (Burton et al., 2010; Phillips et al., 2010). These shifts can greatly complicate conservation and management efforts, particularly if the impact of range expansion on a species' population dynamics is not well understood.

Geographic variation in life-history traits often arises in response to different environmental and demographic gradients experienced across the range of a species (e.g., Roff, 1993; Brown, 1995). For instance, populations not constrained by density-dependent effects often invest less in competitive (K) and more in reproductive (r) capabilities (Charlesworth, 1971; Roughgarden, 1971). In contrast, populations that are density-dependent are often K-selected because successful propagation is related to fitness in high density areas (Charlesworth, 1971; Roughgarden, 1971). Although the "abundant center" distribution does not always occur in natural populations (e.g., Sagarin and Gaines, 2002), range expanding species are expected to exhibit lower population density along the expanding range edge in comparison to more centralized populations (Burton et al., 2010; Phillips et al., 2010). Environmental heterogeneity across a species' range can also drive life-history variation (Brander, 2010). In particular, temperature and the length of the growing season can strongly influence growth and the timing of maturation in fish (Pauly, 1980; Conover, 1990; Pörtner et al., 2001). Spatial variations in predation pressure (e.g., Reznick et al., 1990; Benard, 2004), harvesting (e.g., Jorgensen et al., 2007) and prey availability (e.g., Sherwood et al., 2007) also can influence life-history traits in fish. Collectively, these environmental and biotic processes that mediate the biology of fish species also help determine the amount of biomass that can be sustainably harvested.

Recently, emphasis has been placed on incorporating spatial heterogeneity into marine fisheries management (Ciannelli et al., 2008; Cadrin and Secor, 2009; Pascoe et al., 2009; Lorenzen et al., 2010). Traditionally, stock populations have been managed over large geographic areas where demographic and environmental variables were considered homogenous (Ciannelli et al., 2008). Spatial heterogeneity has largely been ignored due to the substantial complexity it adds to stock assessment models (Pascoe et al., 2009). However, demographic and environmental conditions are rarely homogenous throughout a species' range, and ignoring this heterogeneity may lead to a misunderstanding of the mechanisms regulating population dynamics (Ciannelli et al., 2008; Lorenzen et al., 2010) and subsequent mismatches between harvest levels and stock productivity. Incorporating spatial heterogeneity may be of particular importance for range expanding species that can undergo rapid evolution of life-history traits (Burton et al., 2010). Yet, a big impediment to adaptively managing range shifts is that there often is little information about these species at the leading edge of their newly expanded distributions.

The black sea bass, *Centropristis striata*, is a temperate serranid that is distributed from the Gulf of Mexico to the Gulf of Maine (GOM) (Drohan et al., 2007). Within that range, they are managed as three separate stocks: Gulf of Mexico, Southeast U.S. Continental Shelf and Northeast U.S. Continental Shelf. The Northeast U.S. Continental Shelf stock is further defined as two sub-units, north and south of Hudson Canyon. The Northeast U.S. stock undergoes seasonal migrations, and inhabits the outer continental shelf in the winter vs. nearshore habitat in the spring and summer when spawning occurs (Moser and Shepherd, 2009). They support important commercial and recreational fisheries throughout their range.

Historically, the Northeast U.S. stock ranged from Cape Hatteras, NC to Cape Cod, MA, but in recent years the center of stock biomass has shifted poleward (Bell et al., 2015) and sea bass populations have expanded into the GOM. Very little is known about the population dynamics of sea bass in the GOM. Current stock designations are based on differences in seasonal migrations and life-history traits of sea bass south of Cape Cod, yet it is unclear if the biological characteristics of sea bass in the GOM differ from those of populations farther south. Furthermore, sea bass fisheries have recently developed in the northern GOM outside of stock assessment areas, potentially making this population vulnerable to rapid depletion (Link et al., 2011).

Sea bass are protogynous hermaphrodites (i.e., they are typically born female and transition to male as they increase in size and age), which can complicate management, particularly if accurate information on sex ratios and the mean size at which individuals change sex is not available (Alonzo et al., 2008; Provost and Jensen, 2015). Furthermore, latitudinal variation in growth rates and age-at-maturity has been observed in both the Northeast U.S. (Kolek, 1990; Caruso, 1995) and Southeast U.S. sea bass stocks (McGovern et al., 2002). Kolek (1990) and Caruso (1995) found that sea bass collected in southern Massachusetts grew faster than sea bass from New York and Virginia and Caruso (1995) also noted that sea bass collected from this area were predominantly mature. In addition, McCartney et al. (2013) observed genetic variation across a latitudinal gradient in the northern stock. These studies provide evidence that life-history variation exists within the northern stock, and further emphasize the need to understand how the northern range expansion is influencing population dynamics and structure.

The purpose of this study was to document life-history traits of sea bass collected from southern Massachusetts (i.e., native range) and two regions within the GOM (i.e., newly expanded range). We analyzed diet, growth, condition, and reproduction within these regions, and examined spatial variation that may have implications for stock assessment and management. This study represents one of the first documentations of black sea bass life-history traits at the northern extent of their newly expanded range.

MATERIALS AND METHODS

Sampling Design

To determine if life-history traits of black sea bass differed between native and newly expanded populations, we collected samples from three regions: southern Massachusetts (SMA) (historic northern range limit delineated by Cape Cod), northern Massachusetts (NMA) (newly expanded range north of Cape

Cod) and midcoast Maine (ME) (expanding range edge), between May and October from 2013 to 2016 (**Figure 1**). In SMA, fish were collected by the Massachusetts Division of Marine Fisheries trawl and trap surveys, as well as by commercial lobstermen who caught sea bass as bycatch in their lobster traps. State and federal trap and trawl surveys rarely find sea bass in NMA, so fish were also collected via hook and line by recreational fishers, as well as bycatch from lobster traps. Collecting fish caught as bycatch in lobster traps was the only successful method in Maine. Recreational and commercial sea bass fishing does not occur in this area, and state and federal trawl surveys do not encounter sea bass. Therefore, the only capture method that was the same across regions was bycatch from lobster traps. Black sea bass smaller than 10 cm total length are not commonly captured in lobster traps, but are captured by trawl surveys, so to avoid biased size estimates between capture types, we did not collect sea bass smaller than 10 cm.

The date, location, and capture method were recorded at each site where fish were collected. To explore the influence of season on biological metrics, samples were categorized into seasons defined as spring (May–June), summer (July–August), and fall (September–October). Fish were frozen immediately after capture and transported to the laboratory where they were kept frozen until they were processed. The total length (cm), standard length (cm) and total weight (g) were measured for each fish prior to removing vital organs. Weight was also recorded after the removal of vital organs to obtain the gutted weight (g). The gonads and liver were then weighed individually, and stomachs were retained for stomach content analysis. Sagittal otoliths were removed to determine age and calculate growth rates. Small core subsections (~1 g) were taken from muscle tissue samples to conduct stable isotope analysis to examine the diet of black sea bass.

Size Distribution and Growth

Size-frequency histograms were used to explore regional differences in black sea bass distributions. The Kolmogorov-Smirnov (K-S) test was used to compare the cumulative size frequency distribution among regions. We also compared the cumulative size frequency distribution among capture types in SMA and NMA (only one capture type was used in ME). Age determination was conducted to compare age-at-maturity of sea bass among regions. Aging techniques were adapted from the Massachusetts Division of Marine Fisheries and Northeast Fisheries Science Center protocols for black sea bass (Robillard et al., 2011; Elzey et al., 2015), which age whole otoliths up to age five, and sectioned otoliths for ages six and up. Only six fish collected in this study were six or older, and they were collected by the Massachusetts Division of Marine Fisheries in trap or trawl surveys. The otoliths of these fish were removed prior to arriving

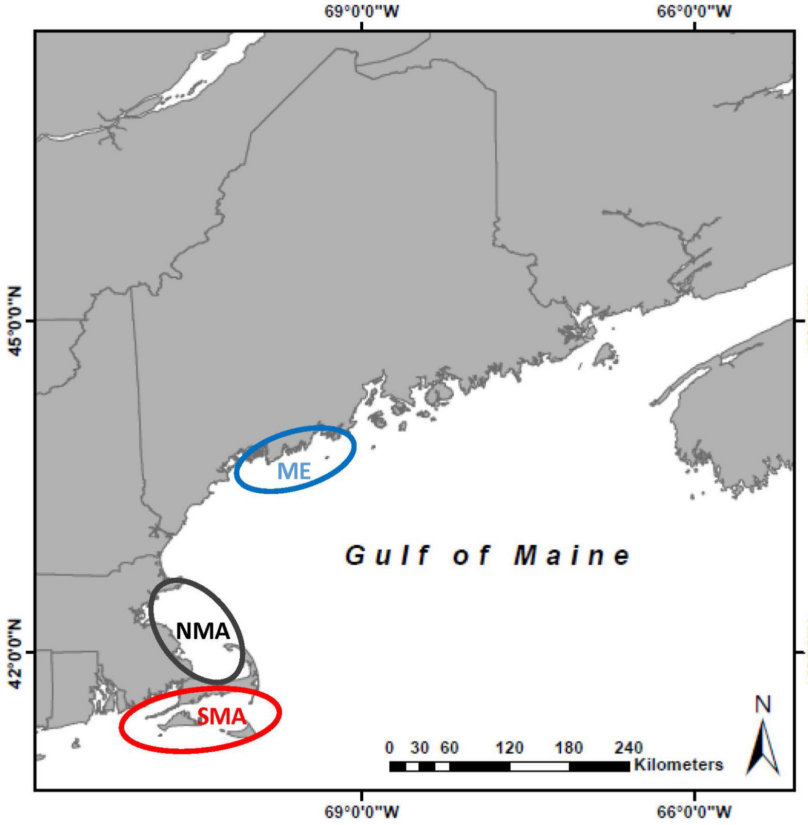

FIGURE 1 | Map of the Gulf of Maine with field sites delineated: Maine (ME) in blue, northern Massachusetts (NMA) in gray, and southern Massachusetts (SMA) in red.

at our lab, and were sectioned and aged at the Division of Marine Fisheries Age and Growth Laboratory. For fish ages five and under, whole sagittal otoliths were immersed in mineral oil on a black background and viewed under a microscope. The number of annuli on each otolith was counted outward from the core to estimate age. Annuli were defined as continuous dark bands with no breaks. Age was calculated based on capture date and seasonal timing of when annuli form and delineate from the otolith edge (Elzey et al., 2015).

Growth was modeled using von Bertalanffy growth function (VBGF) parameter estimates obtained from the non-linear regression function in the "FSA" package (Ogle et al., 2020) in R (R Core Team, 2017) and the following equation:

$$L_t = L_{inf}(1 - e^{(-k(t-t_0))})$$

where L_t is length (cm) at age t, L_{inf} is the asymptotic length, k is the Brody growth coefficient and t_0 is the age at which length is 0. 95% confidence intervals were calculated by bootstrapping and extracting 2.5 and 97.5% quantiles of the parameter estimates. A VBGF curve was established for all regions combined. Separate growth curves were not established for each region due to low sample sizes of the youngest and oldest age classes in NMA and ME.

Diet

Stomach contents were used to compare the diet of sea bass among regions. Stomachs were dissected and contents were weighed, counted and identified to the lowest possible taxon. Prey items were divided into the following groups: pelagic fish (bay anchovy, butterfish, herring, etc.); demersal fish (sculpin, scup, black sea bass, etc.); squid (long-fin squid); crabs (various species); shrimp (various species); lobster; benthic invertebrates (mollusks, polychetes, amphipods, algae, etc.); and unidentified fish. Partial fullness index (PFI) of prey was calculated for each fish, and mean PFI was used to compare the relative importance of prey groups among regions. Mean PFI provides a length-standardized way to determine relative volumetric prey importance (Bowering and Lilly, 1992), and was calculated as:

$$\text{Mean PFI} = \frac{1}{\text{n}} \times \sum \frac{w_{ij}}{L_j^3} \times 10^4$$

where w_{ij} is the weight of prey i for fish j, L_j is the length of fish j and n is the total number of fish sampled.

Stable isotope ratios of nitrogen (δ^{15}N) and carbon (δ^{13}C) can be used to determine the trophic position of an organism (Zanden and Rasmussen, 1999) and the source of carbon (e.g., benthic, demersal, pelagic, etc.) in marine food webs (Owens, 1987; Fry, 1988; Sherwood and Rose, 2005), respectively. Muscle tissue samples were dried in a drying oven at 60°C for 48 h, ground to a fine powder using a mortar and pestle, and weighed and packaged in 4 × 6 mm tin capsules. Samples were sent to the Colorado Plateau Stable Isotope Laboratory (Northern Arizona University, Flagstaff, AZ, United States) for analysis. Samples were combusted to produce CO_2 and N_2, from which stable nitrogen and carbon isotope ratios were analyzed using an elemental analyzer followed by gas chromatograph separation interfaced via continuous flow to an isotope ratio mass spectrometer. Stable carbon and nitrogen ratios were expressed in delta (δ) notation and defined as parts per thousand deviations from the following standard materials: Pee Dee Belemnite for δ^{13}C, and N_2 in air for δ^{15}N. To determine the level of precision of isotope results, 8% of the samples were analyzed in duplicate.

Distinctions in the overall diet among groups were assessed using a permutational multivariate analysis of variance (PerMANOVA) using the "vegan" package in R (R Core Team, 2017). Specifically, PerMANOVA was used to test the effects of region, sex, season and their interactions on the PFI's of each prey group. PerMANOVA requires the use of a matrix of dissimilarity indices, rather than raw response values, which we calculated prior to analysis. Gower's index was used as the dissimilarity measure because it allows for the use of double zeroes (Gower, 1971). The multivariate dispersions of each group matrix were compared using beta diversity tests to identify potential violations of PerMANOVA assumptions.

A two-step modeling approach using GLMs was used to analyze individual prey categories, similar to Stefánsson (1996). First, the presence of prey was analyzed using generalized linear models (GLMs) with binomial error distribution and logit link functions. Second, prey category abundance (i.e., PFI $\neq$ 0) was analyzed using GLMs with gamma error distributions and identity link functions. A similar approach using generalized additive models has also commonly been employed in diet studies (Stefánsson and Pálsson, 1997; Santos et al., 2013; Buchheister and Latour, 2015), however, GLMs are more appropriate when utilizing multiple factors (Stefánsson, 1996; Stefánsson and Pálsson, 1997). Fixed effects in both binomial and gamma GLMs included region, sex, season, and all interactions. Capture method was also included as a fixed effect, but not as an interaction term because capture method was unequally represented across the levels of the other factors. Total length was included as a covariate when analyzing prey presence, but not abundance, since PFI is a length standardized measure. Akaike information criteria (AIC) was used to assess fit and select the most parsimonious model(s). Separate three-way ANOVAs were used to test the effect of region, season and size class on carbon and nitrogen stable isotope ratios. Size classes were categorized as 10–19 cm (juveniles), 20–29 cm (50–95% mature), 30–39 cm (reproductive adults), and 40 + cm total length ($\geq$50% male).

Condition

The length-weight relationship was estimated for all regions combined ($n = 288$) using the "FSA" (Ogle et al., 2020) and "stats" packages in R and a linearized version of the following equation:

$$W = aL^b$$

where W is the whole body weight (g), L is the total length (cm), a is the intercept of the regression and b is the regression coefficient. Linearization of this equation results in the errors being additive (as opposed to multiplicative) and stabilizes the variances about the model (Ogle, 2013), allowing for linear regression methods to be used. The linear model was calculated as:

$$log(W) = \log(a) + b\log(L)$$

with $y = log(W)$, $x = log(L)$, slope = b, and intercept = $log(a)$.

We considered two indices of physiological condition: Fulton's condition factor K, and liver-somatic index (LSI). K is primarily an indicator of energy reserves available for somatic growth (i.e., muscle mass), while LSI is a measure of energy reserves available for reproduction (i.e., lipid storage). A length-standardized measure of Fulton's condition factor was calculated to determine the effects of region and season on condition (Le Cren, 1951; Froese, 2006):

$$K_{rel} = \frac{W_g}{aL^b}$$

where W_g is the gutted fish weight (g), L is the total length (cm), and a and b are the parameters of the length-weight relationship defined above. We also calculated Fulton's condition factor by standardizing for season, rather than size, to examine how condition varies with size and related diet ontogeny (Sherwood et al., 2007):

$$K_{adj} = K - K_{avg}$$

where K is Fulton's condition factor and K_{avg} is the average condition factor (all sizes and regions) by season. LSI was calculated as:

$$LSI = \frac{W_l}{W_g} \times 100$$

where W_l is the liver weight and W_g is the gutted fish weight. A seasonally adjusted value was also calculated for LSI:

$$LSI_{adj} = LSI - LSI_{avg}$$

where LSI_{avg} is the average LSI (all sizes and regions) by season (spring, summer and fall).

The standardized residuals from the least-squares regression of total length and LSI or GSI were used to account for the effect of size on LSI and GSI. K_{rel}, residual LSI and residual GSI were analyzed using separate two-way ANOVAs where region, season, and their interaction were included as fixed effects. *Post hoc* multiple comparison tests were conducted using the glht function in the "multcomp" package, which conducts simultaneous tests and computes confidence intervals for parametric models (Hothorn et al., 2008; Bretz et al., 2010). Regional differences in K_{adj} and LSI_{adj} were qualitatively explored within 2 cm size intervals.

Reproduction

Sex and reproductive maturity were determined macroscopically using techniques modeled from Wuenschel et al. (2011). Macroscopic gonad analysis was sufficient for identifying developing, spawning capable and spent stages, and therefore allowed us to classify samples as mature or immature for subsequent analyses.

The gonadosomatic index (GSI) of each fish was calculated using the following equation:

$$GSI = \frac{W_g}{W_t - W_g} \cdot 100$$

where W_g is gonad weight and W_t is total weight. The sex ratio-at-length was determined separately for males and females using a logistic regression in R (R Core Team, 2017) with the following equation:

$$p = \frac{1}{1 + e^{-k(L - L_{50})}}$$

where p is the proportion of males or females at length L, k is a slope parameter, and L_{50} is the length at which 50% of the fish are male or female, respectively. Maturity-at-length for both sexes combined was determined using the same equation, where p is the proportion of mature fish at length L, and L_{50} is the length at which 50% of the fish are mature. Sex ratio-at-length and maturity-at-length were calculated using all regions combined, due to the small sample size within each 1 cm size bin when regions were separated. Age-at-maturity for both sexes combined was determined for all regions combined, as well as each region separately, using a logistic regression in R (R Core Team, 2017) with the following equation:

$$p = \frac{1}{1 + e^{-k(A - A_{50})}}$$

where p is the proportion of mature fish at age A, k is a slope parameter, and A_{50} is the age at which 50% of the fish are mature. We chose to combine sexes to determine length-at-maturity and age-at-maturity because this was the method used in the most recent black sea bass stock assessment (Northeast Fisheries Science Center [NEFSC], 2016). 95% confidence intervals were calculated for sex ratio-, maturity-, and age-at-length by bootstrapping and extracting 2.5 and 97.5% quantiles of the parameter estimates using the "FSA" package (Ogle et al., 2020) in R (R Core Team, 2017). We explored whether the proportion of males and females, as well as the proportion of mature and immature fish, differed among region using Chi-Square tests.

RESULTS

Size Frequency and Growth

Of the 288 sea bass collected between 2013 and 2016, 131 were captured in SMA, 109 in NMA and 48 in ME. There was no significant difference in the cumulative size frequency of sea bass collected among capture types in NMA and SMA (K-S test, $p > 0.05$ for all comparisons). Large sea bass were significantly more frequent in NMA compared to ME and SMA (K-S test, $p < 0.001$ for both comparisons) and small sea bass were significantly more frequent in ME compared to SMA (K-S test, $p = 0.01$; **Figure 2**). The VBGF curve for all regions combined revealed greater length-at-age estimates than the 2016 black sea bass stock assessment, particularly for younger fish (**Table 1** and **Figure 3**).

Diet

Sea bass diet varied among region and season, and also varied with size (**Figure 4**). Demersal fish, pelagic fish and squid comprised 47–66% of sea bass diet in SMA, but only 20–29% in NMA and 8% in ME. Meanwhile, crustaceans (e.g., shrimp, crabs, lobster) accounted for 31–53% of sea bass diet in SMA,

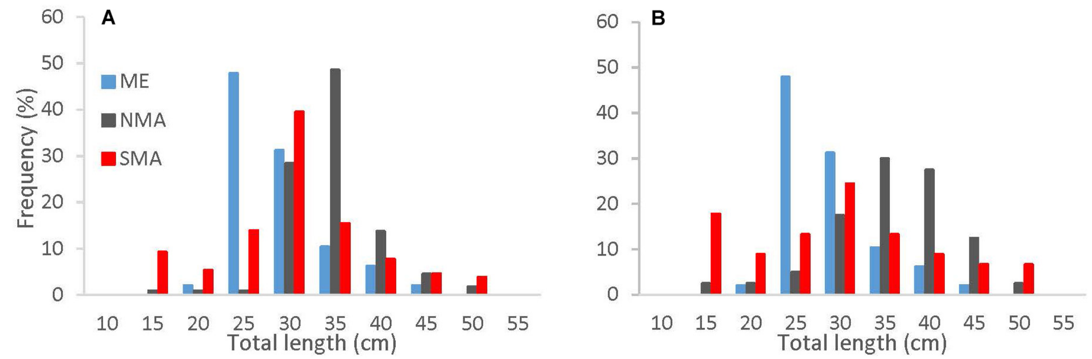

FIGURE 2 | Cumulative length frequency distribution of black sea bass collected in Maine (blue), northern Massachusetts (gray) and southern Massachusetts (red) for **(A)** all capture methods combined, and **(B)** trap caught fish only.

69–76% in NMA and 78% in ME (**Table 1**). The best fitting binomial and gamma GLMs included various combinations of explanatory variables. Region and season were typically the two most important factors in the models, emphasizing the importance of both spatial and temporal dynamics in trophic interactions. Sex did not significantly influence the presence or abundance of prey. Overall, total length and capture method did not significantly influence presence or abundance for the majority of prey groups (**Supplementary Figure S1**).

The presence of demersal fish significantly differed by region ($x^2 = 23.5$, $p < 0.001$), season ($x^2 = 39.2$, $p < 0.001$) and total length ($x^2 = 9.5$, $p = 0.002$). Demersal fish were more frequent in the stomachs of SMA fish compared to NMA (Tukey's HSD, $p < 0.001$) and ME (Tukey's HSD, $p = 0.01$) fish, and significantly more frequent in the fall compared to the summer (Tukey's HSD, $p = 0.001$). No demersal fish were found in the stomachs of fish collected in the spring. Demersal fish regularly occurred in the diet of sea bass measuring 24–40 cm total length, but were more variable in smaller and larger fish. None of the factors tested significantly influenced the abundance of demersal fish.

The presence of squid significantly differed by region ($x^2 = 10.86$, $p < 0.001$) and season ($x^2 = 21.59$, $p < 0.001$). Squid were significantly more frequent in the stomachs of fish collected in the fall compared to the summer (Tukey's HSD, $p = 0.008$) and spring (Tukey's HSD, $p = 0.009$), and significantly more frequent in SMA fish compared to NMA fish (Tukey's HSD, $p = 0.003$). No squid were found in the diet of fish captured in ME.

There was a significant interaction between region and season ($x^2 = 21.81$, $p < 0.001$) on the presence of shrimp biomass in black sea bass stomachs. Shrimp were significantly more frequent in the stomachs of fish collected in SMA in the spring compared to summer (Tukey's HSD, $p = 0.012$) and fall (Tukey's HSD, $p = 0.013$). Similar to presence, there was an interaction between region and season on shrimp abundance ($x^2 = 3.35$, p = 0.001). Shrimp were less abundant in SMA in the fall compared to spring (Tukey's HSD, $p < 0.001$) and summer (Tukey's HSD, $p < 0.001$), and more abundant in the summer in SMA compared to ME (Tukey's HSD, $p = 0.03$).

The presence of crabs significantly differed by region ($x^2 = 29.70$, $p < 0.001$) and season ($x^2 = 26.64$, $p < 0.001$) independently. Crabs were significantly more frequent in the stomachs of fish collected in NMA compared to ME (Tukey's HSD, $p < 0.001$) and in the fall compared to the spring (Tukey's HSD, $p < 0.001$). The abundance of crabs significantly differed by capture method ($x^2 = 9.35$, $p = 0.012$). There was a significantly greater abundance of crabs in the stomachs of hook and line caught fish compared to trap (Tukey's HSD, $p = 0.022$) and trawl (Tukey's HSD, $p = 0.05$) caught fish.

The consumption of benthic invertebrates (e.g., mollusks, polychetes, tunicates) significantly differed by region ($x^2 = 14.15$, $p < 0.001$) and season ($x^2 = 34.99$, $p < 0.001$). The presence of benthic inverts was significantly greater in SMA compared to ME (Tukey's HSD, $p = 0.012$), and significantly lower in the summer compared to spring (Tukey's HSD, $p = 0.011$) and fall (Tukey's HSD, $p < 0.001$). The lobster and pelagic fish prey groups were not modeled using GLMs due to a small sample size. However, it is worth noting that lobsters were found in the diet of fish from all regions, while pelagic fish were only found in SMA and NMA fish.

Stable isotope analysis indicated that sea bass diets likely differ among region and season, but not size class (**Table 1** and **Figure 5**). There was a significant interaction between region and season on both δ^{13}C [ANOVA, $F_{(4,\ 160)} = 5.94$, $p = 0.0002$] and δ^{15}N [ANOVA, $F_{(4,\ 160)} = 2.55$, $p = 0.04$]. The δ^{13}C values of SMA and NMA fish indicated that their diets were more pelagic in the spring, whereas the diet of ME fish was more pelagic in the fall. δ^{13}C values were significantly lower for ME fish in the fall compared to the spring and summer (Tukey's HSD, $p < 0.001$), and significantly lower for NMA fish in spring compared to fall. There was a trend of lower δ^{13}C values for SMA fish in the spring compared to summer and fall, but this effect was not significant. Finally, δ^{13}C values of ME fish in the spring were significantly higher than those for SMA and NMA fish (Tukey's HSD, $p < 0.05$ for both comparisons). Similarly, in the fall, δ^{13}C values of NMA fish were significantly greater than those of ME fish (Tukey's HSD, $p < 0.001$), and there was a trend of greater δ^{13}C values in fish in NMA than in SMA fish (Tukey's HSD, $p = 0.15$).

There was a trend of higher δ^{15}N values in SMA fish compared to those in NMA and ME. δ^{15}N values were significantly higher for SMA fish compared to NMA fish in the spring, summer and

TABLE 1 | Black sea bass sample sizes and life-history parameter estimates by region and season.

	ME			NMA			SMA		
	Spring	**Summer**	**Fall**	**Spring**	**Summer**	**Fall**	**Spring**	**Summer**	**Fall**
N									
Capture type									
Trap	10	14	24	15	17	5	0	38	0
Hook and Line	0	0	0	1	22	25	0	0	0
Trawl	0	0	0	11	0	13	44	0	49
Growth									
VBGF	*Linf* = 59.2 cm (95% UCI-LCI = 77.5–50.7 cm), *k* = 0.21 (95% UCI-LCI = 0.31–0.13), t_0 = −0.88 (95% UCI-LCI = −0.49 to −1.46)								
Diet									
Mean PFI									
Demersal fish		0.07			0.23			0.90	
Pelagic fish		0.00			0.02			0.19	
UNID fish		0.03			0.09			0.19	
Benthic inverts		0.20			0.04			0.10	
Squid		0.00			0.18			0.56	
Crabs		0.40			0.98			0.51	
Lobster		0.16			0.14			0.09	
Shrimp		0.47			0.10			0.27	
Stable isotopes									
δ^{13}C ± 1 SE	−16.88 ± 0.25	−17.16 ± 0.19	−17.68 ± 0.31	−17.73 ± 0.08	−17.28 ± 0.13	−17.05 ± 0.07	−17.75 ± 0.11	−17.23 ± 0.10	−17.51 ± 0.10
δ^{15}N ± 1 SE	13.73 ± 0.19	13.57 ± 0.21	14.14 ± 0.18	13.49 ± 0.11	13.67 ± 0.15	13.80 ± 0.11	13.92 ± 0.22	14.56 ± 0.14	14.18 ± 0.13
Condition									
K_{rel} ± 1 SE	0.89 ± 0.02	0.90 ± 0.03	1.10 ± 0.02	0.97 ± 0.02	0.97 ± 0.02	1.10 ± 0.02	1.03 ± 0.02	0.96 ± 0.02	1.07 ± 0.02
Residual LSI ± 1SE	−0.15 ± 0.11	−0.35 ± 0.10	0.29 ± 0.11	0.03 ± 0.08	0.26 ± 0.10	0.48 ± 0.13	−0.16 ± 0.06	−0.30 ± 0.06	−0.53 ± 0.04
Reproduction									
Residual GSI ± 1SE	1.14 ± 0.67	0.51 ± 0.41	−1.11 ± 0.09	1.77 ± 0.44	1.47 ± 0.38	−1.14 ± 0.13	0.65 ± 0.15	−1.43 ± 0.16	−1.36 ± 0.04
Sex ratio		33% male/67% female			56% male/44% female			22% male/78% female	
L_{50}/A_{50}	26.60 cm (95% UCI-LCI = 27.1–25.6 cm)/1.78 (95% UCI-LCI = 1.94–1.62)								

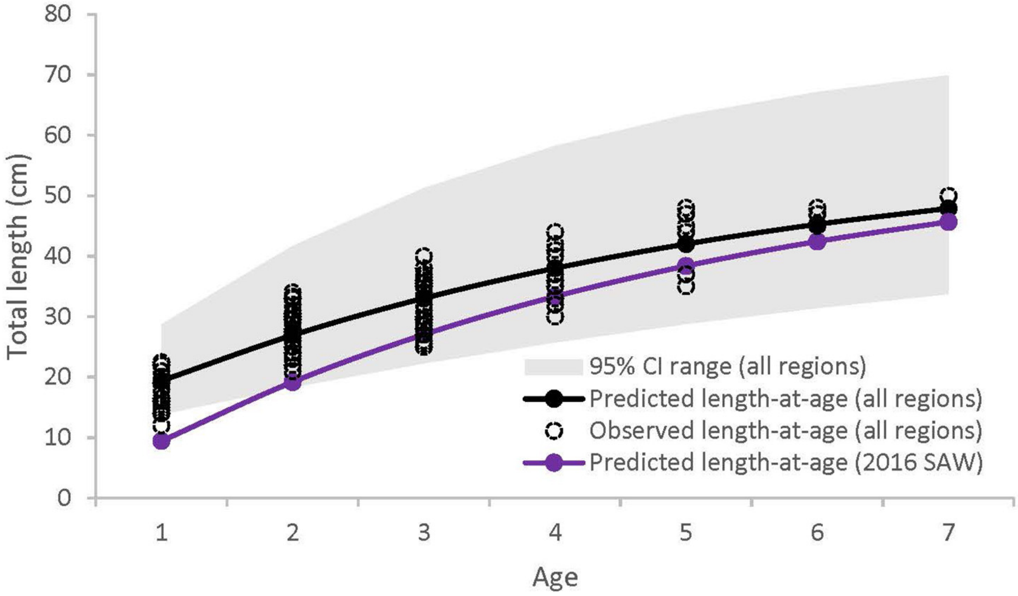

FIGURE 3 | Von Bertalanffy growth curves for black sea bass from all regions combined (black), and from the 2016 Black Sea Bass Stock Assessment (purple) (Northeast Fisheries Science Center [NEFSC], 2016). Gray shaded area represents 95% confidence intervals for all regions combined (95% confidence intervals not available for 2016 Black Sea Bass Stock Assessment).

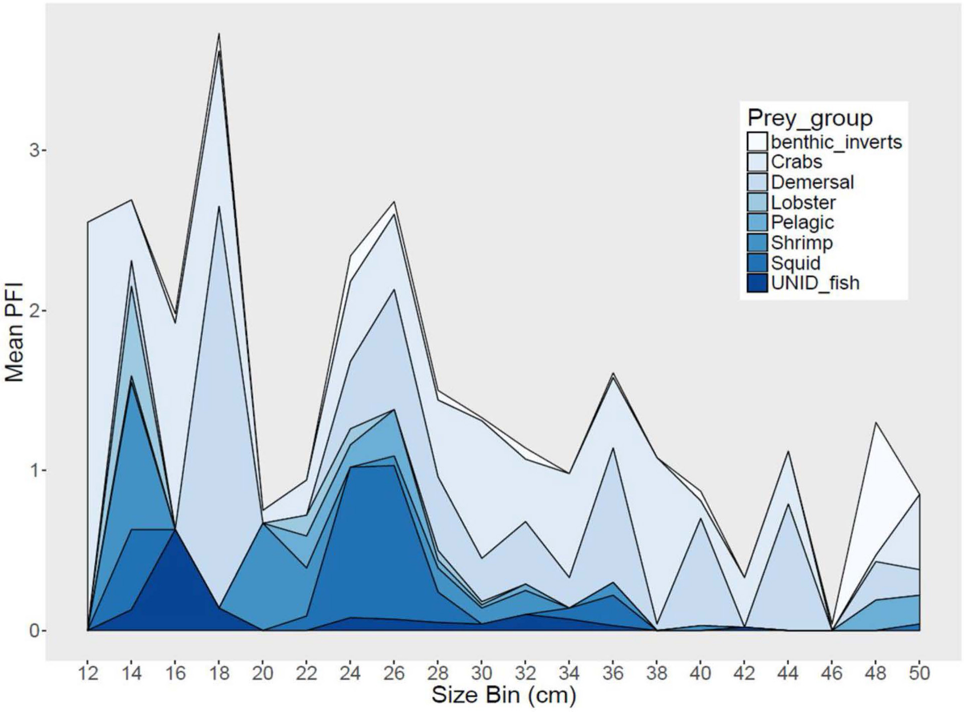

FIGURE 4 | Stacked area graph of mean partial fullness index (Mean PFI) by 2 cm size bins for black sea bass from all regions combined.

fall (Tukey's HSD, $p < 0.05$), and significantly higher than ME fish in the summer. In addition, $\delta^{15}N$ values of ME fish were significantly higher than those of NMA fish. Finally, $\delta^{15}N$ values for ME fish were significantly higher in the fall compared to spring and summer, for SMA fish were significantly higher in the summer compared to spring and fall, and for NMA fish were significantly higher in the fall compared to spring (Tukey's HSD, $p > 0.05$ for all comparisons).

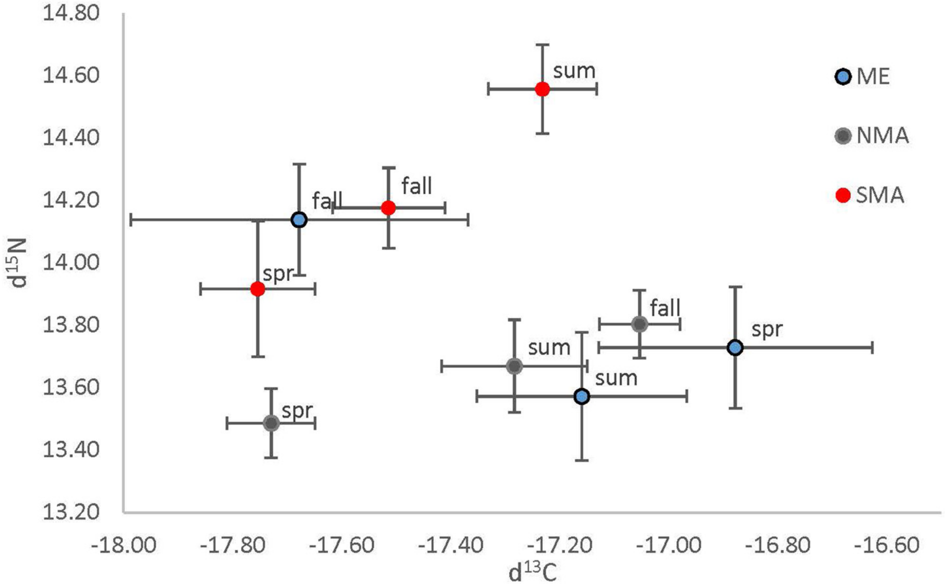

FIGURE 5 | Mean (± 1 SE) δ13C plotted against mean (± 1 SE) δ15N, separated by region (Maine = blue, northern Massachusetts = gray and southern Massachusetts = red) and season (spring = spr, summer = sum and fall = fall).

Condition

The equation $W_g = 0.02 * L_t{}^{2.86}$ explained > 97% of the variance between length and weight of sea bass from all regions combined (**Supplementary Figure S2**). There was a significant interaction effect between region and season on K_{rel} [ANOVA, $F_{(4,\ 254)} = 3.36$, $p = 0.01$, **Figure 6A**]. K_{rel} was significantly greater for NMA and ME fish in the fall compared to the spring and summer, and significantly lower for SMA fish in the summer compared to spring and fall (Tukey's HSD, $p < 0.05$ for all comparisons). K_{rel} was also greater for SMA fish in the spring compared to ME fish (Tukey's HSD, $p = 0.009$). Mean (± 1 SE) values of K_{adj} (binned into 2 cm sea bass length intervals) varied greatly, but there was a decreasing trend in K_{adj} between 28 and 36 cm for all regions combined (**Figure 7**).

There was a significant interaction between region and season [ANOVA, $F_{(4,\ 251)} = 7.36$, $p < 0.001$, **Figure 6B**] on residual LSI. Residual LSI was significantly lower for SMA fish in the fall compared to the spring and summer, significantly greater for ME fish in fall compared to summer, and significantly greater for NMA fish in fall compared to spring (Tukey's HSD, $p < 0.05$ for all comparisons). LSI was also greater in the fall for NMA and ME fish compared to SMA fish, and greater in the summer for NMA fish compared to ME and SMA fish (Tukey's HSD, $p < 0.05$ for all comparisons). Mean (± 1SE) values of LSI_{adj} (binned into 2 cm sea bass length intervals) also varied greatly, but contrary to K_{adj} results, there was a trend of increasing LSI_{adj} between 26 and 36 cm for all regions combined (**Figure 7**).

Reproduction

There was a significant interaction between region and season [ANOVA, $F_{(4,\ 240)} = 7.36$, $p < 0.001$] on residual GSI (**Table 1** and **Figure 6C**). Residual GSI was lower for NMA and ME fish in the fall compared to spring and summer, and greater for SMA fish in the spring compared to summer and fall (Tukey's HSD, $p < 0.05$ for all comparisons). Residual GSI was also lower in the spring for SMA fish compared to NMA fish, and lower in the summer for SMA fish compared to both NMA and ME fish (Tukey's HSD, $p < 0.05$ for all comparisons).

There were significantly more females than males in SMA and ME (x^2, $p < 0.05$), and slightly more males than females in NMA, but this was not significant. The black sea bass sex ratio-at-length for all regions combined is shown in **Figure 8A**. The length at which 50% of the population was female was 33.9 cm (lower and upper 95% CI = 31.9 and 36.8 cm). Mean length at 50% maturity for all regions combined was 26.6 cm (lower and upper 95% CI = 25.6 and 27.1 cm; **Figure 8B**), and the age at 50% maturity for all regions combined was 1.78 (lower and upper 95% CI = 1.62 and 1.94; **Figure 8C**). Age-at-maturity varied among regions, with SMA having the highest age-at-maturity and NMA having the lowest. There were significantly more mature than immature sea bass collected in NMA (x^2, $p < 0.05$). The proportion of mature fish collected in SMA and ME did not differ (x^2, $p > 0.05$).

DISCUSSION

In the past decade, black sea bass have expanded their range into the GOM where historically cold oceans waters are now warming faster than 99% of the world's oceans (Pershing et al., 2015), causing a shift in the distribution of suitable habitat for many species. Observations of black sea bass from SMA (i.e., historic northern range limit), NMA (i.e., newly expanded range) and ME (i.e., upper limit of newly expanded range edge), revealed variation in life-history traits across a relatively

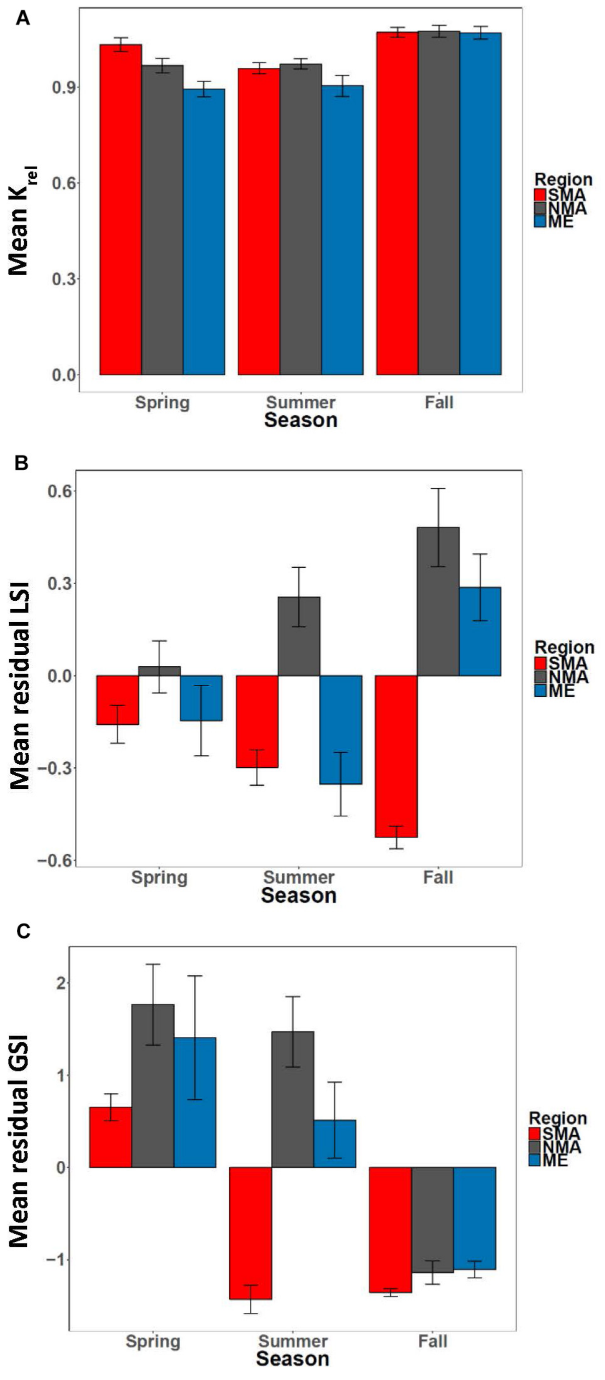

FIGURE 6 | (A) Mean Krel, **(B)** mean residual LSI and **(C)** mean residual GSI by season for Maine (ME), northern Massachusetts (NMA) and southern Massachusetts (SMA).

small geographic area. Significant spatial differences in size, diet, condition, maturity and sex ratio were observed. Although small sample sizes across years prevented us from analyzing inter-annual variation, which may have biased our results, our findings pooled across years suggest that range expanding sea bass may exhibit life-history strategies that differ from their southern counterparts.

Growth and Reproduction

Length-at-age estimates for all regions combined were greater than the length-at-age estimate established in the 2016 Black Sea Bass Stock Assessment, which combines length and age data from populations throughout the northern range, from Cape Hatteras to Cape Cod (Northeast Fisheries Science Center [NEFSC], 2016). We also found that sea bass from NMA and ME reach reproductive maturity at a younger age than sea bass from SMA, and that the length-at-maturity for all regions combined (L_{50} = 26.6 cm) was greater than the length-at-maturity utilized in the most recent sea bass assessment (L_{50} = 21 cm; Northeast Fisheries Science Center [NEFSC], 2016). These observed differences may have arisen from latitudinal variation in temperature and the length of the growing season. Organisms at higher latitudes may be locally adapted to grow within a lower range of temperatures, may have growth rates that evolve inversely with the length of the growing season (i.e., countergradient variation), or may exhibit some combination of these adaptations (Yamahira and Conover, 2002). For instance, Conover and Present (1990) found that fish from colder regions were adapted to a shorter growing season and grew faster than their southern counterparts. This effect may be due, in part, to northern fish having greater food conversion efficiencies (Present and Conover, 1992).

It is also possible that the observed differences in growth and maturity may be related to differences in migration strategies. In their native range, sea bass migrate off of the continental shelf in the winter and migrate back to nearshore habitat in the spring (Shepherd, 2008). However, very little is known about the migration patterns of sea bass in the GOM. Three potential different migration strategies could be occurring: (1) sea bass overwinter in the GOM, (2) sea bass overwinter in the Mid-Atlantic and return to the GOM each year, or (3) sea bass overwinter in the Mid-Atlantic and randomly re-occupy northern areas each year. Given the observed differences in biological metrics found in this study, it may be more likely that sea bass are overwintering in the GOM or returning to the same areas each year. Anecdotal evidence from fishers suggests that sea bass are occasionally found in offshore regions of the GOM during the winter months, further indicating that resident populations may exist. Differences in the bioenergetics of resident vs. migratory fish populations has been well documented (e.g., Forseth et al., 1999; Morinville and Rasmussen, 2003; Kerr and Secor, 2009). In particular, Morinville and Rasmussen (2003) found that resident brook trout have higher growth efficiency as a result of lower total metabolic costs. Further studies focusing on both the migration patterns and bioenergetics of sea bass in the Gulf of Maine are warranted, and may begin to uncover the mechanisms driving the latitudinal variation in growth and maturity found in this study. Furthermore, the variation in life history traits observed could have far reaching management implications as the northern stock of sea bass continues to expand poleward (Pinsky and Mantua, 2014; Hare et al., 2016; Kleisner et al., 2016, 2017).

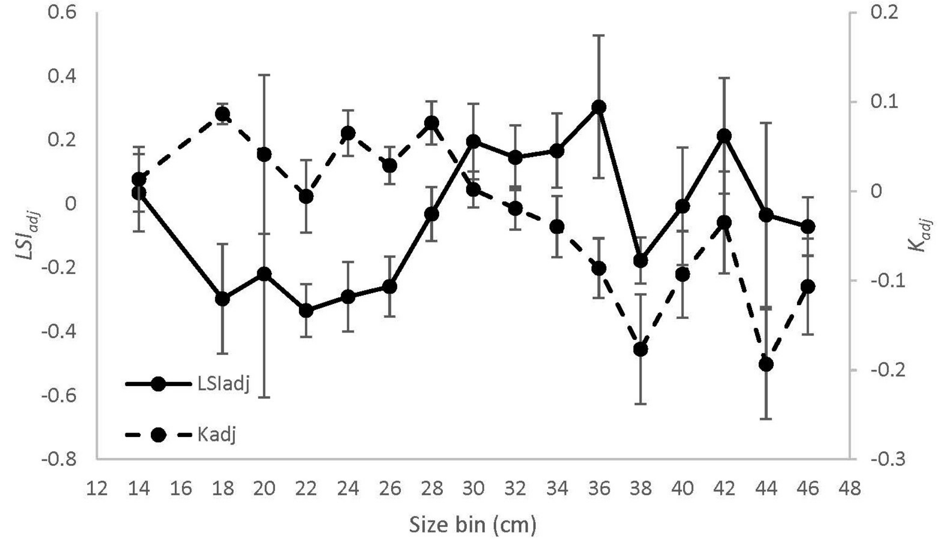

FIGURE 7 | Mean (± 1 SE) values of Kadj (dashed line) and LSIadj (solid line) by 2 cm size bins for black sea bass from all regions combined.

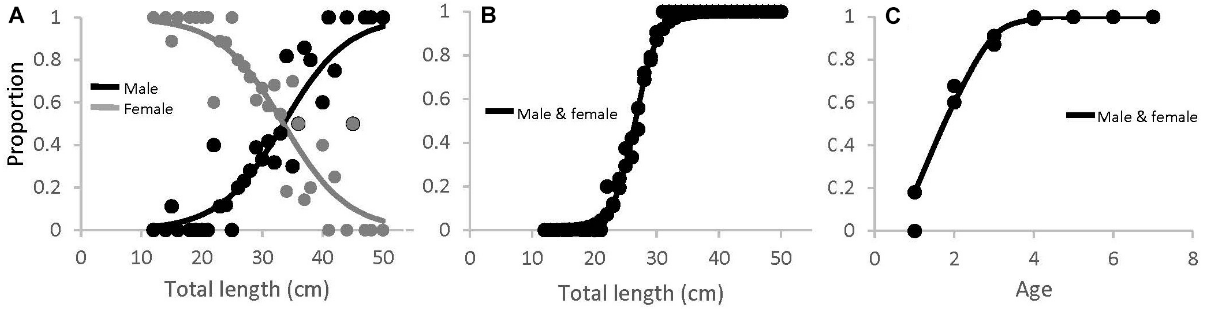

FIGURE 8 | (A) Proportion of male (black) and female (gray) black sea bass as a function of total length for all regions combined (M_{50} = 33.5 cm), **(B)** length-at-maturity (L_{50} = 26.6 cm), and **(C)** age-at-maturity (A_{50} = 1.78 years) for all regions and sexes combined.

Demographic patterns of abundance may also be influencing sea bass growth and reproduction. Range expanding sea bass populations are likely at lower densities, as evidenced by low capture rates by both fisheries dependent and independent sources, and therefore may not be subject to density-dependent competition (Burton et al., 2010; Phillips et al., 2010). These range expanding sea bass appear to be growing faster and achieving reproductive maturity at a younger age, but larger size, which follows r-K selection theory (Charlesworth, 1971; Roughgarden, 1971). Faster growth rates result in fish achieving reproductive maturity at a younger age, which promotes rapid population growth. Spatial variation in conspecific density can influence life-history traits in fish, including growth, maturation, and diet (Jones, 1987; Caselle et al., 2003, 2011; Samhouri, 2009). For example, Caselle et al. (2011) found that high density populations of California sheephead were smaller in size, had lower fecundity, and changed sex at smaller sizes, and Samhouri (2009) found that aggressive interactions in high density populations of damselfish resulted in reduced growth and reproductive output. Similar density-dependent effects may be influencing the spatial variation in black sea bass life-history traits observed among our study sites, as well as between our data and the most recent sea bass stock assessment from farther south where these effects are likely stronger (Northeast Fisheries Science Center [NEFSC], 2016).

Interspecific competition may also differ between the GOM and regions farther south. Atlantic cod, a historically dominant large bodied predator in the GOM, has rapidly decreased in abundance in recent decades, and spawning stock biomass is currently estimated to be at 5–8% of the target level (Palmer, 2017). In general, large groundfish species are functionally absent in much of the nearshore ecosystem, and have been largely replaced by smaller-bodied fish, such as sculpin and cunner (Witman and Sebens, 1992; Steneck, 1997). Sea bass are an aggressive and territorial species, and may easily outcompete small-bodied native GOM fish. For example, SCUBA and video surveys in NMA and ME have captured sea bass aggressively interacting with cunner and small pollock, generally driving them away from sea bass territories (McMahan and Grabowski, unpublished data). Therefore, in addition to potentially experiencing reduced intraspecific competition, sea bass in the GOM may also be subjected to reduced interspecific competition in comparison to those in southern regions, further minimizing the reproductive-growth trade-offs encountered in a highly competitive environment (Burton et al., 2010).

Diet and Condition

We found both regional and seasonal variability in K_{rel}, but overall there was a decreasing trend with latitude which may be due, in part, to variations in diet. We found that the diversity and quality of prey items in the diet of sea bass decreased with latitude. The diet of SMA sea bass was dominated by lipid rich demersal and pelagic fish, as well as squid, whereas the diet of NMA and ME sea bass was dominated by small crustaceans. Diet trends in NMA and ME were similar to results from previous studies suggesting that sea bass rely heavily on crabs and other benthic invertebrates (Mack and Bowman, 1983; Steimle and Figley, 1996; Garrison and Link, 2000). Within this study area, heterogeneity in prey availability is likely driving regional differences. For instance, many prey items found in the diet of SMA sea bass (e.g., bay anchovy, scup, squid) are rare or found in lower abundance in the GOM. However, it is unclear why SMA sea bass would consume more fish and squid than populations farther south. Stable isotope signatures reflected many of the dietary trends revealed in the stomach content analysis. ME fish had the highest δ13C values in the spring, which was also when the most shrimp and benthic invertebrate prey were found in their diet. SMA and NMA fish had higher δ13C values in the fall, which was when the greatest amount of crabs were found in their diet. δ13C values were lowest for SMA and NMA fish in the spring, however, this was also the period of time when very few fish and squid were found in their diet. Therefore, there may be a prey source that these fish consume in the spring (i.e., when sea bass are migrating from the continental shelf to nearshore spawning habitat) that was not found in stomach content results.

Ontogenetic trends in diet revealed that feeding habits also fluctuated with fish size and that Kadj closely tracked diet trends. We were unable to compare ontogenetic trends in diet and condition among regions due to low sample sizes. However, in general, we found that fish between 28 and 36 cm total length decreased their feeding and shifted from consuming predominantly squid and fish to crabs, which coincided with a decrease in their K_{adj}. Sherwood et al. (2002) found that prey switching often occurs when condition starts to decline, suggesting that these diet changes may be necessary to overcome energetic bottlenecks. Yet, counterintuitively, LSI_{adj} increased within this size range, suggesting that further research will likely be needed to resolve whether it is an energetic bottleneck. It is also possible that the allocation of energy shifts during certain growth phases, causing liver and somatic condition to diverge. As individuals allocate energy to fat reserves (i.e., lipid storage in the liver) they must reduce energy allocation to somatic growth. Therefore, sea bass storing energy for periods without feeding, such as spawning, may exhibit decreased somatic growth and increased lipid storage.

The range of LSI and GSI values obtained in this study were similar to values previously reported for sea bass collected in SMA (Wuenschel et al., 2013). LSI varied among season, but was highest in the fall for NMA and ME, and was inversely correlated with GSI. This finding may indicate that sea bass in the GOM are using energy reserves in the liver while spawning, and that those reserves are replenished when spawning concludes in the late summer and fall. It is also possible that this energy allocation strategy relates to the fall migration of sea bass in the GOM, however, very little is known about seasonal movement patterns of sea bass in this newly expanded region. The opposite energy allocation trend was found in SMA. LSI decreased from spring to fall and was positively correlated with GSI. LSI values in SMA were also lower than in NMA and ME. We speculate that this could have been related to increased consumption of fish and squid in SMA. As spawning decreased from spring to fall for SMA fish, consumption may have rapidly increased. A substantial increase in body weight would sharply increase the denominator of the LSI equation, leading to decreased LSI values (Brown and Murphy, 2004). Overall, these results suggest that sea bass in SMA may exhibit different energetic strategies than sea bass in the GOM, and that parameters from sea bass caught within the historic range may not accurately predict the biology and population dynamics of sea bass in the GOM. Further investigation of how energetic strategies vary with latitude is warranted.

Regional differences in GSI may reflect a latitudinal gradient in the length of the spawning season. Sea bass in SMA are likely able to spawn earlier in the spring due to warmer temperatures and a shorter migration from offshore winter habitat. We collected sea bass between mid-May and mid-June in the spring season. In SMA, GSI may have already begun to decrease during this period if spawning began earlier than mid-May. Conversely, GSI was much higher in NMA and ME during the spring, perhaps because spawning is delayed at higher latitudes. In the summer season, GSI was greatly reduced in SMA as spawning was likely ending, and GSI values were similarly low among all regions in the fall.

Size and Sex Ratio

We found that the sex ratio of all regions combined was 100% female for the smallest sizes and approached 100% male for the largest sizes. This pattern is typical of a hermaphroditic species that matures as a female and transitions to male as it grows, however, our results were markedly different from previous black sea bass work that has found sex ratios of approximately 30% male below 30 cm, and 30–40% female above 45 cm (Wuenschel et al., 2011; Northeast Fisheries Science Center [NEFSC], 2012, 2016; Blaylock and Shepherd, 2016). Indeed, the northern stock of black sea bass in its historic range is distinguished from typical protogynous hermaphrodites because of the presence of secondary mature males and the abundance of large females in their population (Blaylock and Shepherd, 2016). Blaylock and Shepherd (2016) concluded that black sea bass are likely more resilient to fisheries exploitation because of these unique sex ratios. Our results did not reveal a similar abundance of smaller males and larger females, which may be a consequence of small sample sizes of the smallest and largest black sea bass size categories. We analyzed a total of 288 sea bass, whereas the stock assessment utilizes results from thousands of sea bass throughout the northern range (but south of Cape Cod). However, it is also possible that range expanding populations do not reflect the same sex-ratio trends as populations near the center of their range.

In addition, we found that sex ratios varied with region, with 20–30% males and 70–80% females in SMA and ME, and 55% males and 45% females in NMA. We also found that sea bass were larger in NMA and predominantly mature. Caruso (1995) observed that the majority of sea bass recruiting to SMA where mature, and at the time of these observations (early 1990s), SMA was considered the range edge of the northern stock. These results indicate that sea bass populations have shifted, and that large, mature fish are now recruiting to NMA. Meanwhile, small, immature fish (i.e., those that can be outcompeted by larger fish) are common farther north in ME, where conspecific density is lower, but habitat may be suboptimal (i.e., colder temperature and less diverse prey availability).

CONCLUSION

Collectively, these results suggest that demographic patterns and life-history strategies of range expanding sea bass differ from more centralized populations, and that important stock metrics, such as growth and maturity, vary over relatively short distances. Previous black sea bass stock assessment reviews explicitly called for the incorporation of spatial structure within the northern stock due to concern that incomplete mixing was occurring (Northeast Fisheries Science Center [NEFSC], 2016). In response, the most recent sea bass stock assessment incorporated a spatial divide at the Hudson Canyon and found that the two-area model better represented overall population dynamics (Northeast Fisheries Science Center [NEFSC], 2016). However, our results suggest that latitudinal heterogeneity exists in sea bass populations north of the Hudson Canyon divide. Furthermore, the poleward range expansion of black sea bass is predicted to continue as additional warming occurs along the U.S. Northeast Continental Shelf (Kleisner et al., 2016, 2017), which could result in further divergence of life-history traits of range expanding sea bass away from more centralized populations. We recommend that future assessments target GOM sea bass to build upon these initial findings and enhance our understanding of the biology and population dynamics of sea bass in their newly expanded range. Finally, these findings apply more broadly to the global redistribution of species that is currently underway and expected to intensify (Pecl et al., 2017), and emphasize the need to incorporate alternative assessment and management approaches to range shifting species.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

Ethical review and approval was not required for this animal study as samples were obtained by fishermen or state/federal agencies (Maine Department of Marine Resource, Massachusetts Division of Marine Fisheries, and the Northeast Fisheries Science Center).

AUTHOR CONTRIBUTIONS

MM and JG designed and carried out the research. MM conducted the analyses. MM, JG, and GS contributed to writing and reviewing the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

Funding for this project was provided by the Graduate Women in Science Nell Mondy Fellowship, the Switzer Environmental Fellowship, crowd funding sourced through Experiment, and the NOAA Saltonstall-Kennedy Grant Program: Award # NA18NMF4270189.

ACKNOWLEDGMENTS

We thank the Massachusetts Division of Marine Fisheries, Maine Department of Marine Resources, Kevin Cheung, William Lister, Jim McMahan, and Richard Nelson for collecting sea bass. We also thank R. Waller, S. Elzey, K. O'Brien, K. Schultz, A. Scrippa, and C. Lawrence for assistance in the laboratory. Finally, this manuscript was greatly improved thanks to comments and edits provided by three reviewers.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.567758/full#supplementary-material

REFERENCES

Alonzo, S. H., Ish, T., Key, M., MacCall, A. D., and Mangel, M. (2008). The importance of incorporating protogynous sex change into stock assessments. *Bull. Mar. Sci.* 83, 163–179.

Bell, R. J., Richardson, D. E., Hare, J. A., Lynch, P. D., and Fratantoni, P. S. (2015). Disentangling the effects of climate, abundance, and size on the distribution of marine fish: an example based on four stocks from the Northeast US shelf. *ICES J. Mar. Sci.* 72, 1311–1322. doi: 10.1093/icesjms/fsu217

Benard, M. F. (2004). Predator-induced phenotypic plasticity in organisms with complex life histories. *Annu. Rev. Ecol. Evol. Syst.* 35, 651–673. doi: 10.1146/annurev.ecolsys.35.021004.112426

Blaylock, J., and Shepherd, G. R. (2016). Evaluating the vulnerability of an atypical protogynous hermaphrodite to fishery exploitation: results from a population model for black sea bass (*Centropristis striata*). *Fishery Bull.* 114, 476–489. doi: 10.7755/FB.114.4.9

Bowering, W. R., and Lilly, G. R. (1992). Greenland halibut (*Reinhardtius hippoglossoides*) off southern Labrador and northeastern Newfoundland

(Northwest Atlantic) feed primarily on capelin (*Mallotus villosus*). *Neth. J. Sea Res.* 29, 211–222. doi: 10.1016/0077-7579(92)90021-6

Brander, K. (2010). Impacts of climate change on fisheries. *J. Mar. Syst.* 79, 389–402. doi: 10.1016/j.jmarsys.2008.12.015

Bretz, F., Hothorn, T., and Westfall, P. (2010). *Multiple Comparisons Using R*. Boca Raton, FL: CRC Press.

Brown, J. H. (1995). *Macroecology*. Chicago, IL: University of Chicago Press.

Brown, M. L., and Murphy, B. R. (2004). Seasonal dynamics of direct and indirect condition indices in relation to energy allocation in largemouth bass *Micropterus salmoides* (Lacepede). *Ecol. Freshw. Fish* 13, 23–36. doi: 10.1111/j.0906-6691.2004.00031.x

Buchheister, A., and Latour, R. J. (2015). Dynamic trophic linkages in a large estuarine system—support for supply-driven dietary changes using delta generalized additive mixed models. *Can. J. Fish. Aquat. Sci.* 73, 5–17. doi: 10.1139/cjfas-2014-0441

Burton, O. J., Phillips, B. L., and Travis, J. M. (2010). Trade-offs and the evolution of life-histories during range expansion. *Ecol. Lett.* 13, 1210–1220. doi: 10.1111/j.1461-0248.2010.01505.x

Cadrin, S. X., and Secor, D. H. (2009). "Accounting for spatial population structure in stock assessment: past, present, and future," in *The Future of Fisheries Science in North America*, eds R. J. Beamish and B. J. Rothschild (Dordrecht: Springer), 405–426. doi: 10.1007/978-1-4020-9210-7_22

Caruso, P. G. (1995). *The Age, Growth, and Spawning of Black Sea Bass (Centropristis striata, Linneaus) in Massachusetts Waters*. Master's thesis, University of Rhode Island, Kingston, RI, 117.

Caselle, J. E., Hamilton, S. L., Schroeder, D. M., Love, M. S., Standish, J. D., Rosales-Casian, J. A., et al. (2011). Geographic variation in density, demography, and life history traits of a harvested, sex-changing, temperate reef fish. *Can. J. Fish. Aquat. Sci.* 68, 288–303. doi: 10.1139/F10-140

Caselle, J. E., Hamilton, S. L., and Warner, R. R. (2003). The interaction of retention, recruitment, and density-dependent mortality in the spatial placement of marine reserves. *Gulf Caribbean Res.* 14, 107–116. doi: 10.18785/gcr.1402.08

Charlesworth, B. (1971). Selection in density-regulated populations. *Ecology* 52, 469–474. doi: 10.2307/1937629

Ciannelli, L., Fauchald, P., Chan, K. S., Agostini, V. N., and Dingsør, G. E. (2008). Spatial fisheries ecology: recent progress and future prospects. *J. Mar. Syst.* 71, 223–236. doi: 10.1016/j.jmarsys.2007.02.031

Conover, D. O. (1990). The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. *Trans. Am. Fish. Soc.* 119, 416–430. doi: 10.1577/1548-8659(1990)119<0416:TRBCFG>2.3.CO;2

Conover, D. O., and Present, T. M. (1990). Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia* 83, 316–324. doi: 10.1007/BF00317554

Drohan, A. F., Manderson, J. P., and Packer, D. B. (2007). *Essential Fish Habitat Source Document: Black Sea Bass, Centropristis striata, Life History and Habitat Characteristics*, 2nd Edn. Available online at: http://www.nefsc.noaa.gov/nefsc/publications/tm/tm200/ (accessed September, 2014).

Elzey, S. P., Trull, K. J., and Rogers, K. A. (2015). *Massachusetts Division of Marine Fisheries Age and Growth Laboratory: Fish Aging Protocols*. Gloucester, MA: Massachusetts Division of Marine Fisheries.

Forseth, T., Naesje, T. F., Jonsson, B., and Harsåker, K. (1999). Juvenile migration in brown trout: a consequence of energetic state. *J. Anim. Ecol.* 68, 783–793. doi: 10.1046/j.1365-2656.1999.00329.x

Froese, R. (2006). Cube law, condition factor and Length-Weight relationships: history, meta-analysis and recommendations. *Appl. Ichthyol.* 22, 241–253. doi: 10.1111/j.1439-0426.2006.00805.x

Fry, B. (1988). Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnol. Oceanogr.* 33, 1182–1190. doi: 10.4319/lo.1988.33.5.1182

Garrison, L. P., and Link, J. S. (2000). Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. *Mar. Ecol. Prog. Ser.* 202, 231–240. doi: 10.3354/meps202231

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics* 27, 857–874. doi: 10.2307/2528823

Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., et al. (2016). A vulnerability assessment of fish and invertebrates to climate change on the Northeast US Continental Shelf. *PLoS One* 11:e0146756. doi: 10.1371/journal.pone.0146756

Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous inference in general parametric models. *Biom. J.* 50, 346–363. doi: 10.1002/bimj.200810425

Jones, G. P. (1987). Competitive interactions among adults and juveniles of a coral reef fish. *Ecology* 68, 1534–1547. doi: 10.2307/1939237

Jorgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., et al. (2007). Ecology-Managing evolving fish stocks. *Science* 318, 1247–1248. doi: 10.1126/science.1148089

Kerr, L. A., and Secor, D. H. (2009). Bioenergetic trajectories underlying partial migration in Patuxent River (Chesapeake Bay) white perch (Morone americana). *Can. J. Fish. Aquat. Sci.* 66, 602–612. doi: 10.1139/F09-027

Kleisner, K. M., Fogarty, M. J., McGee, S., Barnett, A., Fratantoni, P., Greene, J., et al. (2016). The effects of sub-regional climate velocity on the distribution and spatial extent of marine species assemblages. *PLoS One* 11:e0149220. doi: 10.1371/journal.pone.0149220

Kleisner, K. M., Fogarty, M. J., McGee, S., Hare, J. A., Moret, S., Perretti, C. T., et al. (2017). Marine species distribution shifts on the US Northeast Continental Shelf under continued ocean warming. *Prog. Oceanogr.* 153, 24–36. doi: 10.1016/j.pocean.2017.04.001

Kolek, D. (1990). *Homing of Black Sea Bass, Centropristis striata, in Nantucket Sound with Comments on Seasonal Distribution, Growth Rates, and Fisheries of the Species*. Boston, MA: Massachusetts Division of Marine Fisheries, 12.

Lawing, A. M., and Polly, P. D. (2011). Pleistocene climate, phenology, and climate envelope models: an integrative approach to better understand species' response to climate change. *PLoS One* 6:e28554. doi: 10.1371/journal.pone.0028554

Le Cren, E. D. (1951). The length-weight relationships and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *J. Anim. Ecol.* 20, 201–219.

Link, J. S., Nye, J. A., and Hare, J. A. (2011). Guidelines for incorporating fish distribution shifts into a fisheries management context. *Fish Fish.* 12, 461–469.

Lorenzen, K., Steneck, R. S., Warner, R. R., Parma, A. M., Coleman, F. C., and Leber, K. M. (2010). The spatial dimensions of fisheries: putting it all in place. *Bull. Mar. Sci.* 86, 169–177.

Mack, R. G. Jr., and Bowman, R. E. (1983). *Food and Feeding of Black Sea Bass (Centropristis striata). Woods Hole Laboratory Reference Document*. Woods Hole, MA: Northeast Fisheries Center.

McCartney, M. A., Burton, M. L., and Lima, T. G. (2013). Mitochondrial DNA differentiation between populations of black sea bass (*Centropristis striata*) across Cape Hatteras, North Carolina (USA). *J. Biogeogr.* 40, 1386–1398.

McGovern, J. C., Collins, M. R., Pashuk, O., and Meister, H. S. (2002). Temporal and spatial differences in life history parameters of black sea bass in the southeastern United States. *North Am. J. Fish. Manage.* 22, 1151–1163.

Morinville, G. R., and Rasmussen, J. B. (2003). Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci.* 60, 401–410. doi: 10.1139/F03-036

Moser, J., and Shepherd, G. R. (2009). Seasonal distribution and movement of black sea bass (*Centropristis striata*) in the Northwest Atlantic as determined from a mark-recapture experiment. *J. Northwest Atl. Fishery Sci.* 40, 17–28.

Northeast Fisheries Science Center [NEFSC] (2012). *53rd Northeast Regional Stock Assessment Workshop (53rd SAW) Assessment Report. US Department of Commerce, Northeast Fisheries Science Center Reference Document*. Woods Hole, MA: National Marine Fisheries Service.

Northeast Fisheries Science Center [NEFSC] (2016). *62nd Northeast Regional Stock Assessment Workshop (62nd SAW) Assessment Report. US Department of Commerce, Northeast Fisheries Science Center Reference Document*. Woods Hole, MA: National Marine Fisheries Service.

Ogle, D. H. (2013). *fishR Vignette: Length-Weight Relationships*. Ashland, WI: Northland College.

Ogle, D. H., Wheeler, P., and Dinno, A. (2020). *FSA: Fisheries Stock Analysis. R package version* 0.8.30.9000. Available online at: https://github.com/droglenc/FSA (accessed July 6, 2020).

Owens, N. J. P. (1987). Natural variation in 15N in the marine environment. *Adv. Mar. Biol.* 24, 389–450. doi: 10.1016/S0065-2881(08)60077-2

Palmer, M. (2017). *Gulf of Maine Atlantic Cod 2017 Assessment Update Report*. Woods Hole, MA: National Marine Fisheries Service.

Parmesan, C., and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42. doi: 10.1038/nature01286

Pascoe, S., Bustamante, R., Wilcox, C., and Gibbs, M. (2009). Spatial fisheries management: a framework for multi-objective qualitative assessment. *Ocean Coast. Manage.* 52, 130–138. doi: 10.1016/j.ocecoaman.2008.10.009

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES J. Mar. Sci.* 39, 175–192. doi: 10.1093/icesjms/39.2.175

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., et al. (2017). Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355:eaai9214. doi: 10.1126/science.aai9214

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science* 308, 1912–1915. doi: 10.1126/science.1111322

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., et al. (2015). Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350, 809–812. doi: 10.1126/science.aac9819

Phillips, B. L., Brown, G. P., and Shine, R. (2010). Life-history evolution in range-shifting populations. *Ecology* 91, 1617–1627. doi: 10.1890/09-0910.1

Pinsky, M. L., and Mantua, N. J. (2014). Emerging adaptation approaches for climate-ready fisheries management. *Oceanography* 27, 146–159. doi: 10.5670/oceanog.2014.93

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., et al. (2013). Global imprint of climate change on marine life. *Nat. Clim. Change* 3, 919–925. doi: 10.1038/nclimate1958

Pörtner, H. O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., et al. (2001). Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Cont. Shelf Res.* 21, 1975–1997. doi: 10.1016/S0278-4343(01)00038-3

Present, T. M. C., and Conover, D. O. (1992). Physiological basis of latitudinal growth differences in *Menidia menidia*: variation in consumption or efficiency? *Funct. Ecol.* 6, 23–31. doi: 10.2307/2389767

Provost, M. M., and Jensen, O. P. (2015). The impacts of fishing on hermaphroditic and treatment of sex change in stock assessments. *Fisheries* 40, 536–545. doi: 10.1080/03632415.2015.1093471

R Core Team (2017). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Reznick, D. A., Bryga, H., and Endler, J. A. (1990). Experimentally induced life-history evolution in a natural population. *Nature* 346, 357–359. doi: 10.1038/346357a0

Robillard, E., Gregg, J. W., Dayton, J., and Gartland, J. (2011). *Validation of Black Sea Bass, Centropristis striata, Ages Using Oxytetracycline Marking and Scale Margin Increments. SARC* 62 Working Paper. Woods Hole, MA: Northeast Fisheries Science Center.

Roff, D. (ed.) (1993). *Evolution of Life. (Histories): Theory and Analysis*. New York, NY: Chapman and Hall.

Roughgarden, J. (1971). Density-dependent natural selection. *Ecology* 52, 453–468. doi: 10.2307/1937628

Sagarin, R. D., and Gaines, S. D. (2002). The 'abundant center' distribution: to what extent is it a biogeographical rule? *Ecol. Lett.* 5, 137–147. doi: 10.1046/j.1461-0248.2002.00297.x

Samhouri, J. F. (2009). Food supply influences offspring provisioning but not density-dependent fecundity in a marine fish. *Ecology* 90, 3478–3488. doi: 10.1890/08-1732.1

Santos, M., German, I., Correia, D., Read, F., Martinez Cedeira, J., Caldas, M., et al. (2013). Long-term variation in common dolphin diet in relation to prey abundance. *Mar. Ecol. Prog. Ser.* 481, 249–268. doi: 10.3354/meps10233

Shepherd, G. R. (2008). *Black Sea Bass. The Northeast Data Poor Stocks Working Group Report*. Available online at: file:///C:/Users/ELCOT/Downloads/NEFSC_RD_09_02.pdf (accessed November 24, 2017).

Sherwood, G. D., Pazzia, I., Moeser, A., Hontela, A., and Rasmussen, J. B. (2002). Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. *Can. J. Fish. Aquat. Sci.* 59, 229–241. doi: 10.1139/f02-001

Sherwood, G. D., Rideout, R. M., Fudge, S. B., and Rose, G. A. (2007). Influence of diet on growth, condition and reproductive capacity in Newfoundland and Labrador cod (Gadus morhua): insights from stable carbon isotopes (δ 13 C). *Deep Sea Res Part II Top. Stud. Oceanogr.* 54, 2794–2809. doi: 10.1016/j.dsr2.2007.08.007

Sherwood, G. D., and Rose, G. A. (2005). Stable isotope analysis of some representative fish and invertebrates of the Newfoundland and Labrador continental shelf food web. *Estuar. Coast. Shelf Sci.* 63, 537–549. doi: 10.1016/j.ecss.2004.12.010

Stefánsson, G. (1996). Analysis of groundfish survey abundance data: combining the GLM and delta approaches. *ICES J. Mar. Sci.* 53, 577–588. doi: 10.1006/jmsc.1996.0079

Stefánsson, G., and Pálsson, Ó. K. (1997). Statistical evaluation and modelling of the stomach contents of Icelandic cod (Gadus morhua). *Can. J. Fish. Aquat. Sci.* 54, 169–181. doi: 10.1139/f96-246

Steimle, F. W., and Figley, W. (1996). The importance of artificial reef epifauna to black sea bass diets in the Middle Atlantic Bight. *North Am. J. Fish. Manage.* 16, 433–439. doi: 10.1577/1548-8675(1996)016<0433:TIOARE>2.3.CO;2

Steneck, R. S. (1997). "Fisheries-induced biological changes to the structure and function of the Gulf of Maine ecosystem," in *Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop. RARGOM Report*, eds G. T. Wallace and E. F. Braasch (Hanover, NH: Regional Association for Research on the Gulf of Maine), 151–165.

Witman, J. D., and Sebens, K. P. (1992). Regional variation in fish predation intensity: a historical perspective in the Gulf of Maine. *Oecologia* 90, 305–315. doi: 10.1007/BF00317686

Wuenschel, M. J., McBride, R. S., and Fitzhugh, G. R. (2013). Relations between total gonad energy and physiological measures of condition in the period leading up to spawning: results of a laboratory experiment on black sea bass (*Centropristis striata*). *Fish. Res.* 138, 110–119. doi: 10.1016/j.fishres.2012.05.012

Wuenschel, M. J., Shepherd, G. R., McBride, R. S., Jorgensen, R., Oliveira, K., Robillard, E., et al. (2011). *Sex and Maturity Of Black Sea Bass Collected in Massachusetts and Rhode Island Waters; Preliminary Results Based on Macroscopic Staging of Gonads with a Comparison to Survey Data*. Silver Spring, MD: National Oceanic and Atmospheric Administration.

Yamahira, K., and Conover, D. O. (2002). Intra- vs interspecific latitudinal variation in growth: adaptation to temperature or seasonality? *Ecology* 83, 1252–1262. doi: 10.1890/0012-9658(2002)083[1252:IVILVI]2.0.CO;2

Zanden, M. J. V., and Rasmussen, J. B. (1999). Primary consumer δ13C and δ15N and the trophic position of aquatic consumers. *Ecology* 80, 1395–1404. doi: 10.1890/0012-9658(1999)080[1395:PCCANA]2.0.CO;2

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 30 September 2020
doi: 10.3389/fmars.2020.565699

The Cumulative Effects of Fishing, Plankton Productivity, and Marine Mammal Consumption in a Marine Ecosystem

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OPEN ACCESS

Edited by:
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Reviewed by:
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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: *26 May 2020*
Accepted: *15 September 2020*
Published: *30 September 2020*

Citation:
Fu C, Xu Y, Guo C, Olsen N, Grüss A, Liu H, Barrier N, Verley P and Shin Y-J (2020) The Cumulative Effects of Fishing, Plankton Productivity, and Marine Mammal Consumption in a Marine Ecosystem. Front. Mar. Sci. 7:565699. doi: 10.3389/fmars.2020.565699

The marine ecosystem off British Columbia (BC), Canada, has experienced various changes in the last two decades, including reduced lipid-rich zooplankton biomass, increased marine mammals, and deteriorated commercial fisheries, particularly those targeting pelagic species such as Pacific Herring (*Clupea pallasii*). Understanding how stressors interactively and cumulatively affect commercially important fish species is key to moving toward ecosystem-based fisheries management. Because it is challenging to assess the cumulative effects of multiple stressors by using empirical data alone, a dynamic, individual-based spatially explicit ecosystem modeling platform such as Object-oriented Simulator of Marine Ecosystems (OSMOSE) represents a valuable tool to simulate ecological processes and comprehensively evaluate how stressors cumulatively impact modeled species. In this study, we employed OSMOSE to investigate the cumulative effects of fishing, plankton biomass change, and marine mammal consumption on the dynamics of some fish species and the BC marine ecosystem as a whole. We specifically simulated ecosystem dynamics during the last 20 years under two sets of scenarios: (1) unfavorable conditions from the perspective of commercial fish species (i.e., doubling fishing mortality rates, halving plankton biomass, and doubling marine mammal biomass, acting individually or collectively); and (2) favorable conditions with the three factors having opposite changes (i.e., halving fishing mortality rates, doubling plankton biomass, and halving marine mammal biomass, acting individually or collectively). Our results indicate that, under unfavorable conditions, the degree to which species biomass was reduced varied among species, and that negative synergistic and negative dampened effects were dominant under historical and doubled fishing mortality rates, respectively. Under favorable conditions, species biomasses did not increase as much as expected due to the existence of complex predator-prey interactions among fish species, and positive synergistic and positive dampened effects were prevailing under historical and halved fishing mortality rates, respectively. The ecosystem total biomass and the biomass to fisheries yield ratio were found to be good ecological indicators to represent ecosystem changes and track the impacts from the multiple drivers of change. Our research provides insights on how fisheries management should adapt to prepare for potential future impacts of climate change.

Keywords: cumulative effect, ecosystem-based fisheries management, ecological indicator, ecosystem modeling, synergism

INTRODUCTION

Marine ecosystems have been increasingly impacted by both climate- and human-induced drivers that have caused drastic changes in the ecosystems at multiple trophic levels and spatial scales, potentially resulting in species redistributions, altered biodiversity, ecosystem resilience and integrity, and affecting the reference points that are critical for effective resource management (e.g., Stenseth et al., 2002; Fulton, 2011; García-Reyes et al., 2013; Quetglas et al., 2013; Feld et al., 2016; Samhouri et al., 2017; Bonebrake et al., 2018; Le Bris et al., 2018; Ortega-Cisneros et al., 2018; Ramírez et al., 2018; Guo et al., 2019). The cumulative impacts from multiple drivers of change can also cause significant disturbances in socio-economic systems (Bograd et al., 2019).

In marine ecosystems, multiple drivers of change may interact and generate synergistic, dampened or antagonistic combined effects with respect to the sum of their individual effects (Crain et al., 2008; Griffith et al., 2011, 2012, 2019; Travers-Trolet et al., 2014; Piggott et al., 2015; Fu et al., 2018). Addressing these interacting drivers of change jointly and understanding how they affect different ecosystem components and ecosystem functioning are important to natural resource managers (Planque et al., 2010; Hidalgo et al., 2011; Giakoumi et al., 2015; Halpern et al., 2015; Feld et al., 2016). Since the review by Crain et al. (2008), studies analyzing the cumulative and interactive effects of drivers of change have moved from species-level research to ecosystem-level research (e.g., Micheli et al., 2013; Feld et al., 2016; Schinegger et al., 2016; Teichert et al., 2016; Mach et al., 2017; Lercari et al., 2018; Ramírez et al., 2018). Nevertheless, a deep understanding of the cumulative effects of drivers of change is often impossible when analysts rely only on statistical analyses of empirical data, which hampers a comprehensive prediction of responses to multiple drivers and, thus, the proper mitigation of cumulative impacts of multiple drivers on marine ecosystems and restoration projects (Segurado et al., 2018). In particular, statistical analyses are generally unable to provide information at the scale of entire ecosystems and for long time periods despite the fact that the consideration of large spatial and temporal scales is critical for reliable projections of the potential future effects of drivers of change (Boyd et al., 2018; Hodgson and Halpern, 2019).

In contrast to statistical analyses, simulation experiments using ecosystem models can easily consider the large spatial and temporal scales at which the cumulative effects of multiple drivers of change manifest (Griffith et al., 2011; Fu et al., 2018). Simulation experiments employing ecosystems models have been increasingly conducted during the past 10 years to provide a mechanistic understanding of the impacts of natural and human-induced drivers of changes on marine ecosystems (Griffith et al., 2011, 2012, 2019; Travers-Trolet et al., 2014; Weijerman et al., 2015; Fu et al., 2018, 2019; Ortega-Cisneros et al., 2018). In this study, we applied the ecosystem modeling platform Object-oriented Simulator of Marine Ecosystems (OSMOSE) Shin and Cury, 2004; Fu et al., 2017) to the British Columbia (BC) marine ecosystem (**Figure 1**) to understand the cumulative impacts of multiple drivers on this ecosystem.

Object-oriented Simulator of Marine Ecosystems is an individual-based model that simulates species dynamics in a spatiotemporally explicit fashion. One key characteristic of OSMOSE is that it does not predefine species interactions; rather, species interactions are emerging properties that depend on the degree of spatiotemporal overlap between predator and prey species, their size ratios, and their relative abundances (Shin and Cury, 2004), as well as on the accessibility of prey to the predators due to the morphology and vertical distribution patterns of the prey (Fu et al., 2013). Because modeling with OSMOSE necessitates extensive information on entire life cycles of the modeled species, typically no more than 10–15 species are focused. By limiting the number of focus species included in an OSMOSE model, the computation time and memory capacity can be kept reasonable while the complex interactions within the study ecosystem are simplified. However, this limited number of species can cause the OSMOSE model to miss important, and even sometimes major, prey and predators when the study ecosystem is characterized by a relatively high biodiversity. Fu et al. (2017) enhanced the OSMOSE model to allow explicit consideration of nearly all the taxa of a given ecosystem without compromising much of the computation time and without requiring extensive information on whole life cycles. This enhancement was done through the inclusion of "background" taxa, that is, taxa that are of secondary importance for the study but have the potential to be important prey or predators of the modeled focus species. The inclusion of background taxa has allowed OSMOSE to provide a more comprehensive understanding of species interactions within an ecosystem and their implications when management measures are implemented (Fu et al., 2017).

The BC marine ecosystem is located within a dynamic transition zone where the Pacific Ocean Current bifurcates into the northward-flowing Alaska Current and the southward-flowing California Current, and the variability of the bifurcation location influences the species composition of plankton communities and the productivity of higher-trophic-level fish species (Keister et al., 2011; Malick et al., 2017). In the last two

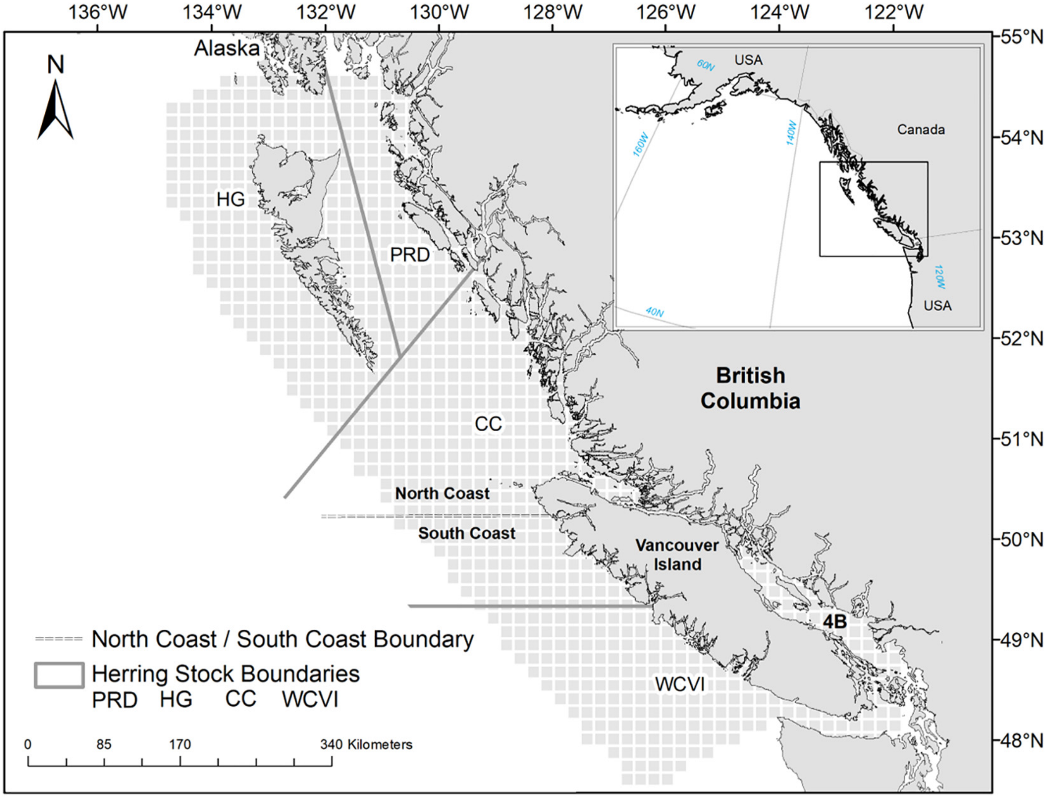

FIGURE 1 | Map of the British Columbia marine ecosystem showing the spatial grid of the OSMOSE-BC model (light gray cells), the four management areas (delineated by solid lines) of Pacific Herring (*C. pallasii*) [Prince Rupert District (PRD), Haida Gwaii (HG), and Central Coast (CC), and West Coast of Vancouver Island (WCVI)], as well as the two management areas (separated by dashed lines) of Pacific Cod (*G. macrocephalus*), Lingcod (*O. elongatus*), and Walleye Pollock (*G. chalcogrammus*) (North and South Coasts).

decades, the BC marine ecosystem has experienced measurable changes in its structure and functioning, potentially due to the spatial redistributions of some marine species in response to changes in climatic conditions. Firstly, the zooplankton community, which used to be dominated by abundant lipid-rich large boreal copepods, has become dominated by gelatinous zooplankton with lower nutritional quality for juvenile fishes (Boldt et al., 2019). Secondly, marine mammals, such as pinnipeds and cetaceans, many of which have experienced a dramatic increase in numbers in the last few decades (Ford, 2014) and may have negatively impacted some commercial fish species (Fu et al., 2017), are increasingly contributing to shaping the functioning of the BC marine ecosystem. Thirdly, some fisheries, particularly those targeting Pacific Herring (*Clupea pallasii*), have contracted or been in moratorium for nearly two decades (Cleary et al., 2018).

In light of the above-mentioned changes, we attempted to understand how fishing pressure, plankton productivity and mammal consumption may have interacted and impacted the BC marine ecosystem, and how fisheries management should be adapted to meet the challenge of climate change. The primary objectives of this study are three-fold. First, at the species level, particularly from the perspectives of commercially and ecologically important species such as Pacific Herring, Pacific Cod (*Gadus macrocephalus*), Lingcod (*Ophiodon elongatus*) and Pacific Halibut (*Hippoglossus stenolepis*), we investigate the impacts on their dynamics of three key drivers, i.e., fishing, change in plankton biomass as suitable food for planktivorous fish, and change in marine mammal biomass as a measure of predatory consumption. Second, at the ecosystem level and from the standpoint of ecological indicators, we examine how these three key drivers influence ecosystem dynamics. Third, from the viewpoint of ecosystem-based fisheries management, we discuss how fisheries management should be adapted to better prepare for potential future climate change.

MATERIALS AND METHODS

Study Area and OSMOSE Model Components

The BC marine ecosystem extends along 27,000 km of the temperate northeast Pacific coastline, and from the coastal watersheds to the outer limit of the continental slope (**Figure 1**). The focus species included in the OSMOSE model for the BC ecosystem ("OSMOSE-BC") are commercially and ecologically important fishes and include Pacific Herring, Pacific Cod, Lingcod, Arrowtooth Flounder (*Atheresthes stomias*), Walleye Pollock (*Gadus chalcogrammus*), and Pacific Halibut (*H. stenolepis*). An additional species group, Euphausiids (*Thysanoessa* spp. and *Euphausia* spp.), is modeled as a focus taxon in the OSMOSE-BC model, as Euphausiids represent an abundant and important food source for higher-trophic-level fish species (Haigh et al., 2015) and baleen whales (Ford, 2014). Following Fu et al. (2017), the focus fish species are modeled either as a single stock (i.e., Arrowtooth Flounder, Pacific Halibut) or multiple stocks in different geographic regions in accordance with the current stock assessment practices (**Figure 1**). Specifically, Pacific Herring has been assessed and managed as four separate stocks in four distinct areas: Prince Rupert District (PRD), Haida Gwaii (HG), Central Coast (CC), and West Coast of Vancouver Island (WCVI). Pacific Cod, Lingcod, and Walleye Pollock are assessed as two separate stocks in two distinct areas: North and South Coasts (**Figure 1**).

In the OSMOSE-BC model, plankton (phytoplankton and zooplankton) are included as spatially distributed biomass pools serving as food for planktivorous fishes. Their biomass time series, minimum and maximum body sizes, trophic levels, and distribution maps at different time steps were set up according to Fu et al. (2017).

Marine mammals are included in the OSMOSE-BC model as background taxa that exert different degrees of predation mortality on other modeled species depending on their abundance, predator-prey size ratio, and spatial distribution (Fu et al., 2017). Included in the OSMOSE-BC model are also 16 additional background taxa (**Table 1**). For some background taxa (e.g., Pacific Hake *Merluccius productus*; Humpback Whale *Megaptera novaeangliae*, and Fin Whale *Balaenoptera physalus*) that are migratory, they do not interact with other modeled taxa when they migrate out of the model spatial domain. Therefore, a map of empty value is used for the out-of-model-domain season.

The OSMOSE-BC model simulates the life cycle of the focus species, from the egg stage to the terminal age, at a time step of 4 months, each representing one season (Winter: December to next March; Summer: April to July; Fall: August to November). At the time step immediately following the production of eggs, the total number of eggs of each population is split into super-individuals called "schools," which are distributed spatially according to input distribution maps (Fu et al., 2017). The distribution maps (15 km × 15 km) are density-based and obtained from geo-referenced data of both commercial fisheries and research surveys (the data archives being maintained by Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC, Canada). The spatial resolution of the distribution maps was set to adequately capture the spatial dynamics of modeled species while also keeping the computation time and memory capacity within reasonable ranges. At each time step, OSMOSE simulates the biological and ecological processes of these schools, including growth, predation, starvation, other natural mortality due to causes unaccounted for by the model, fishing, reproduction, and spatial movement (including migration). The biological information needed for the focus species including growth, reproduction and mortality parameters were obtained from previous studies (Fu et al., 2013, 2017) and stock assessments (Forrest et al., 2015; Holt et al., 2016; Grandin and Forrest, 2017; Cleary et al., 2018; **Table 2**). The rest of the information needed for focus species, including feeding size ranges expressed as minimum and maximum predator/prey size ratios, annual fishing mortality time series obtained from stock assessments, fishing and reproduction seasonality, and distribution maps for different life stages and time steps, was set up following Fu et al. (2017).

For the background taxa, only the predation, spatial distribution and movement processes are simulated. At the beginning of each year, the biomass of background taxa is separated into young-of-the-year, juveniles, and adults. The biomass in each life stage is then converted to abundance based on the average weight of each life stage and subsequently divided into schools. At each time step, these schools for the different life stages interact with schools of the focus species and other background taxa through predator-prey relationships by exerting predation mortality and/or representing a food source. Mortality other than predation mortality, growth, and reproduction are not modeled for the background taxa. Input information of biomass time series, mean length and weight at different stages, minimum and maximum predator/prey size ratios and distribution maps for different life stages and time steps was set up following Fu et al. (2017).

Model Calibration and Simulation Scenarios

The period considered in the OSMOSE-BC model is the period 1940–2018 (including a burn-in period from 1940 to 1950). The natural mortality rate of the first life stage (eggs and first-feeding larvae), i.e., larval mortality rate, is due to different causes (e.g., non-fertilization of eggs, starvation of first feeding larvae, advection, and sinking) and is usually very hard to quantify. Therefore, the first step with the OSMOSE-BC model consisted of estimating the larval mortality rate of the focus species, as in Fu et al. (2017), so that the simulated biomass time series of the populations were as close as possible to those from stock assessments or those reconstructed from survey data. The best calibrated OSMOSE-BC model (i.e., representing historical conditions) was used to derive biomass time series for the focus species, which were then used as baseline scenario such that there was comparability between the scenarios and past realistic projections (Niiranen et al., 2013).

Previous ecosystem simulation studies have explored the cumulative effects of ocean warming and acidification on the dynamics of fish species, communities, and ecosystems (e.g., Griffith et al., 2011, 2012, 2019; Ortega-Cisneros et al., 2018). The long-term warming trend in the BC marine ecosystem has been only 0.08°C per decade for sea surface temperature since recordings started in 1917 and even weaker (0.07°C) for the subsurface (100–150 m) waters (Greenan et al., 2018). Such a slow long-term change in temperature is likely within the optimal temperature range of the studied focus species. In addition, ocean acidification has not been found to have a measurable effect on fish species in the BC marine ecosystem (Haigh et al., 2015). By contrast, the climate-induced variability of the location of the

TABLE 1 | Focus species and background taxa included in the OSMOSE-BC ecosystem simulation model.

Species/Taxon name	Type	Species represented
Euphausiids	Focus species	*Thysanoessa* spp., *Euphausia* spp.
Pacific herring	Focus species	**Pacific Herring (*Clupea pallasi*)**
Arrowtooth Flounder	Focus species	**Arrowtooth Flounder (*Atheresthes stomias*)**
Walleye Pollock	Focus species	**Walleye Pollock (*Gadus chalcogrammus*)**
Pacific Cod	Focus species	**Pacific Cod (*Gadus macrocephalus*)**
Lingcod	Focus species	**Lingcod *(Ophiodon elongatus*)**
Pacific Halibut	Focus species	**Pacific halibut (*Hippoglossus stenolepis*)**
Harbor Seal	Background taxa	**Harbor Seal (*Phoca vitulina*)**
Steller Sea Lion	Background taxa	**Steller Sea Lion (Eumetopias jubatus)**
California Sea Lion	Background taxa	**California Sea Lion (*Zalophus californianus*)**
Humpback Whale	Background taxa	**Humpback Whale (*Megaptera novaeangliae*)**
Fin Whale	Background taxa	**Fin Whale (*Balaenoptera physalus*)**
Pacific Hake	Background taxa	**Pacific Hake (*Merluccius productus*)**
Pacific Ocean Perch	Background taxa	**Pacific Ocean perch (*Sebastes alutus*)**
Spiny Dogfish	Background taxa	**Spiny Dogfish (*Squalus acanthias*)**
Flatfish	Background taxa	**Dover Sole (*Microstomus pacificus*)**, Rock Sole (*Lepidosetta bilineata*), English Sole (*Parophyrys vetulus*), Sand Sole (*Psettichthys melanostictus*), Rex Sole (*Glyptocephalus zachirus*), Flathead Sole (*Hippoglossoides elassodon*)
Petrale Sole	Background taxa	**Petrale sole (*Eopsetta jordani*)**
Shelf Rockfish	Background taxa	**Yellowtail (*Sebastes flavidus*)**, Silvergray (*Sebastes brevispinis*), Bocaccio (*Sebastes paucispinis*), Canary (*Sebastes pinniger*)
Slope Rockfish	Background taxa	**Yellowmouth (*Sebastes reedi*)**, Rougheye *(Sebastes aleutioanus*), Redstripe *(Sebastes proriger*), Sharpchin (*Sebastes zacentrus*), Redbanded (*Sebastes babcocki*), Shortspine Thornyhead (*Sebastolobus altivelis*)
Inshore Rockfish	Background taxa	**Yelloweye (*Sebastes rubberrimus*)**, Quillback (*Sebastes maliger*)
Spotted Ratfish	Background taxa	**Spotted Ratfish (*Hydrolagus colliei*)**
Sablefish	Background taxa	**Sablefish *(Anoplopoma fimbria*)**
Coho Chinook	Background taxa	**Coho Salmon (*Oncorhynchus kisutch*)**, Chinook Salmon (*Oncorhynchus tshawytscha*)
Shallow Benthic Fish	Background taxa	**eelpouts (*Zoarcidae*)**, poachers (*Agonidae*), sculpins (*Cottidae*)
Forage Fish	Background taxa	**Eulachon (*Thaleichthys pacificus*)**, Smelts (*Osmeridae*), Sandlance (*Ammodytes hexapterus*)
Crabs	Background taxa	**Dungeness crab (*Metacarcinus magister*)**, tanner crab (*Chionoecetes sp.*), red rock crab (*Cancer productus*)
Shrimp	Background taxa	**Smooth Shrimp (*Pandalus jordani*)**, Pink Shrimp (*Pandalus goniturus*), Sidestripe Shrimp (*Pandalopsis disbar*), Prawn (*Pandalus platycterus*)
Detritus Benthos	Background taxa	

The reference species of each background taxon (in bold) is used for obtaining mean length and weight at different stages as well as distribution maps for the background taxon.

TABLE 2 | Growth, reproduction and mortality parameters for each of the focus species considered in the OSMOSE-BC model.

	Growth					**Reproduction**		**Survivalship**		
Species	L_∞ **(cm)**	k **(year^{-1})**	t_0 **(year)**	c **(g cm^{-3})**	b	**φ (eggs g^{-l})**	A_{mat} **(year)**	A_{max} **(year)**	A_{rec} **(year)**	M **(year^{-1})**
Euphausiids	1.84	1.68	−0.20	0.0091	2.920	24469	0.3	1.7	0.5	0.10
Pacific Herring	26.3	0.36	−0.03	0.0070	2.997	200	3	10	3	0.12
Arrowtooth Flounder	58.92	0.26	0.48	0.0036	3.251	743	5	25	5	0.15
Walleye Pollock	44.50	0.92	0.57	0.0065	2.997	300	3	10	3	0.25
Pacific Cod	89.48	0.31	−0.12	0.0074	3.096	564	3	10	3	0.25
Lingcod	112.80	0.15	−3.01	0.0013	3.324	26	5	17	5	0.196
Pacific Halibut	130.00	0.23	−0.06	0.0013	3.238	553	8	40	8	0.112

Growth parameters include L_∞*, k, and* t_0 *for the von Bertalanffy growth model as well as parameters c and b for the weight-at-length allometric function. Relative fecundity φ is the number of eggs spawned per gram of mature female per year.* A_{mat}*,* A_{max}*, and* A_{rec} *are, respectively, the age at sexual maturity, the longevity, and the age of recruitment into the fisheries. The mortality rate M is the mortality due to disease, senescence and predation by organisms not represented in the OSMOSE-BC model (e.g., birds).*

Pacific Ocean Current bifurcation has resulted in region-specific enrichment or impoverishment of suitable plankton food for fish species (Keister et al., 2011). Such changes in the plankton community along with increased marine mammals that tend to undergo extensive climate-induced migrations (Sprogis et al., 2018) are two primary drivers of change in the BC marine ecosystem (Fu et al., 2017; Godefroid et al., 2019). The bottom-up forcing of plankton productivity and top-down forcing of predation pressure are also considered to be critical components of ecosystem-based fisheries management (Cury et al., 2011; Weijerman et al., 2015; Ortega-Cisneros et al., 2018).

Therefore, in this study, we specifically investigated how changes in the plankton production and marine mammal consumption may affect the dynamics of other species and the whole marine ecosystem. Considering that plankton and marine mammal biomasses within the BC marine ecosystem can either decrease or increase rapidly as a result of climate-induced spatial redistributions, we carried out simulations under two contrasting sets of scenarios (i.e., favorable and unfavorable from the perspectives of commercial fish species) related to three drivers (i.e., fishing, change in plankton biomass, and change in marine mammal biomass). Under the favorable condition scenarios, fish population biomasses were expected to be higher than under the historical baseline scenario by manipulating the three drivers individually or collectively, including halving fishing mortality rate (HalfF), doubling plankton biomass (DoubPl), and halving marine mammal biomass (HalfMam) during the last 20 years of the simulation period. By contrast, under the unfavorable condition scenarios, fish population biomasses were expected to be lower than under the historical baseline scenario, as fishing mortality rate was doubled (DoubF), plankton biomass was halved (HalfPl), and marine mammal biomass was doubled (DoubMam), separately or simultaneously, during the last 20 years of the simulation. In total, seven (three with a single driver and four with multiple drivers) favorable condition scenarios and seven unfavorable condition scenarios were considered in the present study; these 14 scenarios are detailed in **Table 3**.

TABLE 3 | Acronyms and descriptions of seven simulation scenarios.

Scenarios	Descriptions
BaseF_DoubPL_BaseMam	Baseline fishing mortality rates, doubled plankton biomass, and Baseline marine mammal biomass
BaseF_BasePL_HalfMam	Baseline fishing mortality rates, Baseline plankton biomass, and halved marine mammal biomass
BaseF_DoubPL_HalfMam	Baseline fishing mortality rates, doubled plankton biomass, and halved marine mammal biomass
HalfF_BasePL_BaseMam	Halved fishing mortality rates, Baseline plankton biomass, and Baseline marine mammal biomass
HalfF_DoubPL_BaseMam	Halved fishing mortality rates, doubled plankton biomass, and Baseline marine mammal biomass
HalfF_BasePL_HalfMam	Halved fishing mortality rates, Baseline plankton biomass, and halved marine mammal biomass
HalfF_DoubPL_HalfMam	Halved fishing mortality rates, doubled plankton biomass, and halved marine mammal biomass

Ecological Indicators

Aside from the dynamics of modeled focus species, the three drivers also interactively and cumulatively impact the dynamics of the ecosystem as a whole. Therefore, we also employed nine ecological indicators to help reveal how the 12 stocks of focus fish species as a whole responded to the drivers that cannot be inferred from species-specific indicators (e.g., Fu et al., 2019). The nine indicators include: the biomass to fisheries yield ratio (B/Y); the proportion of predatory fishes (Pred: the proportion of biomass at trophic levels ≥ 4.0); the large fish indicators LFI20 and LFI40, i.e., the proportions (by weight) of fish >20 and >40 cm, respectively; the mean trophic level of the community (TLco: calculated as $\frac{\sum_l (\sum_S \mathrm{B}_{S,l}\mathrm{TL}_l)}{\sum_l (\sum_S \mathrm{B}_{S,l})}$, where TL is for trophic level); the total fish biomass of all-trophic-level species (B); the biomass of lower-trophic-level fish species (B_LTL: the biomass at trophic levels ≤ 3.25); the biomass of higher-trophic-level fish species (B_HTL: the biomass at trophic levels >3.25); and the ratio of B_LTL to B_HTL (B_L2H). All the ecological indicators were calculated based on the OSMOSE-BC model outputs of the 12 fish stocks of the focus fish species (**Table 1**).

Relative Changes and Combined Effects

For each scenario k, the change in a response variable R (i.e., the biomass of a species or the value of an ecological indicator) relative to the baseline scenario b was calculated as: $\Delta R_k = \frac{R_k - R_b}{R_b}$. To understand the cumulative impacts of the three drivers (fishing mortality, plankton biomass, and marine mammal biomass) on the dynamics of the focus species and the whole BC ecosystem, we specifically used the biomasses of the individual focus species and the total biomass of the ecosystem as the response variable, following the Global Ocean Observing System (GOOS) Biology and Ecosystems Panel that identified biomasses as Fish Essential Ocean Variables (Miloslavich et al., 2018). Under an additive effect, the combined effect of multiple drivers is the sum of ΔR_k with each of the three drivers varying independently. Following Fu et al. (2018), we defined the additive effect as the 1:1 line, but added a range of ±0.05 (shown as dashed lines around the 1:1 line in **Figure 2**) to allow for a broadened definition of the additive effect (Ortega-Cisneros et al., 2018). The zones below the additive effect are considered as ecologically risky effects, including negative synergism, negative antagonism, and positive dampened effects (**Figure 2**). By contrast, the zones above the additive effect, including positive synergism, positive antagonism, and negative dampened effects, result in higher fish biomasses than expected under the additive effect and, therefore, there is no ecological risk associated with them (Fu et al., 2018).

RESULTS

Relative Changes in Biomasses and the Ecological Indicators

Under unfavorable conditions, relative biomass changes were negative for all scenarios except DoubF_BasePl_BaseMam for two species: Walleye Pollock and Arrowtooth Flounder (**Figure 3**). As time progressed from the first to the second

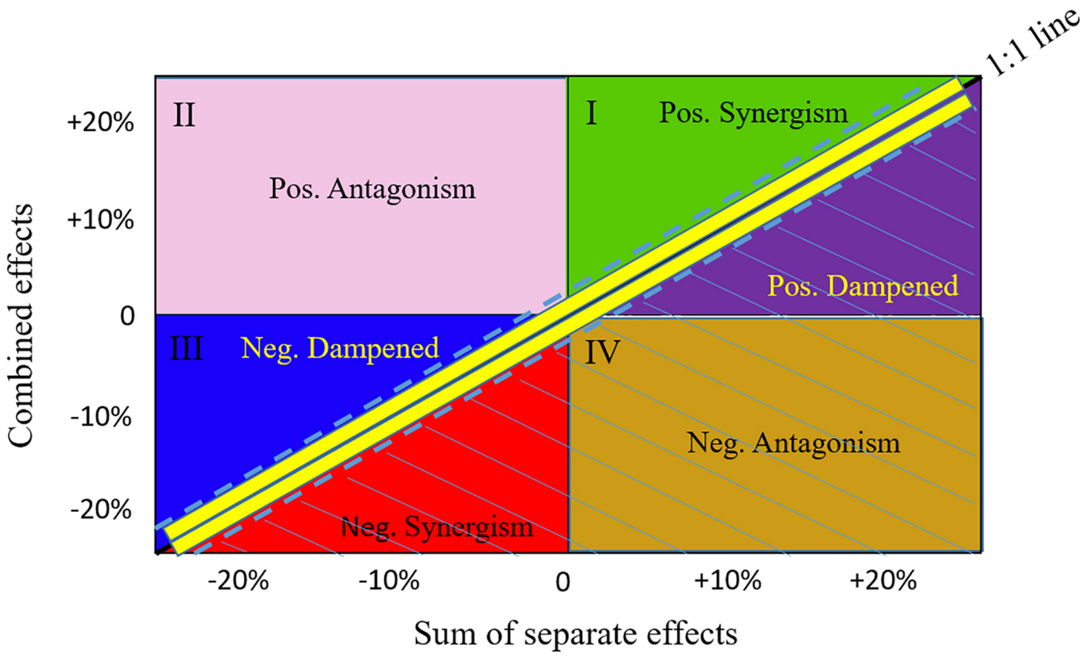

FIGURE 2 | Schematic comparison of the combined versus additive separate effects. Effects are presented as relative change in biomass occurring when fishing and changes in plankton and mammal biomasses act simultaneously (combined effect, *y*-axis) versus separately (*x*-axis). The 1:1 line with a range of ±0.05 (dashed lines) represents combined effects being equal to additive effects. The zones below the lower dashed line are considered as risk zones, including negative synergistic (Neg. Synergism), negative antagonistic (Neg. Antagonism), and positive dampened (Pos. Dampened) effects. The zones above the upper dashed line are considered as not being risky, including positive synergistic (Pos. Synergism), positive antagonistic (Pos. Antagonism), and negative dampened (Neg. Dampened) effects.

10 years of simulation, relative biomass changes tended to become more negative for all species. During the first 10 years, the scenario BaseF_HalfPl_BaseMam resulted in larger biomass reductions than the scenario BaseF_BasePl_DoubMam for Pacific Herring, but not for Pacific Cod, Lingcod, and Walleye Pollock (**Figure 3A**), suggesting that Pacific Herring were more sensitive to plankton biomass halving, while Pacific Cod, Lingcod, and Walleye Pollock were more vulnerable to mammal biomass doubling. Compared to the baseline situation where fishing mortality rates were at historical levels, the scenario DoubF_BasePl_BaseMam resulted in larger biomass reductions for Pacific Cod, Lingcod, and Pacific Halibut, suggesting that these three species were susceptible to the increase in fishing pressure. By contrast, this scenario resulted in the smallest biomass reductions for Pacific Herring, and in biomass increase for Walleye Pollock, and Arrowtooth Flounder contrary to what may be expected. This result may be due to the fact that the depleted predator populations resulting from doubled fishing mortality rates may have led to a reduction of the predation pressure exerted on Pacific Herring, Walleye Pollock, and Arrowtooth Flounder. As time progressed to the second 10 years of simulation, biomass reduction under the scenario BaseF_HalfPl_DoubMam worsened for all species, and resulted in only slightly higher biomass levels than the scenario DoubF_HalfPl_DoubMam where the three drivers of change acted collectively (**Figure 3B**).

Among all the ecological indicators, total biomass was the only indicator that showed significantly negative responses (with 95% confidence intervals all below zero) to the seven unfavorable scenarios during both the first and the second 10 years of simulation (**Figure 4**). In comparison, the biomasses of lower- or higher-trophic-level fish species showed large variability during one of the two 10-year periods (with confidence intervals encompassing zero), suggesting that biomasses are more variable at the functional group level than at the ecosystem level. As a result, the biomass ratio of lower and higher-trophic-level fish species (B_L2H) also showed high variability, particularly during the second 10 years of simulation (**Figure 4B**). The biomass to yield ratio, similar to the total biomass, was generally negative and showed relatively small variability, suggesting that it can appropriately track unfavorable conditions. Contrary to most indicators, the large fish indicator LFI20 increased relative to the baseline scenario under all seven unfavorable scenarios during both the first and the second 10 years. The increases were even greater for the large fish indicator LFI40 (except under the scenario DoubF_BasePl_BaseMam), implying that halving plankton biomass and/or doubling mammal biomass increased the proportion of large fish, particularly those >40 cm. Mean trophic level was largely unaffected by the unfavorable conditions; however, the confidence intervals were large, revealing the strong variability of this indicator, particularly during the first 10 years of simulation.

Biomass changes relative to the baseline scenario were positive under the seven favorable condition scenarios for all six species, and they also tended to be greater during the second 10 years of simulation for most species, especially Pacific

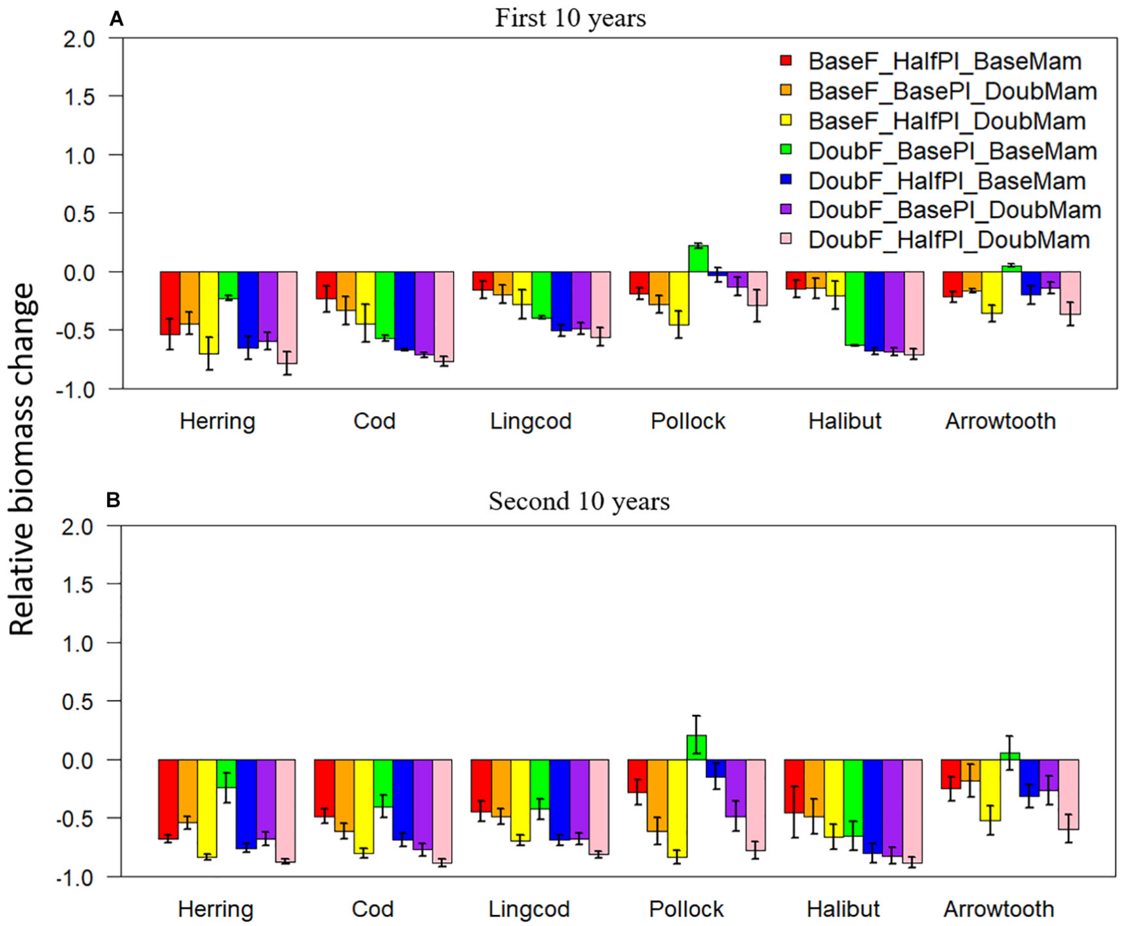

FIGURE 3 | Biomass change relative to the baseline scenario (where fishing mortality rates, plankton biomass, and marine mammal biomass are all set to their historical levels) for six fish species [Herring: Pacific Herring (*Clupea pallasii*), Cod: Pacific Cod (*Gadus macrocephalus*), Lingcod (*Ophiodon elongatus*), Pollock: Walleye Pollock (*Gadus chalcogrammus*), Halibut: Pacific Halibut (*Hippoglossus stenolepis*), and Arrowtooth: Arrowtooth Flounder (*Atheresthes stomias*)] under seven unfavorable condition scenarios where stressors act individually or simultaneously. The acronyms of the seven unfavorable condition scenarios are provided here and their definition can be found in **Table 3**. Panels **(A,B)** are for the first and second 10 years of the 20-year simulation experiment period, respectively.

Herring and Pacific Cod (**Figure 5**). During the first 10 years, the scenario BaseF_DoubPl_HalfMam tended to produce the largest biomass increases for all species except for Pacific Cod, which had the largest biomass increase under the scenario HalfF_DoubPl_HalfMam (**Figure 5A**). This result indicates that Pacific Cod may benefit the most from halved fishing mortality rates. The biomass of all species except Pacific Cod was virtually unchanged under the scenario HalfF_BasePl_BaseMam, implying that the fishing mortality rates for all species except Pacific Cod in the last 20 years of simulation were so small that halving fishing mortality rates had no impact on the status of fish populations. During the first 10 years, the scenario BaseF_DoubPl_BaseMam generally showed larger biomass increases than the scenario BaseF_BasePl_HalfMam, suggesting that doubling plankton biomass had a greater effect on species biomasses than halving mammal biomass. However, this was not true anymore for Pacific Herring during the second 10 years of simulation (**Figure 5B**), suggesting that the effect of reduced mammal predation resulting from halving mammal biomass became incrementally larger as time progressed. During the second 10 years, the scenario HalfF_DoubPl_HalfMam did not result in the largest biomass increases for all species except for Pacific Cod, which entails that the dramatic increase in Pacific Cod biomass may have largely affected all other species either through predation or competition for food.

Under favorable conditions, the biomass to yield ratio, total biomass, and the biomasses of lower- and higher-trophic-level fish species all displayed positive changes relative to the baseline scenario under the seven favorable condition scenarios (**Figure 6**). By contrast, the proportion of predatory fish exhibited either negative or positive changes, implying its unpredictable responses to different favorable drivers. Contrary to most indicators, the large fish indicators LFI20 and LFI40 were reduced under all favorable condition scenarios, particularly under the scenarios where fishing mortality rates were at baseline levels, which was primarily due to the disproportional increase of Pacific Herring, the smallest among the focus key species, as well as density-dependent reduction in somatic growth. Again, mean

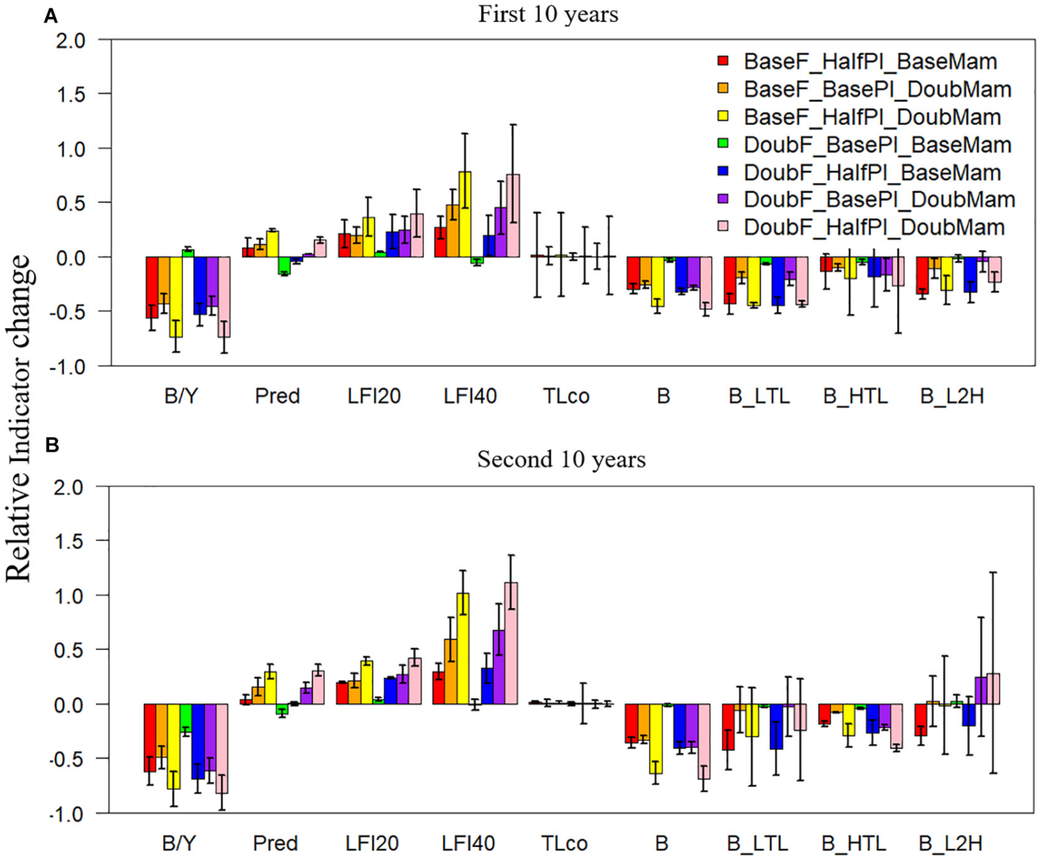

FIGURE 4 | Changes in ecological indicators (B/Y: biomass to fisheries yield ratio, Pred: proportion of predatory fishes, LFI20: proportion of large fish (>20 cm) indicator, LFI40: proportion of large fish (>40 cm) indicator, TLco: mean trophic level of the community, B: total biomass of all-trophic-level taxa, B_LTL: biomass of lower-trophic-level taxa, B_HTL: biomass of higher-trophic-level taxa, and B_L2H: ratio of B_LTL to B_HTL) relative to the baseline scenario (where fishing mortality rates, plankton biomass, and marine mammal biomass are all set to their historical levels) under seven unfavorable condition scenarios where stressors act individually or simultaneously. The acronyms of the seven unfavorable condition scenarios are provided here and their definition can be found in **Table 3**. Panels **(A,B)** are for the first and second 10 years of the 20-year simulation experiment period, respectively.

trophic level was largely unaffected by the drivers of change yet exhibited large variability, revealing the strong variability of this indicator, particularly during the second 10 years of simulation.

Combined Effects

Under unfavorable conditions, the responses to the combined effects of two or three factors varied among the different species (**Figure 7**). During the first 10 years of simulation, Pacific Herring and all species combined showed nearly 100% negative synergism under the scenario BaseF_HalfPl_DoubMam, while Pacific Cod demonstrated nearly 100% negative antagonism (**Figure 7A**). Other species, including Lingcod, Walleye Pollock, and Arrowtooth Flounder, were also affected by negative synergism under this scenario. However, when fishing mortality rates were doubled, regardless of whether mammal biomass was doubled (DoubF_BasePl_DoubMam), plankton biomass was halved (DoubF_HalfPl_BaseMam) or both whether mammal and plankton biomasses were altered (DoubF_HalfPl_DoubMam), negative dampened effects became dominant for all species except Walleye Pollock and Arrowtooth Flounder. For all species combined, additive effects contributed to around 50% when doubled fishing mortality rates were combined with either halved plankton biomass or doubled mammal biomass. During the second 10 years of simulation, additive effects were reduced under the four above-mentioned scenarios (BaseF_HalfPl_DoubMam, DoubF_BasePl_DoubMam, DoubF_HalfPl_BaseMam, and DoubF_HalfPl_DoubMam) (**Figure 7B**). Under the scenario BaseF_HalfPl_DoubMam, all species were predominantly influenced by negative synergism. When fishing mortality rates were doubled (i.e., under the scenarios DoubF_BasePl_DoubMam, DoubF_HalfPl_BaseMam, and DoubF_HalfPl_DoubMam), negative dampened effects became even more prevailing for Pacific Herring, Pacific Cod, Lingcod, and Pacific Halibut. For Walleye Pollock and Arrowtooth Flounder, however, negative synergism became more prevailing during the second 10 years of simulation than during the first 10 years. For all species combined, negative synergism became more dominant during the second 10 years of simulation when doubled fishing mortality rates were combined with either halved plankton biomass or doubled mammal biomass. However, when

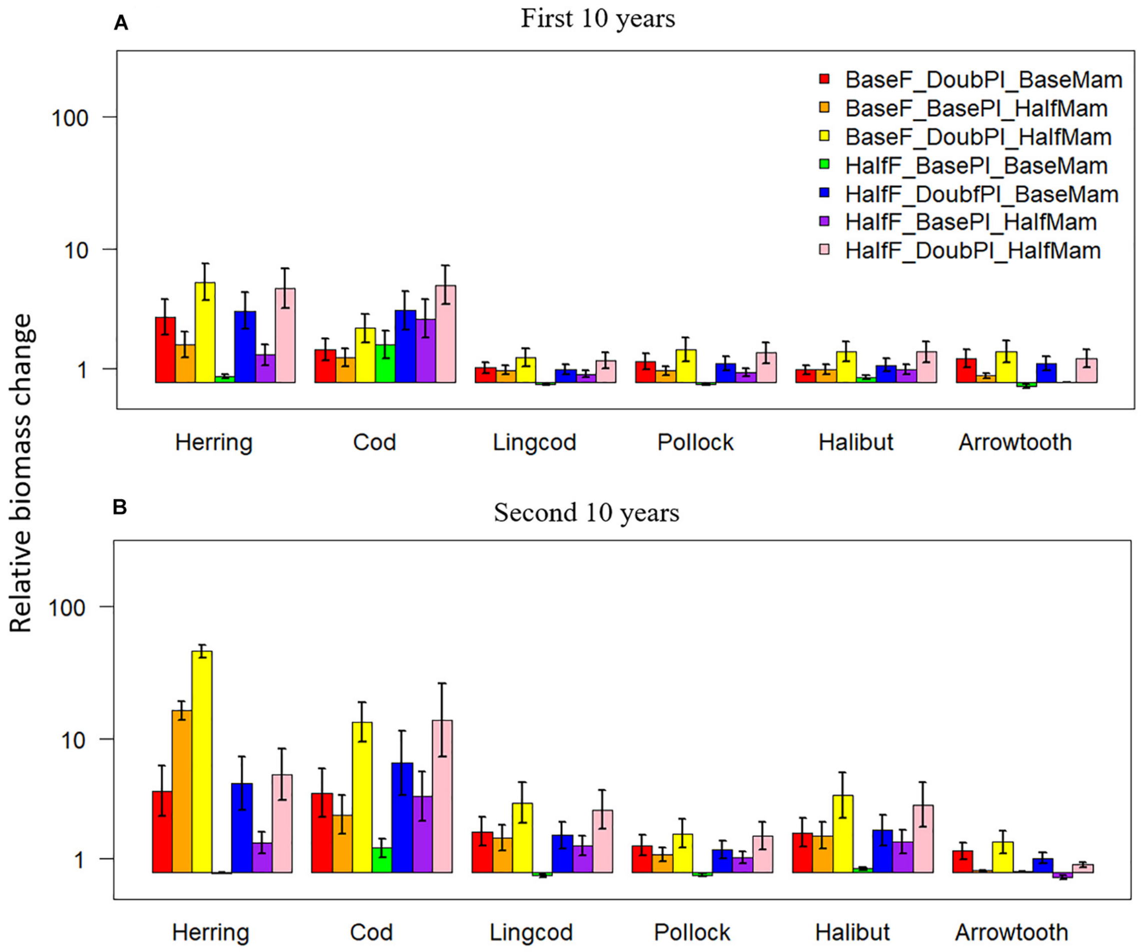

FIGURE 5 | Biomass changes (at a log-10 scale) relative to the baseline scenario (where fishing mortality rates, plankton biomass, and marine mammal biomass are all set to their historical levels) for six fish species [Herring: Pacific Herring (*Clupea pallasii*), Cod: Pacific Cod (*Gadus macrocephalus*), Lingcod (*Ophiodon elongatus*), Pollock: Walleye Pollock (*Gadus chalcogrammus*), Halibut: Pacific Halibut (*Hippoglossus stenolepis*), and Arrowtooth: Arrowtooth Flounder (*Atheresthes stomias*)] under seven favorable condition scenarios where stressors act individually or simultaneously. The acronyms of the seven favorable condition scenarios are provided here and their definition can be found in **Table 3**. Panels **(A,B)** are for the first and second 10 years of the 20-year simulation experiment period, respectively.

all three drivers interacted together, additive effects became dominant while negative synergism largely diminished.

Under favorable conditions, the responses to the combined effects of two or three factors also varied among the different species (**Figure 8**). Pacific Cod benefited the most from all combinations of two or three factors, showing predominantly positive synergism. While Pacific Herring showed largely positive synergism for three of the four combinations during the first 10 years of simulation (**Figure 8A**), the scenario HalfF_BasePl_HalfMam produced predominantly positive dampened effects, which was also true for all species combined. This result suggests that the benefits of halving fishing mortality rates and mammal biomass were compromised when plankton biomass was not increased to meet the food requirement of the increasing Pacific Herring populations and the increased total biomass. Compared to the scenario BaseF_DoubPl_HalfMam, all the scenarios where fishing mortality rates were halved while the biomass of plankton and/or marine mammals was doubled produced less positive synergism for all species except for Pacific Cod. Under the scenario HalfF_DoubPl_HalfMam, positive synergism was dominant for Pacific Herring, Pacific cod, and all species combined. As time progressed to the second 10 years, the relative frequencies of various combined effects for each species were generally unchanged except that there were less additive effects under all four above-mentioned scenarios (HalfF_BasePl_HalfMam, BaseF_DoubPl_HalfMam, HalfF_DoubPl_BaseMam, and HalfF_DoubPl_HalfMam) (**Figure 8B**). For all species combined and for Pacific Herring, there were relatively more positive dampened effects under all four scenarios compared to the first 10 years. Under the scenarios HalfF_DoubPl_BaseMam and HalfF_DoubPl_HalfMam, positive dampened effects tended to be greater for most species (except for Pacific Cod) during the second 10 years of simulation, implying that the benefits of halved fishing mortality rates combined with doubled plankton biomass or even with halved mammal

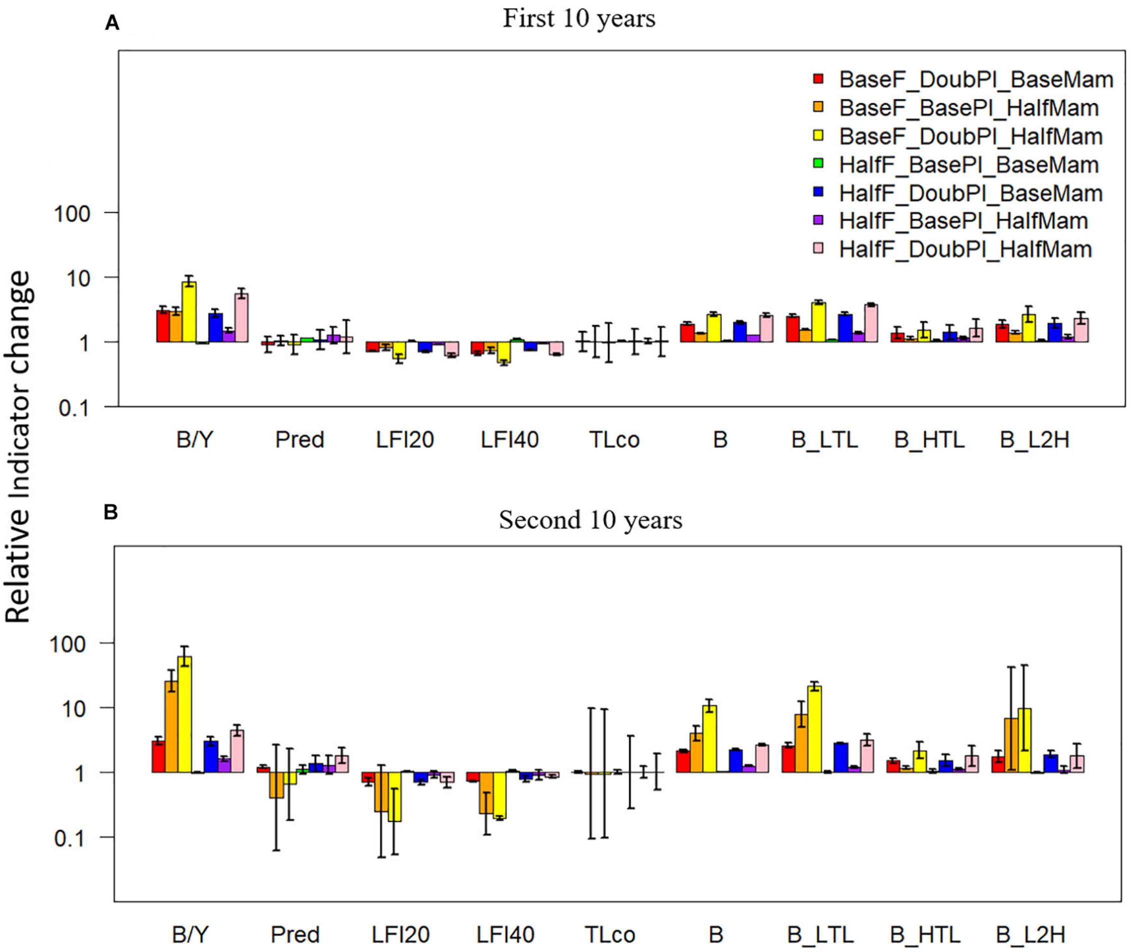

FIGURE 6 | Changes (at a log-10 scale) in ecological indicators (B/Y: biomass to fisheries yield ratio, Pred: proportion of predatory fishes, LFI20: proportion of large fish (>20 cm) indicator, LFI40: proportion of large fish (>40 cm) indicator, TLco: mean trophic level of the community, B: total biomass of all-trophic-level taxa, B_LTL: biomass of lower-trophic-level taxa, B_HTL: biomass of higher-trophic-level taxa, and B_L2H: ratio of B_LTL to B_HTL) relative to the baseline scenario (where fishing mortality rates, plankton biomass, and marine mammal biomass are all set to their historical levels) under seven favorable condition scenarios where stressors act individually or simultaneously. The acronyms of the seven favorable condition scenarios are provided here and their definition can be found in **Table 3**. Panels **(A,B)** are for the first and second 10 years of the 20-year simulation experiment period, respectively.

biomass were less than expected under additive effects as time progressed.

DISCUSSION

The plankton community and marine mammal biomass within the BC marine ecosystem have changed over the last decades partially due to species redistributions as a result of climate change (Keister et al., 2011; Boldt et al., 2019). Such spatial redistributions of marine species are believed to serve as a way of adapting to environmental changes (Miller et al., 2018) and their ecological consequences need to be investigated from an ecosystem perspective, as ecosystem components at different trophic levels interact actively and impact the entire food web (Stenseth et al., 2002; Bonebrake et al., 2018). Using the individual-based ecosystem simulation model OSMOSE-BC, we were able to investigate how fish species biomass and ecological indicators would change relative to the historical (baseline) scenario when the BC ecosystem was hypothetically subjected to changes in three drivers: fishing mortality rates, plankton biomass, and marine mammal biomass. We were also able to examine the cumulative impacts of the three drivers on the dynamics of the focus species as well as the whole BC ecosystem.

We arrived at the following findings. First, under unfavorable conditions for the focus fish species (i.e., doubling fishing mortality rates, halving plankton biomass, and doubling mammal biomass), the total biomass and biomass to yield ratio were reduced consistently, while other indicators had mixed responses and the different focus species exhibited different degrees of biomass reduction among different scenarios. When both plankton biomass was halved and mammal biomass doubled, negative synergistic effects dominated for most species under the historical fishing mortality rates, while negative dampened effects

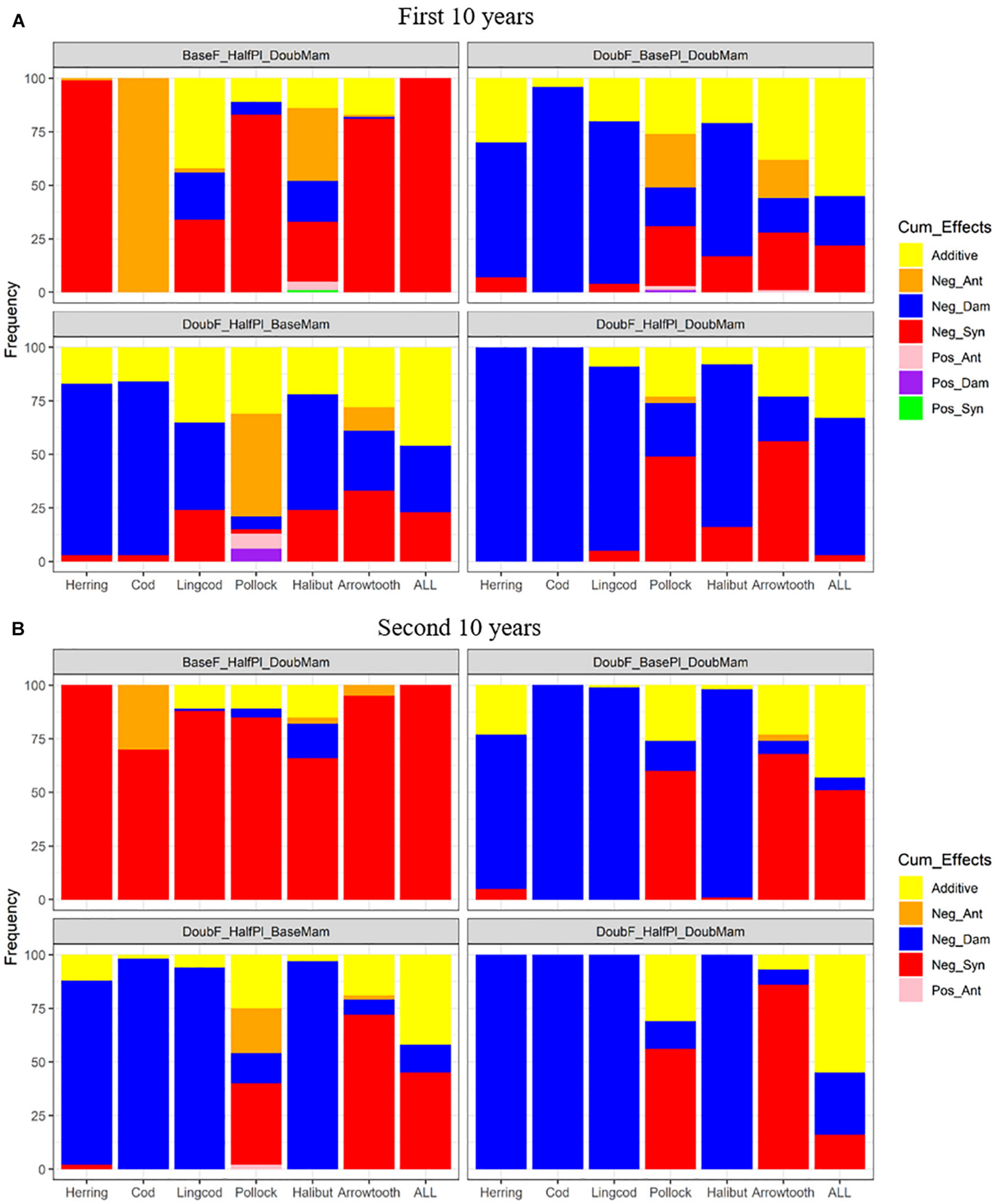

FIGURE 7 | Stacked bar plots of seven combined effects (Additive: additive effect, Nag_Ant: negative antagonism, Neg_Dam: negative dampened, Neg_Syn: negative synergism, Pos_Ant: positive antagonism, Pos_Dam: positive dampened, and Pos_Syn: positive synergism) for the biomasses of six fish species (Herring: Pacific Herring (*Clupea pallasii*), Cod: Pacific Cod (*Gadus macrocephalus*), Lingcod (*Ophiodon elongatus*), Pollock: Walleye Pollock (*Gadus chalcogrammus*), Halibut: Pacific Halibut (*Hippoglossus stenolepis*), and Arrowtooth: Arrowtooth Flounder (*Atheresthes stomias*) and the total biomass of all species (ALL) under four unfavorable condition scenarios where stressors act simultaneously. The acronyms of the unfavorable condition scenarios are provided here and their definition can be found in **Table 3**. Panels **(A,B)** are for the first and second 10 years of the 20-year simulation experiment period, respectively.

became more prevalent under doubled fishing mortality rates. Second, when all factors were favorable from the perspective of sustaining commercial fish biomasses (i.e., halving fishing mortality rates, doubling plankton biomass, and halving mammal biomass), the biomasses of the focus species did not increase as much as would be expected under additive effects, as a result of the complex predator-prey interactions occurring in the modeled system. Total biomass showed consistently positive responses

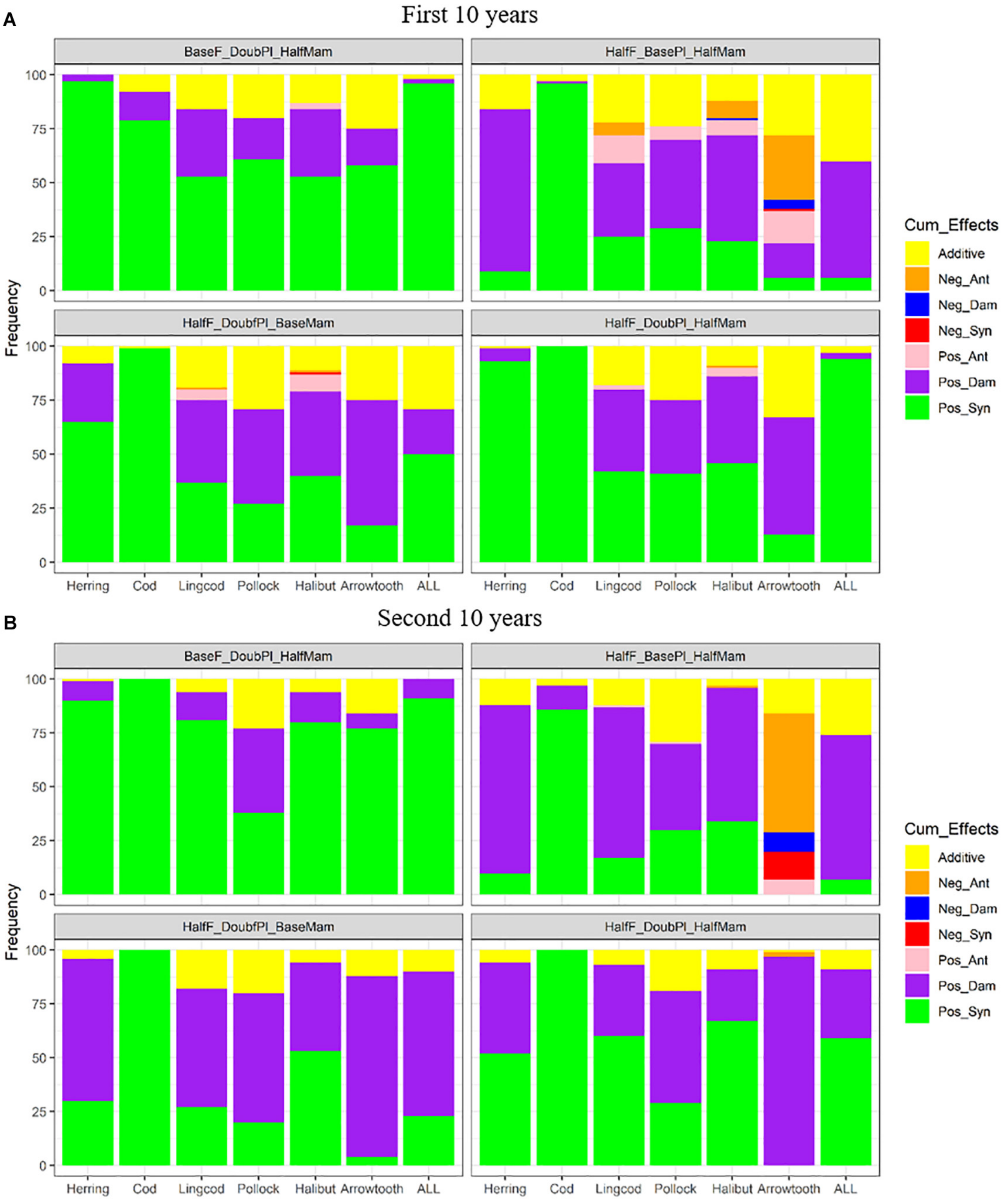

FIGURE 8 | Stacked bar plots of seven combined effects (Additive: additive effect, Nag_Ant: negative antagonism, Neg_Dam: negative dampened, Neg_Syn: negative synergism, Pos_Ant: positive antagonism, Pos_Dam: positive dampened, and Pos_Syn: positive synergism) for the biomasses of six fish species (Herring: Pacific Herring (*Clupea pallasii*), Cod: Pacific Cod (*Gadus macrocephalus*), Lingcod (*Ophiodon elongatus*), Pollock: Walleye Pollock (*Gadus chalcogrammus*), Halibut: Pacific Halibut (*Hippoglossus stenolepis*), and Arrowtooth: Arrowtooth Flounder (*Atheresthes stomias*) and the total biomass of all species (ALL) under four favorable condition scenarios where stressors act simultaneously. The acronyms of the favorable condition scenarios are provided here and their definition can be found in **Table 3**. Panels **(A,B)** are for the first and second 10 years of the 20-year simulation experiment period, respectively.

and was most stable during the first and second 10 years of simulation. While the combined effects of doubling plankton biomass and halving mammal biomass were largely positive synergistic, halving fishing mortality rates tended to produce more positive dampened effects when it was combined with doubling plankton biomass and/or halving mammal biomass.

Implications for Ecosystem-Based Fisheries Management

Fishing, climate change, particularly in the form of extreme climate conditions (Smale et al., 2019; Ainsworth et al., 2020), and trophic interactions, are important factors that act together, resulting in profound changes in many marine ecosystems (Corrales et al., 2017; Foley et al., 2017). Understanding the cumulative impacts of multiple drivers of change on individual fish species, as well as on the studied ecosystem as a whole, is key to moving toward ecosystem-based fisheries management (Rosenberg and McLeod, 2005; Leslie and McLeod, 2007; Ban et al., 2014). This topic has become even more heated in recent years as the entire globe is facing an unprecedented situation where climate change, species distribution shifts, and more intense anthropogenic activities such as increased fisheries exploitation are all interactively affecting the structure and functioning of marine ecosystems (e.g., Kirby et al., 2009; Schinegger et al., 2016; Bonebrake et al., 2018; Ramírez et al., 2018).

Considerable knowledge gaps remain in understanding the interactive and cumulative effects of multiple stressors (Ban et al., 2014; Corrales et al., 2017). Such a lack of understanding may largely be driven by the complexity of marine ecosystems, where interacting components can either propagate or counter the effects of environmental change on individual species and communities (Goldenberg et al., 2018). Therefore, ecological complexities, particularly in the form of climate-induced species redistributions, multi—species interactions, and long—term dynamics at multiple trophic levels, should be considered in forecasting the likely outcomes of different management actions in the context of ecosystem-based fisheries management (Bonebrake et al., 2018). The individual-based ecosystem modeling platform OSMOSE is well-suited to explicitly account for these ecological complexities for assessing the impacts of multiple environmental and anthropogenic drivers at the species, community, and ecosystem levels. The results presented in this study complement a previous study where OSMOSE was used to provide strategic perspectives on ecosystem-based management actions in the face of climate change (Guo et al., 2020). Below, we discuss specific issues that are essential to effective ecosystem-based fisheries management, including properly understanding the species-specific effects of drivers of change, temporal considerations, and the response of ecological indicators.

Properly Understanding the Species-Specific Effects of Drivers of Change

Previous research has indicated that when and how a species responds to multiple drivers depends on its biological characteristics (e.g., life-history traits, trophic level), exploitation history, and the ecosystem being considered (Fuller et al., 2015; Fu et al., 2017, 2018; Serpetti et al., 2017; Miloslavich et al., 2018; Ortega-Cisneros et al., 2018; Rilov et al., 2019). Our simulations indicated that Pacific Herring, an important prey to both predatory fish species and marine mammals, was more sensitive to plankton biomass halving compared to the other modeled species, while other focus species, including Pacific Cod, Lingcod, and Walleye Pollock, were more vulnerable to mammal doubling when fishing mortality rates were set at the baseline levels. This result is consistent with the findings of Fu et al. (2017) regarding the potential factors responsible for the declines of Pacific Herring and Pacific Cod in the BC marine ecosystem (Fu et al., 2017). As fishing mortality rates were doubled for all focus species, biomass reductions were smaller for Pacific Herring, Walleye Pollock, and Arrowtooth Flounder, and greater for Pacific Cod, Lingcod, and Pacific Halibut, suggesting that the latter three species were susceptible to the increase of fishing pressure. This result also suggests that the depleted populations of Pacific Cod, Lingcod, and Pacific Halibut resulting from doubled fishing mortality rates may exert a reduced predation pressure on Pacific Herring, Walleye Pollock, and Arrowtooth Flounder, thereby resulting in less pronounced biomass reductions or even biomass increases for these species. This result is also consistent with findings from many other studies (e.g., Travers-Trolet et al., 2014; Ortega-Cisneros et al., 2018) that suggest that fish species at higher trophic levels are more responsive to fishing, while those at lower trophic levels are primarily affected by plankton biomass changes.

The combined effects of different drivers are also species-specific, and they can be either dampened or amplified through food competition and trophic interactions with bottom-up and top-down processes acting simultaneously (Planque et al., 2010; Boyd et al., 2018). Pacific Herring was the only species that experienced 100% negative synergistic effects when both plankton biomass halved and mammal biomass doubled under the baseline fishing mortality rates. Such negative synergistic effects may explain why some Pacific Herring stocks have never recovered even after the implementation of fishery moratorium for nearly two decades now (Cleary et al., 2018). Both the lack of food and increased consumption by top predators were indeed found to be detrimental to Pacific Herring (Fu et al., 2017). Interestingly, when fishing mortality rates were doubled, negative dampened effects became dominant for most species, including Pacific Herring, Pacific Cod, Lingcod, and Pacific Halibut, regardless of the changes in plankton biomass (halving) or mammal biomass (doubling). From the perspective of Pacific Herring, this phenomenon is due to the fact that doubling fishing mortality rates for other predatory species including Pacific Cod, Lingcod, and Pacific Halibut resulted in reductions of their biomass and subsequent predation on Pacific Herring, while doubling fishing mortality rates for the Pacific Herring stocks did not inflict further harm to Pacific Herring because of the nearly zero baseline levels that had been reached for some Pacific Herring stocks.

In contrast to Pacific Herring, Pacific Cod had 100% negative antagonistic effects when both plankton biomass was halved and mammal biomass was doubled under baseline fishing mortality rates. All other species experienced antagonism less frequently than other combined effects (i.e., synergistic and dampened effects). The rarity of antagonism is consistent with the finding in Fu et al. (2018), akin to the "ecological surprises" reported in natural systems (Lindenmayer et al., 2010). Antagonistic effects may become more prevalent under heightened interactions among climate change and other stressors (Lindenmayer et al., 2010), may tend to be large (Fu et al., 2018), and may warrant extreme vigilance from resource managers to prepare for undesirable ecological surprises. Interestingly, the negative antagonistic effect noted for Pacific Cod totally disappeared when fishing mortality rates were doubled, and negative dampened effects became dominant for Pacific Cod along with other species. Such a drastic shift for Pacific Cod from one combined effect to another may be due to the unique trophic position that Pacific Cod occupies in the ecosystem that result in its biomass being greatly impacted by changes in the biomass of other species as a result of changes in fishing pressure. This points to the importance of considering species-specific exploitation history in formulating information for resource managers (Leslie and McLeod, 2007), and also supports the conclusion from other studies that particular combinations of fishing pressure and climate change may affect different species in different ways (e.g., Fuller et al., 2015). Such species-specific responses to multiple drivers of change and how they impact the ecosystem structure and functioning through complex species interactions need to be explicitly integrated through ecosystem modeling in order to develop ecosystem-based fisheries management and appropriate adaptation strategies for fisheries.

Temporal Considerations

Temporal changes are important considerations when studying cumulative effects (Halpern et al., 2015). We specifically compared the occurrences of different cumulative effects between the first and second 10 years of simulation. In particular, the number of occurrences of antagonism decreased during the second 10 years of simulation, implying that ecological surprises may be less likely as time progresses after an ecosystem shift happened. Under unfavorable conditions, the cumulative effects were increasingly dominated by negative synergism under the baseline fishing mortality rates, and by negative dampened effects under the doubled fishing mortality rates, as we moved from the first decade to the second decade of simulation. Similarly, under favorable conditions, the cumulative effects became increasingly dominated by positive synergism under the baseline fishing mortality rates, and by positive dampened effects under the doubled fishing mortality rates as we moved from the first decade to the second decade of simulation. These results also point to the importance of carefully considering the specific exploitation histories of the different modeled species. Although our experimental design can be deemed reasonable as climatic and ecosystem oscillations typically occur over decadal time scales (Lindegren et al., 2018), we encourage future research to consider additional scenarios combining multiple stressors and also investigate the effects of increasingly long periods of simulation on the responses of species and the whole ecosystem to the combination of multiple stressors. We specifically encourage future research to explore the consequences of altering fishing mortality rates and plankton and mammal biomasses more frequently than every 10 or 20 years.

Ecological Indicators

Ecological indicators, particularly food-web indicators such as the ones presented in this study, are essential metrics that are indicative of ecosystem changes caused by multiple drivers, such as fishing and environmental change (e.g., Fu et al., 2019). These ecological indicators are key to the move toward ecosystem-based fisheries management and the development of appropriate resource management measures to maintain healthy ecosystems and restore degraded ecosystems (Thompson et al., 2020). Over the past 25 years, a large number of ecological indicators has been produced (Jennings, 2005; Shin et al., 2012; Shannon et al., 2014). However, there is no one-size-fit-all, and ecological indicators need to be carefully chosen based on their sensitivity, specificity and/or responsiveness, to properly understand how drivers of change may impact particular marine ecosystems under specific exploitation and environmental conditions. In particular, the sensitivity of indicators, i.e., their capacity to vary significantly in response to a given driver, and their responsiveness, i.e., their capacity to respond rapidly to drivers, are properties that are highly desirable for ecological indicators (Fu et al., 2019).

Recently, the GOOS Biology and Ecosystems Panel considered biomass indicators as being Fish Essential Ocean Variables (Miloslavich et al., 2018). Previous multi-ecosystem comparisons based on either empirical data (Fu et al., 2012) or ecosystem simulation data (Fu et al., 2019) revealed that biomass indicators tended to be more environmentally driven but less sensitive to fishing pressure. Comparisons among the nine ecological indicators in the present study identified total biomass as the most consistent indicator over time and the best indicator for tracking the response of ecosystem components to the three drivers of change (fishing mortality, plankton biomass, and marine mammal biomass). This result was due to the fact that fishing pressure was considerably smaller than the other two drivers of change (plankton biomass and marine mammal biomass). In the BC marine ecosystem with the particular exploitation history of various fisheries and the notable changes in plankton and marine mammal biomasses, total biomass appears to be a prime ecological indicator to assess the response of the BC marine ecosystem to drivers of change and facilitate the move toward ecosystem-based fisheries management. Moreover, the biomass to yield ratio was identified as a second best indicator for tracking drivers of change. This indicator was also found to be most useful for indicating changes in fishing pressure across multiple ecosystems (Fu et al., 2019).

The large fish indicators, size-based metrics that reflect the size structure and life history composition of a fish community, serve as a basis for the North Sea Ecological Quality Objective and are key ecosystem state metrics (Greenstreet et al., 2011). However, we found that, under the unfavorable conditions of halved plankton biomass and/or doubled mammal biomass, the large fish indicators LFI20 or LFI40 generally increased, contrary to the biomass indicators. The increases in the large fish indicators in response to unfavorable conditions may be due to the reduction in small-fish biomasses which led to a decrease in total biomass. Moreover, under the favorable condition scenarios, the two large fish indicators decreased in contrast to the biomass indicators, particularly under the scenarios where fishing mortality rates were at baseline levels. Therefore, we concur with Greenstreet et al. (2012) that using the large fish indicator as a sole indicator of ecosystem health is not sufficient to accurately track changes in marine ecosystems. On the other hand, total biomass and the biomass to fisheries yield ratio are two useful indicators that fisheries managers can employ to move toward ecosystem-based fisheries management in the BC marine ecosystem in a context of climate change.

The response of total biomass to the unfavorable (from the perspective of commercial fish species) conditions of halving plankton biomass and doubling marine mammals was 100% negative synergism under the historical fishing mortality rates. This suggests that under this historical fishing pressure, the BC marine ecosystem as a whole could have been subjected to negative synergistic effects. However, a large portion of the negative synergistic effect turned to additive or negative dampened effects when fishing mortality rates were doubled. This implies that the ecological risk of negative synergism could be reduced if fishing pressure was increased for some predatory fishes. This result highlights the importance of managing fisheries in an ecosystem context, rather than on a single-species basis. By contrast, the response of total biomass to the favorable conditions of doubling plankton biomass but halving marine mammal biomass was largely positive synergism, regardless of fishing pressure. Therefore, when conditions were favorable, fishing pressure was not as critical from the perspective of maintaining ecosystem health. However, when plankton biomass was at the baseline level, a large portion of the positive synergism shifted to positive dampened effects under halved fishing mortality rates and mammal biomass, implying that the benefits of reduced fishing pressure and mammal consumption were compromised when plankton biomass was too low. This points to the necessity of evaluating and projecting the dynamics of plankton productivity in the BC marine ecosystem in the face of climate change.

CONCLUSION

By employing the individual-based spatially explicit ecosystem modeling platform OSMOSE, we were able to draw conclusions on the cumulative effects of fishing, plankton biomass change, and marine mammal consumption on the dynamics of some fish species and the BC marine ecosystem as a whole. It was concluded that the degree to which species biomass was reduced under unfavorable conditions varied among species, and species biomasses did not increase as much as expected under favorable conditions due to the existence of complex predator-prey interactions among fish species. From an ecosystem perspective, the response of ecosystem total biomass to the unfavorable conditions was 100% negative synergism under the historical fishing mortality rates but largely turned to additive or negative dampened effects when fishing mortality rates were doubled, implying that the ecological risk of negative synergism could be reduced if fishing pressure was increased for some predatory fishes. By contrast, the response of ecosystem total biomass to the favorable conditions of doubling plankton biomass but halving marine mammal biomass was largely positive synergism, regardless of fishing pressure. However, when plankton biomass was at the baseline level, a large portion of the positive synergism shifted to positive dampened effects under halved fishing mortality rates and mammal biomass, implying that the benefits of reduced fishing pressure and mammal consumption were compromised when plankton biomass was too low. Both species-specific response and ecosystem response to multiple drivers of change highlight the importance of managing fisheries on an ecosystem basis accounting for external drivers of change as well as complex predator-prey interactions among various species. In addition, our research identified the ecosystem total biomass and the biomass to fisheries yield ratio as two good ecological indicators for tracking ecosystem changes and the impacts from the multiple drivers of change. To conclude, our research provides insights on the cumulative effects of multiple drivers of change and helps fisheries management to prepare for potential future impacts of climate change.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: the databases contain sensitive information. Requests to access these datasets should be directed to Bruce Patten (Bruce.Patten@dfo-mpo.gc.ca).

AUTHOR CONTRIBUTIONS

CF designed and conducted simulations, and drafted the manuscript. YX and CG produced some R code to conduct analyses and generate figures. NO conducted analyses on commercial catch and survey data and produced species distribution maps. HL, NB, PV, Y-JS, AG, and CF contributed to the development of the ecosystem modeling platform. AG and Y-JS made important contributions to the final version of the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

This research is funded by the Strategic Program for Ecosystem-Based Research and Advice in Fisheries and Oceans Canada. Y-JS, NB, and PV were supported by the Biodiversa and Belmont Forum project SOMBEE (BiodivScen program, ANR contract n°ANR-18-EBI4-0003-01).

ACKNOWLEDGMENTS

We are extremely grateful to the following colleagues (listed alphabetically) who have generously provided different types of data: Leslie Barton, Jennifer Boldt, Jaclyn Cleary, Kristen Daniel, Thomas Doniol-Valcroze, John Ford, Robyn Forrest, Moira Galbraith, Chris Grandin, Kendra Holt, Jim Irvine, Sheena Majewski, John Morris, R. Ian Perry, Ian Stewart, Matt Thompson, Marc Trudel, and Strahan Tucker.

REFERENCES

Ainsworth, T. D., Hurd, C. L., Gates, R. D., and Boyd, P. W. (2020). How do we overcome abrupt degradation of marine ecosystems and meet the challenge of heat waves and climate extremes? *Glob. Change Biol.* 26, 343–354. doi: 10.1111/gcb.14901

Ban, S. S., Graham, N. A. J., and Connolly, S. R. (2014). Evidence for multiple stressor interactions and effects on coral reefs. *Glob. Change Biol.* 20, 681–697. doi: 10.1111/gcb.12453

Bograd, S. J., Kang, S., Di Lorenzo, E., Horii, T., Katugin, O. N., King, J. R., et al. (2019). Developing a social–ecological–environmental system framework to address climate change impacts in the North Pacific. *Front. Mar. Sci.* 6:333. doi: 10.3389/fmars.2019.00333

Boldt, J. L., Leonard, J., and Chandler, P. C. (eds) (2019). *State of the Physical, Biological and Selected Fishery Resources of (Pacific) Canadian Marine Ecosystems in 2018*. Can. Tech. Rep. Fish. Aquat. Sci. 3314. Sidney, BC: Fisheries and Oceans Canada, vii+248.

Bonebrake, T. C., Brown, C. J., Bell, J. D., Blanchard, J. L., Chauvenet, A., Champion, C., et al. (2018). Managing consequences of climate-driven species redistribution requires integration of ecology, conservation and social science. *Biol. Rev.* 93, 284–305. doi: 10.1111/brv.12344

Boyd, P. W., Collins, S., Dupont, S., Fabricius, K., Gattuso, J. P., Havenhand, J., et al. (2018). Experimental strategies to assess the biological ramifications of multiple drivers of global ocean change—A review. *Glob. Change Biol.* 24, 2239–2261. doi: 10.1111/gcb.14102

Cleary, J. S., Hawkshaw, S., Grinnell, M. H., and Grandin, C. (2018). *Status of B.C. Pacific Herring (Clupea pallasii) in 2017 and forecasts for 2018*. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/028. Sidney, BC: Fisheries and Oceans Canada, vii+273.

Corrales, X., Coll, M., Ofir, E., Piroddi, C., Goren, M., Edelist, D., et al. (2017). Hindcasting the dynamics of an eastern Mediterranean marine ecosystem under the impacts of multiple stressors. *Mar. Ecol. Prog. Ser*. 580, 17–36. doi: 10.3354/meps12271

Crain, C. M., Kroeker, K., and Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.* 11, 1304–1315. doi: 10.1111/j.1461-0248.2008.01253.x

Cury, P., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J., Furness, R. W., et al. (2011). Global seabird response to forage fish depletion — one-third for the birds. *Science* 334, 1703–1706. doi: 10.1126/science.1212928

Feld, C. K., Birk, S., Eme, D., Gerisch, M., Hering, D., Kernan, M., et al. (2016). Disentangling the effects of land use and geo-climatic factors on diversity in European freshwater ecosystems. *Ecol. Ind.* 60, 71–83. doi: 10.1016/j.ecolind.2015.06.024

Foley, M. M., Mease, L. A., Martone, R. G., Prahler, E. E., Morrison, T. H., Murray, C. C., et al. (2017). The challenges and opportunities in cumulative effects assessment. *Environ. Impact Assess. Rev*. 62, 112–134. doi: 10.1016/j.eiar.2016.06.008

Ford, J. K. (2014). *Marine Mammals of British Columbia*. Victoria, BC: Royal BC Museum, 460.

Forrest, R. E., Rutherford, K. L., Lacko, L., Kronlund, A. R., Starr, P. J., and McClelland, E. K. (2015). *Assessment of Pacific Cod (Gadus macrocephalus) for Hecate Strait (5CD) and Queen Charlotte Sound (5AB) in 2013*. DFO Can. Sci. Advis. Sec. Res. Doc. 2015/052. Sidney, BC: Fisheries and Oceans Canada, xii+197.

Fu, C., Gaichas, S., Link, J. S., Bundy, A., Boldt, J. L., Cook, A. M., et al. (2012). Relative importance of fishing, trophodynamic and environmental drivers in a series of marine ecosystems. *Mar. Ecol. Prog. Ser.* 459, 169–184. doi: 10.3354/meps09805

Fu, C., Olsen, N., Taylor, N., Grüss, A., Batten, S., Liu, H., et al. (2017). Spatial and temporal dynamics of predator-prey species interactions off western Canada. *ICES J. Mar. Sci.* 74, 2107–2119. doi: 10.1093/icesjms/fsx056

Fu, C., Perry, R. I., Shin, Y.-J., Schweigert, J., and Liu, H. (2013). An ecosystem modelling framework for incorporating climate regime shifts into fisheries management. *Prog. Oceanogr.* 115, 53–64. doi: 10.1016/j.pocean.2013.03.003

Fu, C., Travers-Trolet, M., Velez, L., Grüss, A., Bundy, A., Shannon, L. J., et al. (2018). Risky business: the combined effects of fishing and changes in primary productivity on fish communities. *Ecol. Modelling* 368, 265–276. doi: 10.1016/j.ecolmodel.2017.12.003

Fu, C., Xu, Y., Bundy, A., Grüss, A., Coll, M., Heymans, J. J., et al. (2019). Making ecological indicators management ready: assessing their ability to detect impacts of fishing and environmental change. *Ecol. Ind.* 105, 16–28. doi: 10.1016/j.ecolind.2019.05.055

Fuller, E., Brush, E., and Pinsky, M. L. (2015). The persistence of populations facing climate shifts and harvest. *Ecosphere* 6, 1–16. doi: 10.1890/ES14-00533.1

Fulton, E. A. (2011). Interesting times: winners, losers, and system shifts under climate change around Australia. *ICES J. Mar. Sci.* 68, 1329–1342. doi: 10.1093/icesjms/fsr032

García-Reyes, M., Sydeman, W. J., Thompson, S. A., Black, B. A., Rykaczewski, R. R., Thayer, J. A., et al. (2013). Integrated assessment of wind effects on central California×s pelagic ecosystem. *Ecosystems* 16, 722–735. doi: 10.1007/s10021-013-9643-6

Giakoumi, S., Halpern, B. S., Michel, L. N., Gobert, S., Sini, M., Boudouresque, C. F., et al. (2015). Towards a framework for assessment and management of cumulative human impacts on marine food webs. *Conserv. Biol.* 29, 1228–1234. doi: 10.1111/cobi.12468

Godefroid, M., Boldt, J. L., Thorsonb, J. T., Forrest, F., Gauthier, S., Flostrand, L., et al. (2019). Spatio-temporal models provide new insights on the biotic and abiotic drivers shaping Pacific Herring (*Clupea pallasi*) distribution. *Prog. Oceanogr.* 178:102198. doi: 10.1016/j.pocean.2019.102198

Goldenberg, S. U., nagelkerken, I., Marangon, E., Bonnet, A., Ferreira, C. M., and Connell, S. D. (2018). Ecological complexity buffers the impacts of future climate on marine consumers. *Nat. Clim. Change* 8, 229–233. doi: 10.1038/s41558-018-0086-0

Grandin, C., and Forrest, R. (2017). *Arrowtooth Flounder (Atheresthes stomias) Stock Assessment for the West Coast of British Columbia*. DFO Can. Sci. Advis. Sec. Res. Doc. 2017/025. Sidney, BC: Fisheries and Oceans Canada, v+87.

Greenan, B. J. W., James, T. S., Loder, J. W., Pepin, P., Azetsu-Scott, K., Ianson, D., et al. (2018). "Changes in oceans surrounding Canada," in *Canada's Changing Climate Report*, eds E. Bush and D. S. Lemmen (Ottawa, ON: Government of Canada), 343–423.

Greenstreet, S. P. R., Fraser, H. M., Rogers, S. I., Trenkel, V. M., Simpson, S. D., and Pinnegar, J. K. (2012). Redundancy in metrics describing the composition, structure, and functioning of the North Sea demersal fish community. *ICES J. Mar. Sci.* 69, 8–22. doi: 10.1093/icesjms/fsr188

Greenstreet, S. P. R., Rogers, S. I., Rice, J. C., Piet, G. J., Guirey, E. J., Fraser, H. M., et al. (2011). Development of the EcoQO for fish communities in the North Sea. *ICES J. Mar. Sci.* 68, 1–11. doi: 10.1093/icesjms/fsq156

Griffith, G. P., Fulton, E. A., Gorton, R., and Richardson, A. J. (2012). Predicting Interactions among fishing, ocean warming, and ocean acidification in a marine system with whole-ecosystem models. *Conserv. Biol.* 26, 1145–1152. doi: 10.1111/j.1523-1739.2012.01937.x

Griffith, G. P., Fulton, E. A., and Richardson, A. J. (2011). Effects of fishing and acidification-related benthic mortality on the southeast Australian marine ecosystem. *Glob. Change Biol.* 17, 3058–3074. doi: 10.1111/j.1365-2486.2011.02453.x

Griffith, G. P., Strutton, P. G., Semmens, J. M., and Fulton, E. A. (2019). Identifying important species that amplify or mitigate the interaction effects of human impacts on marine food webs. *Cons. Biol.* 33, 403–412. doi: 10.1111/cobi.13202

Guo, C., Fu, C., Forrest, R., Olsen, N., Liu, H., Verley, P., et al. (2019). Ecosystem-based reference points under varying plankton productivity states and fisheries management strategies. *ICES J. Mar. Sci.* 76, 2045–2059. doi: 10.1093/icesjms/fsz120

Guo, C., Fu, C., Olsen, N., Xu, Y., Grüss, A., Liu, H., et al. (2020). Incorporating environmental forcing in developing ecosystem-based fisheries management strategies. *ICES J. Mar. Sci.* 77, 500–514. doi: 10.1093/icesjms/fsz246

Haigh, R., Ianson, D., Holt, C. A., Neate, H. E., and Edwards, A. M. (2015). Effects of ocean acidification on temperate coastal marine ecosystems and fisheries in the Northeast Pacific. *PLoS One* 10:e0117533. doi: 10.1371/journal.pone.0117533

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., et al. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nat. Commun.* 6:7615. doi: 10.1038/ncomms8615

Hidalgo, M., Rouyer, T., Molinero, J. C., Massutí, E., Moranta, J., Guijarro, B., et al. (2011). Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Mar. Ecol. Prog. Ser.* 426, 1–12. doi: 10.3354/meps09077

Hodgson, E. E., and Halpern, B. S. (2019). Investigating cumulative effects across ecological scales. *Conserv. Biol.* 33, 22–32. doi: 10.1111/cobi.13125

Holt, K., King, J. R., and Krishka, B. A. (2016). *Stock Assessment for Lingcod (Ophiodon elongatus) in the Strait of Georgia, British Columbia in 2014*. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/013. Sidney, BC: Fisheries and Oceans Canada, xi+186.

Jennings, S. (2005). Indicators to support an ecosystem approach to fisheries. *Fish Fish.* 6, 212–232. doi: 10.1111/j.1467-2979.2005.00189.x

Keister, J. E., Di Lorenzo, E., Morgan, C. A., Combes, V., and Peterson, W. T. (2011). Zooplankton species composition is linked to ocean transport in the Northern California Current. *Glob. Change Biol.* 17, 2498–2511. doi: 10.1111/j.1365-2486.2010.02383.x

Kirby, R., Beaugrand, G., and Lindley, J. (2009). Synergistic effects of climate and fishing in a marine ecosystem. *Ecosystems* 12, 548–561. doi: 10.1007/s10021-009-9241-9

Le Bris, A., Mills, K. E., Wahle, R. A., Chen, Y., Alexander, M. A., Allyn, A. J., et al. (2018). Climate vulnerability and resilience in the most valuable North American fishery. *Proc. Natl. Acad. Sci. U.S.A.* 115, 1831–1836. doi: 10.1073/pnas.1711122115

Lercari, D., Defeo, O., Ortega, L., Orlando, L., Gianelli, I., and Celentano, E. (2018). Long-term structural and functional changes driven by climate variability and fishery regimes in a sandy beach ecosystem. *Ecol. Modelling* 368, 41–51. doi: 10.1016/j.ecolmodel.2017.11.007

Leslie, H. M., and McLeod, K. L. (2007). Confronting the challenges of implementing marine ecosystem based management. *Front. Ecol. Environ.* 5:540–548. doi: 10.1890/060093

Lindegren, M., Checkley, D. M., Koslow, J. A., Goericke, R., and Ohman, M. D. (2018). Climate-mediated changes in marine ecosystem regulation during El Niño. *Glob. Change Biol.* 24, 796–809. doi: 10.1111/gcb.13993

Lindenmayer, D. B., Likens, G. E., Krebs, C. J., and Hobbs, R. J. (2010). Improved probability of detection of ecological "surprises". *Proc. Natl. Acad. Sci. U.S.A.* 107, 21957–21962. doi: 10.1073/pnas.1015696107

Mach, M. E., Wedding, L. M., Reiter, S. M., Micheli, F., Fujita, R. M., and Martone, R. G. (2017). Assessment and management of cumulative impacts in California's network of marine protected areas. *Ocean Coast. Manag.* 137, 1–11. doi: 10.1016/j.ocecoaman.2016.11.028

Malick, M. J., Cox, S. P., Mueter, F. J., Dorner, B., and Peterman, R. M. (2017). Effects on the North Pacific Current on the productivity of 163 Pacific salmon stocks. *Fish. Oceanogr.* 26, 268–281. doi: 10.1111/fog.12190

Micheli, F., Halpern, B. S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., et al. (2013). Cumulative human impacts on Mediterranean and Black Sea marine ecosystems: assessing current pressures and opportunities. *PLoS One* 8:e79889. doi: 10.1371/journal.pone.0079889

Miller, D. D., Ota, Y., Sumaila, U. R., Cisneros-Montemayor, A. M., and Cheung, W. W. L. (2018). Adaptation strategies to climate change in marine systems. *Glob. Change Biol.* 24, e1–e14. doi: 10.1111/gcb.13829

Miloslavich, P., Bax, N. J., Simmons, S. E., Klein, E., Appeltans, W., Aburto-Oropeza, O., et al. (2018). Essential ocean variables for global sustained observations of biodiversity and ecosystem changes. *Glob. Change Biol.* 24, 2416–2433. doi: 10.1111/gcb.14108

Niiranen, S., Yletyinen, J., Tomczak, M. T., Blenckner, T., Hjerne, O., Mackenzie, B. R., et al. (2013). Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. *Glob. Change Biol.* 19, 3327–3342. doi: 10.1111/gcb.12309

Ortega-Cisneros, K., Cochrane, K. L., Fulton, E. A., Gorton, R., and Popova, E. (2018). Evaluating the effects of climate change in the southern Benguela upwelling system using the Atlantis modelling framework. *Fish. Oceanogr.* 27, 489–503. doi: 10.1111/fog.12268

Piggott, J. J., Townsend, C. R., and Matthaei, C. D. (2015). Reconceptualizing synergism and antagonism among multiple stressors. *Ecol. Evol.* 5, 1538–1547. doi: 10.1002/ece3.1465

Planque, B., Fromentin, J.-M., Cury, P., Drinkwate, K. F., Jennings, S., Perry, R. L., et al. (2010). How does fishing alter marine populations and ecosystems sensitivity to climate? *J. Mar. Syst.* 79, 403–417. doi: 10.1016/j.jmarsys.2008.12.018

Quetglas, A., Ordines, F., Hidalgo, M., Monserrat, S., Ruiz, S., Amores, A., et al. (2013). Synchronous combined effects of fishing and climate within a demersal community. *ICES J. Mar. Sci.* 70, 319–328. doi: 10.1093/icesjms/fss181

Ramírez, F., Coll, M., Navarro, J., Bustamante, J., and Green, A. J. (2018). Spatial congruence between multiple stressors in the Mediterranean Sea may reduce its resilience to climate impacts. *Sci. Rep.* 8:14871. doi: 10.1038/s41598-018-33237-w

Rilov, G., Mazaris, A. D., Stelzenmüller, V., Helmuth, B., Wahl, M., Guy-Haim, T., et al. (2019). Adaptive marine conservation planning in the face of climate change: what can we learn from physiological, ecological and genetic studies? *Glob. Ecol. Conserv.* 17:e00566. doi: 10.1016/j.gecco.2019.e00566

Rosenberg, A. A., and McLeod, K. L. (2005). Implementing ecosystem-based approaches to management for the conservation of ecosystem services. *Mar. Ecol. Prog. Ser.* 300, 270–274. doi: 10.3354/meps300270

Samhouri, J. F., Andrews, K., Fay, G., Harvey, C. J., Hazen, E. L., Hennessy, S. M., et al. (2017). Defining ecosystem thresholds for human activities and environmental pressures in the California Current. *Ecosphere* 8:e01860. doi: 10.1002/ecs2.1860

Schinegger, R., Palt, M., Segurado, P., and Schmutz, S. (2016). Untangling the effects of multiple human stressors and their impacts on fish assemblages in European running waters. *Sci. Total Environ.* 573, 1079–1088. doi: 10.1016/j.scitotenv.2016.08.143

Segurado, P., Almeida, C., Neves, R., Ferreira, M. T., and Branco, P. (2018). Understanding multiple stressors in a Mediterranean basin: combined effects of land use, water scarcity and nutrient enrichment. *Sci. Total Environ.* 624, 1221–1233. doi: 10.1016/j.scitotenv.2017.12.201

Serpetti, N., Baudron, A. R., Burrows, M. T., Payne, B. L., Helaouët, P., Fernandes, P. G., et al. (2017). Impact of ocean warming on sustainable fisheries management informs the ecosystem approach to fisheries. *Sci. Rep.* 7:3438. doi: 10.1038/s41598-017-13220-7

Shannon, L. J., Coll, M., Bundy, A., Gascuel, D., Heymans, J. J., Kleisner, K., et al. (2014). Trophic level-based indicators to track fishing impacts across marine ecosystems. *Mar. Ecol. Prog. Ser.* 512, 115–140. doi: 10.3354/meps10821

Shin, Y.-J., Bundy, A., Shannon, L. J., Blanchard, J. L., Chuenpagdee, R., Coll, M., et al. (2012). Global in scope and regionally rich: an IndiSeas workshop helps shape the future of marine ecosystem indicators. *Rev. Fish Biol. Fish.* 22, 835–845. doi: 10.1007/s11160-012-9252-z

Shin, Y.-J., and Cury, P. (2004). Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Can. J. Fish. Aquat. Sci.* 61, 414–431. doi: 10.1139/f03-154

Smale, D. A., Wernberg, T., Oliver, E. C. J., Thomsen, M., Harvey, B. P., Straub, S. C., et al. (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Change* 9, 306–312. doi: 10.1038/s41558-019-0412-1

Sprogis, K. R., Christiansen, F., Wandres, M., and Bejder, L. (2018). El Niño Southern Oscillation influences the abundance and movements of a marine top predator in coastal waters. *Glob. Change Biol.* 24, 1085–1096. doi: 10.1111/gcb.13892

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K. S., and Lima, M. (2002). Ecological effects of climate fluctuations. *Science* 297, 1292–1296. doi: 10.1126/science.1071281

Teichert, N., Borja, A., Chust, G., Uriarte, A., and Lepage, M. (2016). Restoring fish ecological quality in estuaries: implication of interactive and cumulative effects among anthropogenic stressors. *Sci. Total Environ.* 542, 383–393. doi: 10.1016/j.scitotenv.2015.10.068

Thompson, M. S. A., Pontalier, H., Spence, M. A., Pinnegar, J. K., Greenstreet, S., Moriarty, M., et al. (2020). A feeding guild indicator to assess environmental change impacts on marine ecosystem structure and functioning. *J. Appl. Ecol.* 57, 1769–1781. doi: 10.1111/1365-2664.13662

Travers-Trolet, M., Shin, Y.-J., Shannon, L. J., Moloney, C. L., and Field, J. G. (2014). Combined fishing and climate forcing in the southern benguela upwelling ecosystem: an end-to-end modelling approach reveals dampened effects. *PLoS One* 9:e94286. doi: 10.1371/journal.pone.0094286

Weijerman, M., Fulton, E. A., Kaplan, I. C., Gorton, R., Leemans, R., Mooij, W. M., et al. (2015). An integrated coral reef ecosystem model to support resource management under a changing climate. *PLoS One* 10:e0144165. doi: 10.1371/journal.pone.0144165

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.

The handling editor declared a past co-authorship with several of the authors CF, AG, and Y-JS.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 16 October 2020
doi: 10.3389/fmars.2020.567877

Advancing Global Ecological Modeling Capabilities to Simulate Future Trajectories of Change in Marine Ecosystems

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OPEN ACCESS

Edited by:
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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: 30 May 2020
Accepted: 13 August 2020
Published: 16 October 2020

Citation:
Coll M, Steenbeek J, Pennino MG, Buszowski J, Kaschner K, Lotze HK, Rousseau Y, Tittensor DP, Walters C, Watson RA and Christensen V (2020) Advancing Global Ecological Modeling Capabilities to Simulate Future Trajectories of Change in Marine Ecosystems. Front. Mar. Sci. 7:567877. doi: 10.3389/fmars.2020.567877

Considerable effort is being deployed to predict the impacts of climate change and anthropogenic activities on the ocean's biophysical environment, biodiversity, and natural resources to better understand how marine ecosystems and provided services to humans are likely to change and explore alternative pathways and options. We present an updated version of EcoOcean (v2), a spatial-temporal ecosystem modeling complex of the global ocean that spans food-web dynamics from primary producers to top predators. Advancements include an enhanced ability to reproduce spatial-temporal ecosystem dynamics by linking species productivity, distributions, and trophic interactions to the impacts of climate change and worldwide fisheries. The updated modeling platform is used to simulate past and future scenarios of change, where we quantify the impacts of alternative configurations of the ecological model, responses to climate-change scenarios, and the additional impacts of fishing. Climate-change scenarios are obtained from two Earth-System Models (ESMs, GFDL-ESM2M, and IPSL-CMA5-LR) and two contrasting emission pathways (RCPs 2.6 and 8.5) for historical (1950–2005) and future (2006–2100) periods. Standardized ecological indicators and biomasses of selected species groups are used to compare simulations. Results show how future ecological trajectories are sensitive to alternative configurations of EcoOcean, and yield moderate differences when looking at ecological indicators and larger differences for biomasses of species groups. Ecological trajectories are also sensitive to environmental drivers from alternative ESM outputs and RCPs, and show spatial variability and more severe changes when IPSL and RCP 8.5 are used. Under a non-fishing configuration, larger organisms show decreasing trends, while smaller organisms show mixed or increasing results. Fishing intensifies the negative effects predicted by climate change, again stronger under IPSL and RCP 8.5, which results in stronger biomass declines for species already losing under climate change, or dampened positive impacts for those increasing. Several species groups that win under climate change become losers under combined impacts, while only a few (small benthopelagic fish and cephalopods) species are projected to show positive biomass changes under cumulative impacts. EcoOcean v2 can contribute to the quantification of cumulative impact assessments of multiple stressors and of plausible ocean-based solutions to prevent, mitigate and adapt to global change.

Keywords: marine ecosystems, climate change, fishing, future trajectories, projections, food web spatial-temporal model, model uncertainty

INTRODUCTION

The world's oceans are experiencing rapid ecological, socioeconomic, and institutional changes due to Global Environmental Change (Poloczanska et al., 2016; Pecl et al., 2017; Trisos et al., 2020). Direct drivers of global change that affect marine life include intense fishing, the loss of habitats, pollution, invasions of alien species, and climate change impacts such as rising water temperatures, acidification, and declining oxygen. These drivers are widely distributed and spatially overlapping (Halpern et al., 2015, 2019), may accumulate over time, and are increasing in severity in many parts of the world (Sala et al., 2000; Poloczanska et al., 2013; Mengerink et al., 2014; Levin and Le Bris, 2015; McCauley et al., 2015). Global environmental change drivers impact biophysical and ecological properties of the ocean and affect multiple levels of biological organization including genes, species, populations, communities, and ecological interactions (Parmesan, 2006; Worm et al., 2006; Hoegh-Guldberg and Bruno, 2010; Poloczanska et al., 2016; Scheffers et al., 2016; Pecl et al., 2017; Beaugrand and Kirby, 2018). They can also strongly influence species geographic distributions (Stenseth et al., 2002; Perry et al., 2005; Hoegh-Guldberg and Bruno, 2010).

A transformation to sustainability is key to adapt our social-ecological systems to changing environments (Abson et al., 2017; Colloff et al., 2017), but scientific understanding about how the oceans will continue to change into the future is limited. This understanding can only be attained with studies at multiple scales, where global studies are essential as environmental changes and socio-economic interactions are often coupled and cascading impacts of ecological disturbances affect human use of ecosystem services across vast distances through ocean currents, species movements, and fishing fleet mobility (Worm et al., 2006; Drakou et al., 2017; Kroodsma et al., 2018). In response, there is a strong push to advance ecosystem-based management of marine resources, which includes the establishment of management initiatives such as large Marine Protected Areas, MPAs, the protection of areas beyond national jurisdiction (Toonen et al., 2013; Lubchenco and Grorud-Colvert, 2015; Roberts et al., 2017; Jones et al., 2020) and, in general, area-based fisheries management measures and other effective spatial conservation measures (FAO, 2019).

Quantifying past and future trends of marine ecosystems caused by global change is critical to inform ongoing climate change and biodiversity assessments, and to guide feasible pathways toward achieving key policy objectives globally (Visbeck, 2018; Hoegh-Guldberg et al., 2019). To predict the future of marine biodiversity and ecosystem services we need to adopt an integrated view of the ocean as a social-ecological system, encompassing the dynamics of commercial and non-commercial species and their interactions, the dynamics of resource users and their interactions, and how those are affected by changing environmental conditions and management interventions (Urban et al., 2016). This implies a need for powerful modeling approaches able to better analyze past and project trajectories of change, and to better understand the impacts that humans and a changing climate may pose (Alder et al., 2007; Christensen et al., 2009; Fulton et al., 2015).

In this context, the last decades have witnessed extensive development of modeling techniques both in terrestrial and marine domains (Urban et al., 2016; Bonan and Doney, 2018). Rapid development of atmospheric-ocean circulation models, including biogeochemical processes in Earth System Models (ESM), has improved the scientific capability to project the climate system, which in turn has helped inform the United Nation (UN) Intergovernmental Panel on Climate Change (IPCC) (IPCC, 2018, 2019). Separately, ecosystem models have been developed to help explore the functioning of marine ecosystems beyond primary producers. These models are conceptual and theoretical frameworks that represent a synthesized understanding of all major parts of an ecosystem (Fulton, 2010). Over the last three decades, there has been a dramatic increase in the development of such modeling frameworks, especially in the marine realm (Tittensor et al., 2018). These Marine Ecosystem Models (MEMs) are used to project changes in marine ecosystems at regional or global scales, including the impacts of fishing and other human activities and stressors (e.g., Travers et al., 2009; Fulton, 2010; Maury, 2010; Blanchard et al., 2012; Barange et al., 2014; Christensen et al., 2015; Fernandes et al., 2015; Fulton et al., 2015; Jennings and Collingridge, 2015; Cheung et al., 2016b; Coll et al., 2016; Galbraith et al., 2017; du Pontavice et al., 2020). These initiatives have been used to analyze past and future dynamics of marine ecosystems, including their emergent properties (Link et al., 2015), and are now being synthesized into ensemble model projections, contributing toward extending the scientific capability to project what the future oceans may look like, how different scenarios may play out, and what the range of uncertainty is for different components and processes (Tittensor et al., 2018; Bryndum-Buchholz et al., 2019; Lotze et al., 2019). The EcoOcean model is a modeling complex with a trophodynamic core that represents one of these initiatives with a global scope (Tittensor et al., 2018).

However, despite the advances in ecological modeling to describe past and future ocean dynamics, the unprecedented development of ESMs and MEMs, and capabilities to project the climate system, available models have limitations in terms of evaluating the combined impacts of environmental change on marine ecosystems and how they can be used to inform management and policy processes integrating socio-ecological dynamics. For example, they may fail to consider direct and indirect ecological dynamics from primary producers to predators, and to capture the multilevel impacts of global change on a diversity of spatial-temporal processes (Travis et al., 2014; Brander, 2015; O'Connor et al., 2015; Koenigstein et al., 2016; Peck et al., 2016; Urban et al., 2016). They are limited in capturing species capacity to invade new ecosystems, which can be important when predicting future climate and global impacts in marine ecosystems (Blois et al., 2013; Urban et al., 2016). Last, most current state-of-the-art models are limited in their ability to consider how eco-evolutionary dynamics may interact to condition and modify species traits, patterns, and interactions (Lavergne et al., 2010; Norberg et al., 2012; Barraclough, 2015; Koenigstein et al., 2016; Peck et al., 2016; Fulton et al., 2019).

Therefore, there is a need to build upon existing approaches and extend the ability to project ocean biodiversity, associated ecosystem services and use patterns, and how these linked social-ecological systems will change. These are essential contributions to international initiatives and treaties such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (Brondizio et al., 2019) and the Convention of Biological Diversity (CBD, 2013) and its post-2020 global biodiversity framework, as well as to inform the UN Sustainable Development Goals, SDGs (UN, 2020), in particular SDG14 on the conservation and sustainable use of the oceans, seas, and marine resources (Claudet et al., 2020; Heymans et al., 2020).

EcoOcean

The first global ocean model with the Ecopath with Ecosim (EwE) modeling approach (Polovina, 1984; Christensen and Walters, 2004) at its core was developed in response to a growing demand by scientists and managers for tools to explore the future of fisheries and marine biodiversity in the ocean (Alder et al., 2007). This model applied historical fishing effort for five types of fleets to the 19 global fishing areas defined by the UN Food and Agricultural Organization (FAO), and its predictions were used to describe how biomass, landings, and profits may change under different policy scenarios. Its application to explore the scenarios proposed by the UN Environmental Programme Global Environment Outlook and the International Assessment for Agricultural Science, Technology and Development further demonstrated the ability of this model to inform future fisheries management decisions. Christensen et al. (2009) applied the same approach on 66 Large Marine Ecosystems (LMEs) while developing a new methodology to create database-driven ecosystem models. Spatial models were driven by fishing effort and primary production to obtain a first estimate of fish biomass in the world's LMEs.

This modeling complex was expanded to EcoOcean v1 (Christensen et al., 2015), with the ability to include ocean climate model forcing to hindcast ecosystem dynamics, considering the interplay between food-web dynamics, niche modeling, environmental change, and fisheries, and their impact on global seafood production (Christensen et al., 2015). EcoOcean v1 was included in the Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP) to investigate, as part of a model ensemble, changes in global fish biomass using past and future standardized environmental forcings from ESM outputs (Tittensor et al., 2018; Lotze et al., 2019).

Here we present an improved spatially and temporally explicit ecosystem modeling complex of the global ocean (EcoOcean v2) that includes spatial-temporal food-web dynamics from primary producers to top predators and considers worldwide fisheries. In this new version, we enhanced EcoOcean's ability to reproduce spatial-temporal ecosystem dynamics by further linking species productivity and distribution to major environmental conditions under climate change (e.g., primary production, sea surface temperature), accounting for varying species compositions of functional groups of the model over time and space. The updated modeling platform is then used to test alternative configurations of the ecological model and alternative input drivers using standardized outputs from ESMs and contrasting emission scenarios (Representative Concentration Pathways, RCPs) for historical (1950–2005) and future (2006–2100) periods, under a fishing and a non-fishing simulation. We compare changes in standardized aggregated ecological indicators and the biomass of marine species groupings among simulations and time periods.

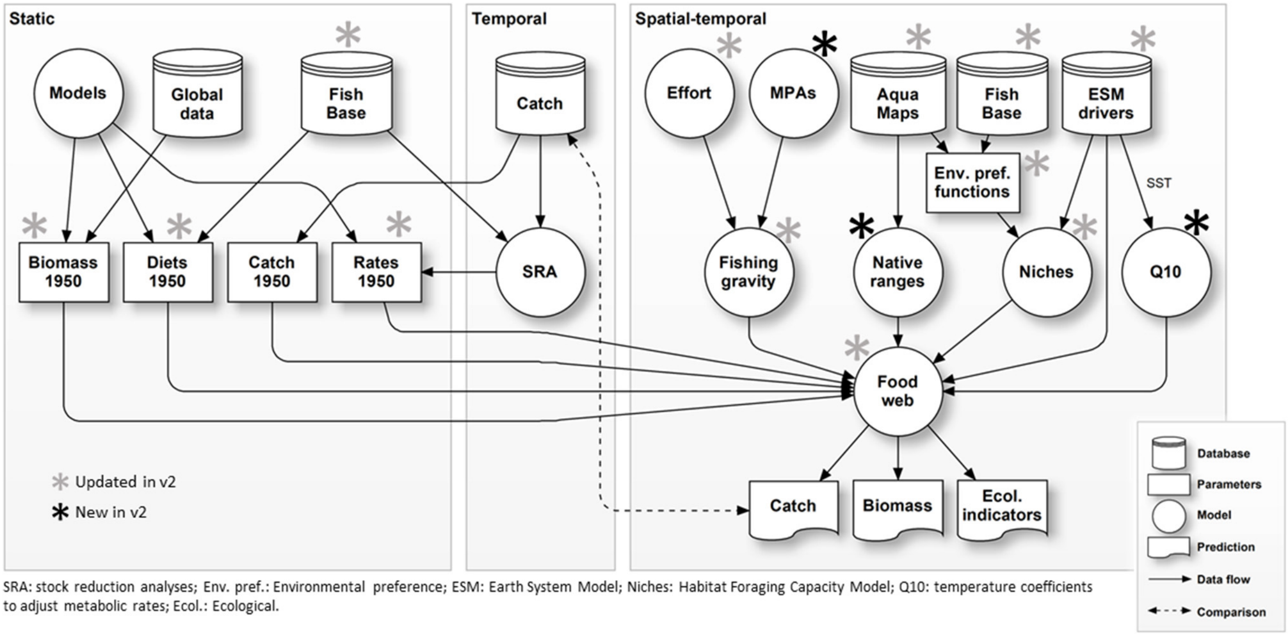
MATERIALS AND METHODS

EcoOcean v1: The Global Model Is an Ecosystem

The EcoOcean v1 modeling complex was initially created to evaluate how alternative management actions impacted the supply of seafood, within an ecosystem context, considering the combined impact of environmental parameters and fisheries at the global scale (Christensen et al., 2015). EcoOcean v1 was spatial-temporally explicit (2D) at ½° or 1° spatial resolution, running from 1950 to 2100 with monthly time steps. Detailed descriptions, diagnostics, and model skill evaluation can be found at Christensen et al. (2015), Tittensor et al. (2018), and Lotze et al. (2019).

EcoOcean v1 was composed of a series of interlinked models including (i) a biogeochemistry and primary production component, (ii) an ecosystem component linked within a food web considering a large variety of organisms from low to high trophic levels and with commercial and non-commercial interest, and (iii) a fisheries component considering main fleets and targeted species (**Figure 1**). Initial developments, parametrizations, capabilities, and specific details of model components are well-documented elsewhere (Christensen et al., 2015) and are briefly summarized below:

- In EcoOcean v1, a simulation of the Modular Ocean Model (MOM4.1) coupled to the COBALT biogeochemical model (Stock et al., 2014) was first used to obtain spatial-temporal outputs of production rates for large phytoplankton, small phytoplankton, and diazotrophs. Additional runs of EcoOcean v1 developed under FishMIP Phase I (Tittensor et al., 2018)



SRA: stock reduction analyses; Env. pref.: Environmental preference; ESM: Earth System Model; Niches: Habitat Foraging Capacity Model; Q10: temperature coefficients to adjust metabolic rates; Ecol.: Ecological.

FIGURE 1 | Schematic structure of EcoOcean v2 modeling complex.

used forcings from two contrasting fully-coupled atmosphere, ocean and biogeochemical ESM from the Coupled Model Intercomparison Project Phase 5 (CMIP5): GFDL-ESM2M using COBALT and IPSL-CMA5-LR using PISCES (both historical and for four RCPs: 2.6, 4.5, 6.0, and 8.5 scenarios) (Bopp et al., 2013).

- The ecosystem component consisted of a customized version of the Ecopath with Ecosim (EwE) food-web modeling approach (Christensen and Walters, 2004) following the definitions and methodologies established by Christensen et al. (2009). The food web explicitly considered standardized 51 functional groups or species groupings (spanning from bacteria to marine mammals and seabirds), each including organisms that share similar biological and ecological traits. Groups composed of fishes were separated into "small fish" (with asymptotic length, $L_\infty < 30$ cm), "medium fish" ($L_\infty = 30 - 90$ cm) and "large fish" ($L_\infty > 90$ cm). Fish species were further grouped as pelagics, demersals, bahypelagics, bathydemersals, benthopelagics, reef fishes, sharks, rays, and flatfishes. The large pelagic fishes were modeled considering two life-stages with an age-structured model (Walters et al., 2010). Invertebrate species were separated into different groups divided into commercial and non-commercial species.

An important feature of the food-web model used in EcoOcean was that predator-prey dynamics were based on the "Foraging Arena Theory" (Walters and Juanes, 1993; Ahrens et al., 2012), which added behavior-driven non-linearity to the mass-action terms included in traditional multispecies models. A formal fitting procedure with historical fishing effort and catch data was developed using a customized version of the time-dynamic model Ecosim (Walters et al., 1997) to estimate key vulnerability parameters. This enabled the model to hindcast marine resources and ecosystem services dynamics for the period 1950–2006, projecting the combined impact of environmental parameters and fisheries on global seafood production (Christensen et al., 2015; Lotze et al., 2019) (**Supplementary Material A**).

Another important feature of EcoOcean v1 was the inclusion of the impact of changes in environmental parameters using the relative habitat capacity of each functional group as a cell-specific attribute through the implementation of the "Habitat Foraging Capacity Model (HFCM)" framework (Christensen et al., 2014) in the spatial-temporal model Ecospace (Walters et al., 1999) through a data exchange engine for Ecospace (Steenbeek et al., 2013). Environmental parameters used to drive cell capacity per functional group were depth, primary production, and sea surface temperature for large pelagic fishes. For depth, information from 1,418 fish and invertebrate species was obtained from FishBase[1] and SeaLifeBase[2] and was used to define depth distribution based on individual triangular distributions.

The movements of organisms across spatial cells depended on cell suitability and response of organisms to local predation risks and feeding conditions (Walters et al., 1999; Martell et al., 2005; Christensen et al., 2014). When dispersing, species had a higher chance of moving to a neighboring cell if feeding is better, and the risk of depredation lower. To incorporate the active movement of organisms across space, EcoOcean v1 used the dispersal mechanisms established in the spatial-temporal Ecospace model (Walters et al., 1999; Martell et al., 2005). EcoOcean v1 used relative magnitudes of dispersal rates (3, 30,

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[1] www.fishbase.org

[2] www.sealifebase.org

and 300 km/year) representing non-dispersing, demersal, and pelagic groups, respectively, and body-sizes (Martell et al., 2005; Bradbury et al., 2008).

- The fisheries model was based on the existing gravity model implemented in Ecospace, where the effort allocated to each spatial cell is based on the profitability of fishing estimated as the difference between expected income and costs of fishing in each cell (Walters et al., 1999). The cost of fishing was assumed proportional to the distance (km) from the nearest coast. Expected income was estimated using prices per functional groups from a global price database available based on average prices in 2000 (Sumaila et al., 2007).

  Time series of fishing effort were obtained from a global spatial effort database that covered 1950 to 2006 and provided information by country and fishing gear specific fleets for 1,365 fleets (Anticamara et al., 2011; Watson et al., 2013). The effort was standardized and the 14 gear types included in the global database were used as global fleets in the fisheries model, which were allocated spatially by LME (Christensen et al., 2015). The effort allocation was set based on historical effort and was scaled per LME as a proportion of the total effort across all fished cells within each LME. The effort included an annual increase of 2% related to technological development (Pauly and Palomares, 2010). Finally, global catch estimates available from the Sea Around Us project (www.seaaroundus.org) were used in two ways: (i) to parameterize the landings by fleet in the initial conditions (1950) and (ii) as observed catches to evaluate the historical model runs from 1951 to 2006 (Christensen et al., 2015).

EcoOcean v2: Key Updates to Further Represent the Global Ocean Dynamics

Here we substantially updated the EcoOcean framework (**Figure 1**), with the principal aim to (i) improve representation of species contributions to ecosystem dynamics, (ii) improve responses of the marine food web to different environmental drivers, such as changes in sea temperature and primary productivity, and (iii) explore the sensitivity of results to alternative configurations of the ecological model and simulations of climate-change and fishing. These developments were facilitated through the modular design of EcoOcean (**Figure 1**) and its underlying code structure, which allows access to databases, integration with other models (Steenbeek et al., 2016) and geospatial driver data (Steenbeek et al., 2013; Christensen et al., 2014), and provides control to enable or disable the representation of ecological mechanisms throughout the complex. EcoOcean v2 was implemented in. NET and R software and runs spatial-temporally explicit simulations at 1° spatial resolution, from 1950 to 2100 with monthly time steps.

Improved Representation of Species Contributions

The food web at the core of EcoOcean was extended to explicitly consider over 3,400 individual species (v1 included over 1,400 species-specific information) and better represent marine biodiversity and environmental sensitivities. Species-specific information was added to the functional groups of benthic primary producers, jellyfish, corals, soft corals and sponges, dolphins and porpoises, baleen whales, toothed whales, pinnipeds, and seabirds. Overall, the species resolution contributes to the initial parameterization and spatial-temporal dynamics of each functional group with a weighted average of specific traits (such as biomass, consumption and production rates, catches, environmental tolerances, and preferences, etc.). These modifications to EcoOcean v2 did not change the initial parameterization, but the representation of species within functional groups to explicitly capture diversity in species traits and their contributions to functional group spatial-temporal dynamics.

In addition, a new functional group for marine turtles was added with specific information for the seven living species of marine turtles occurring today.

Improved Responses to Environmental Drivers

Native ranges

When developing global analyses, spatial allocation of species purely based on affinity for habitats, depth and environmental drivers will mean that species may end up at locations where they have never been observed. To account for this, EcoOcean v2 limited the spatial distribution of each species groupings at the start of a simulation with the observed historical native ranges (NR) of its species.

The species groups-wide native ranges were constructed as presence/absence maps from the species within a functional group, and their maximum range extents as defined by Kaschner et al. (2016). These groups-wide native ranges were then incorporated as input capacity layers to the HFCM (Christensen et al., 2014) at the beginning of each spatial-temporal simulation, preventing a species group to occur outside its observed range initially. Within these confines, the species groups were distributed according to affinity for habitats, depth, and environmental drivers. At the end of the first-time simulation step, these range restrictions were released, allowing the species groups to distribute freely according to changing environmental and habitat conditions for the remaining of the simulation (**Supplementary Figure 1**).

Cell-specific responses

EcoOcean uses the HFCM to determine cell habitat foraging capacity, or cell suitability, per functional group (Christensen et al., 2014) (**Supplementary Figure 2**). In the HFCM, for each species grouping, cell suitability is the product of three foraging capacity terms: (i) input capacity as obtained from external niche models; (ii) optional foraging capacity derived from affinities for specific habitat types and habitat distributions; and (3) optional functional responses to environmental drivers (**Supplementary Figure 1**). Cell suitability is expressed as a per-group multiplier to the foraging arena size, thus varying the suitability of a cell for foraging, which then impacts growth and consumption of functional groups.

In EcoOcean, cell suitability was derived from the product of preferences for (or tolerances to) depth, environmental factors (such as temperature), and affinity for specific type of habitat where applicable. Environmental factors change with time and space by driving the HFCM with ESM outputs. Using the HFCM and information about environmental envelopes and response functions available, new response functions to most functional groups were added (**Supplementary Table 1**).

An important modification to EcoOcean v2 was the ability to evaluate species groups functional responses to temperature based on the probability of presence of a group's species per cell (**Supplementary Figure 3**). This means that the actual response function to temperature of each functional group changed with space and per time step according to the presumed composition of each group in each cell. As functional groups are expressed globally, but the species within vary greatly in distributions due to individual thermal tolerances, EcoOcean v2 combined groups' species compositions, species' environmental preferences, and species' likelihood of presence to evaluate how well a species group may tolerate local conditions in a cell. Lacking continuous range predictions for species, we numerically resolved this as follows: for each species within a species group, for each cell, tolerance to local temperature was determined from AquaMaps responses to temperature (Kaschner et al., 2016). Only species that exhibited some form of tolerance to the local temperature were considered within that cell. Furthermore, species that natively occur within the cell contributed fully to the group-wide temperature response; species outside their native range contribute for 10% to the group-wide temperature response. As we do not have reliable biomass distribution data for species over time and space, species' contributions to the functional response were currently not weighted by biomass. These assumptions still allow functional groups to move to new areas if and when suitable conditions were to develop (**Supplementary Figure 3**).

Temperature-adjusted metabolic rates

The global mass-balanced parameters that are used to initialize EcoOcean are a necessary global average, parameterized to a global averaged temperature. However, aerobic metabolism rates of species vary from optimal average temperatures, and species' capacity for activity, growth, and reproduction exhibit a measure of adaptation on exposure to long-term temperature deviations from the mean (Rao and Bullock, 1954; Lefevre, 2016). This means that for global ecosystem models with globally distributed functional groups, global averages or unadjusted averages or species' mass-balanced conditions and parameters only realistically apply to narrow temperature bands around the globe; elsewhere, species' capacity for activity, growth, and reproduction fundamentally differs due to marked changes in environmental conditions.

To take this into account, in EcoOcean v2 we explored the viability of a Q_{10} approach in a global ecosystem model context by spatially varying the initial mass-balance parameters such as consumption and production rates as a function of near-evolutionary scale average global temperatures (**Supplementary Material**). The Q_{10} temperature coefficient is a measure of the rate of change of a biological or chemical system as a consequence of increasing the temperature by 10 °C. Selecting one single Q_{10} value for an entire ecosystem is incorrect as Q_{10} values are available for a large number of organisms and can vary substantially (Lefevre et al., 2017). As a first experiment, the current version of EcoOcean v2 used two values of Q_{10} to represent only differences between fish and macro-invertebrates based on literature estimates (White et al., 2005), while the rest of the functional groups were left unaffected.

Historical fishing effort and spatial management

A new version of a global fishing effort dataset (Rousseau et al., 2019) was used to replace previous estimates incorporated into EcoOcean, extended from 1950 to 2015. We updated the effort allocation per LME as a proportion of total global effort and kept the annual effort creep of 2% (Pauly and Palomares, 2010). A dynamic module to explore the effectiveness of spatial-temporal management measures such as MPAs, seasonal closures or a combination of both, was also added (**Figure 1**).

Sensitivity to Alternative Configurations of the Ecological Model and Simulations of Climate Change and Fishing

In this study, we used EcoOcean v2 as an experimental modeling platform to investigate the impact on ecological trajectories of alternative configurations of the ecological model, in addition to the impact of combinations of drivers (e.g., changes in ESM inputs and RCP scenarios, under non-fishing and fishing configurations).

In this study we present the results of three experiments, conducted through 13 simulations (**Table 1**):

Experiment 1—ecological configurations

We tested the impact of using alternative configurations of the ecological model (or a combination of them) on spatial and temporal trajectories of ecological dynamics. We tested five different main configurations (**Table 1**): (i) food-web dynamics, habitat affinities and depth preferences as drivers of species distributions, (ii) adding to (i) cell-specific environmental responses to sea surface temperature, (iii) adding to (i) with the Q_{10} implementation to adjust the temperature-specific metabolic rates, (iv) adding to (i) native ranges constrains to initial conditions, and (v) combining all ecological mechanisms. All these simulations were run from 1950 to 2100 using the same moderate environmental scenario (GFDL ESM2M—Historical/RCP2.6 from CMIP5) (**Supplementary Figure 4**), considering changes in sea surface temperature and in three primary producers groups (large phytoplankton, small phytoplankton and diazotrophs) driven using the same protocol as in Tittensor et al. (2018). Fishing was disabled.

Experiment 2—climate impacts

We tested how contrasting climate-change scenarios would impact the ecological trajectories of EcoOcean (**Table 1**) using both GFDL ESM2M—Historical/RCP2.6 and Historical/RCP8.5 and IPSL CMA5-LR—Historical/RCP2.6 and Historical/RCP8.5, both from CMIP5. All these simulations were run from 1950 to 2100 using changes in sea surface temperature and in two or three primary producer groups (large phytoplankton, small phytoplankton, and diazotrophs; this last group was not available for IPSL) (**Supplementary Figures 4**, **5**). Climate change impacts

TABLE 1 | EcoOcean experiments and simulations used to test the relative influence of alternative configurations of the ecological model (experiment 1, simulations 1–5), ESM and RCP scenarios (experiment 2, simulations 6–9), and the additional impact of fishing (experiment 3, simulations 10–13) on projected results.

#	Experiment	Simulation	Depth and habitat	Environ. drivers	Q10	Native ranges	ESM	Scenarios	Fishing
1	1	E-Base	✓				GFDL	Hist + RCP2.6	
2	1	E-Env	✓	✓			GFDL	Hist + RCP2.6	
3	1	E-Met	✓		✓		GFDL	Hist + RCP2.6	
4	1	E-Nr	✓			✓	GFDL	Hist + RCP2.6	
5	1	E-All	✓	✓	✓	✓	GFDL	Hist + RCP2.6	
6	2	C-GFDL2.6	✓	✓	✓	✓	GFDL	Hist + RCP2.6	
7	2	C-GFDL8.5	✓	✓	✓	✓	GFDL	Hist + RCP8.5	
8	2	C-IPSL2.6	✓	✓	✓	✓	IPSL	Hist + RCP2.6	
9	2	C-IPSL8.5	✓	✓	✓	✓	IPSL	Hist + RCP8.5	
10	3	F-GFDL2.6	✓	✓	✓	✓	GFDL	Hist + RCP2.6	✓
11	3	F-GFDL8.5	✓	✓	✓	✓	GFDL	Hist + RCP8.5	✓
12	3	F-IPSL2.6	✓	✓	✓	✓	IPSL	Hist + RCP2.6	✓
13	3	F-IPSL8.5	✓	✓	✓	✓	IPSL	Hist + RCP8.5	✓

were included through spatial-temporal variability in primary production using the same protocol as in Tittensor et al. (2018), through cell suitability per functional group and through temperature-adjusted metabolic rates as described in previous sections. In this experiment, fishing was disabled.

Experiment 3—fishing impacts

We tested the combined impact of contrasting climate-change scenarios and fishing. We repeated the climate-change scenarios of experiment 2 but added historical fishing effort that was kept constant per LME after 2005 following EcoOcean v1 (Christensen et al., 2015) (**Table 1**). All these simulations were run from 1950 to 2100 using changes in sea surface temperature and in three primary producer groups (large phytoplankton, small phytoplankton, and diazotrophs) (**Supplementary Figures 4, 5**). As in experiment 2, climate change impacts were included through spatial-temporal variability in primary production using the same protocol as in Tittensor et al. (2018), through cell suitability per functional group and through temperature-adjusted metabolic rates as described in previous sections.

Spatial-temporal simulations of EcoOcean v2 under the three experiments were run from 1950 to 2100 using a burn-in (or spin-up) period of 10 years and were analyzed via a series of selected standardized aggregated ecological indicators following previous scientific community efforts to compare marine ecosystem modeling outputs (Tittensor et al., 2018) from 1970 to 2100: Total System Biomass (TSB), Total Biomass of Consumers (TBC), Biomass of commercial species (Bcom), Biomass of consumers >10 cm (B10) and Biomass of consumers >30 cm (B30) (**Supplementary Table 1**). These indicators were initially expressed as t·km^2. In addition, the biomasses of functional groups or species groupings (organized in various groups of marine mammals, seabirds, marine turtles, elasmobranchs, pelagic and demersal fish, and invertebrates) were used to identify "winners and losers" under climate-change impact and climate-change and fisheries impacts. Results were compared (i) as integrated time series of the global ocean spatial dynamics and (ii) as time series by FAO sub-oceans, both as relative changes with time from year 1970. We also compared results (iii) as annually averaged maps for 1970–1979 and 2090–2099, from where we calculated relative changes computed as (final value-initial value)/initial value *100%. The mean and the coefficient of variation were also calculated for aggregated indicators and specific species groupings spatially. Analyses were performed with R version 3.6.3. We used R to plot all the temporal and spatial data. The "ggplot" package (Wickham et al., 2016) was used to apply a smoothing function to capture the general patterns in the temporal trends of biomass, while also reducing the noise. With this methodology, each series show a 95% confidence interval for the original lowess. The "maptools" (Bivand et al., 2020) and "raster" (Hijmans et al., 2015) packages were used to map the spatial-results.

RESULTS

Experiment 1—Ecological Configurations

Temporal Changes

Under the alternative configurations of the ecological model and the same climate-change scenario and absence of fishing, trajectories of ecological indicators resulted in moderate differences of temporal change (**Figure 2** and **Supplementary Figure 6**). Changes were small (±2%) for TSB and TCB indicators, and larger for B10, B30, and Bcom (ranging from −1.5 to +21%) (**Table 2a**). Overall, changes under configurations E-Env, E-Met, and E-Nr (**Table 1**) produced projections with small declines by 2100, while the baseline run (E-Base) and the configuration including all the ecological mechanisms (E-All) produced projections with increases by 2100 (**Table 2a**).

Spatial Changes

Our results showed spatial variability of biomass trajectories under the different ecological configurations (**Figures 3A,B** and **Supplementary Figure 7**), which was larger in tropical

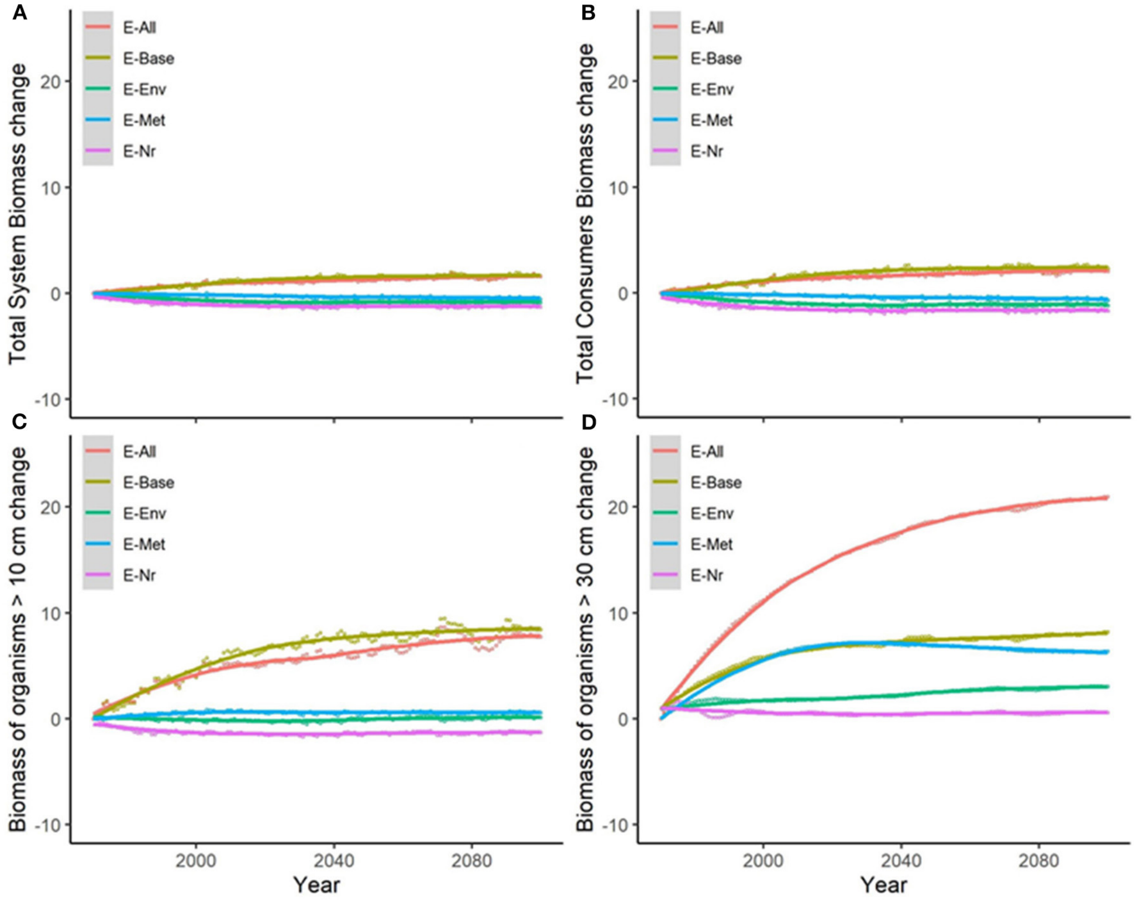

FIGURE 2 | Experiment 1 (Ecological configurations, **Table 1**)—Relative temporal change of ecological indicators (%) obtained under the different ecological configurations of the model: **(A)** Total System Biomass, **(B)** Total Consumer Biomass, **(C)** Biomass of organisms >10 cm, and **(D)** Biomass of organisms >30 cm. **Supplementary Figure 6** shows results for Biomass of commercial species.

TABLE 2 | (a) Experiment 1 (Ecological configurations, **Table 1**) and (b) Experiment 2 (Climate impacts, **Table 1**)—Temporal relative change (%) of ecological indicators between 1970 and 2100 (**Figure 2**).

	Change (%) 2100 vs. 1970								
	(a) Experiment 1					**(b) Experiment 2**			
	E-Base	**E-Env**	**E-Met**	**E-Nr**	**E-All**	**C-GFD2.6**	**C-GFDL8.5**	**C-IPSL2.6**	**C-IPSL8.5**
TSB	1.7	−0.9	−0.5	−1.3	1.6	1.6	1.7	−5.9	−11
TCB	2.3	−1.2	−0.7	−1.7	2.1	2.1	3	−9.6	−10.2
Bcom	8.7	0.1	0.5	−1.5	7.9	7.9	10.4	−12.8	−21.8
B10	8.4	0.1	0.6	−1.3	7.7	7.7	10.2	−12.7	−21.6
B30	8.2	3.1	6.4	0.6	21	21	24.3	−12.5	7.5

TSB, Total System Biomass; TCB, Total Consumers Biomass; Bcom, Biomass of commercial species; B10, Biomass of organisms > 10 cm; B30, Biomass of organisms > 30 cm.

areas (especially in the Indian and Pacific Ocean) and the Poles (**Figure 3C**). Spatial differences were evident between the different configurations of the model (**Supplementary Figure 7**), with a concentration of biomass in higher latitude areas under E-Met, and a wider spread of biomass concentrations under E-Env and E-Nr (**Table 1**). The baseline run (E-Base) presented larger concentrations in specific areas of the Indian and Atlantic Ocean, and the combination of ecological configurations (E-All) showed a gradient of biomass concentration increasing with latitude (**Figure 3C**). The average change for all five ecological configurations showed negative changes in the tropical areas and positive changes in higher latitude areas (**Figure 3D**).

Changes by Species Groups

When comparing the outcomes of the alternative configurations of the ecological model, trajectories of biomass by species groups showed larger differences than when examining aggregated ecological indicators. As an example, predicted changes of "Large reef fish" over time showed slight increases under E-Nr and E-All (+5 to +8%) (**Table 1**), and important declines under the rest of simulations (−35 to −75%) (**Figure 4A**). Simulations produced also different spatial distributions (**Supplementary Figure 8**), with larger variability between configurations in coastal areas (**Figure 4B**). Under E-All, the species tended to increase their biomass in higher latitudes (**Figure 4C**). The relative change under the five alternative configurations showed overall negative declines in coastal areas with time, with spatial variability depending on the ecological configuration underlying each run (**Supplementary Figure 9**). While under E-Env and E-Nr the declines were widely distributed, under E-Met they tended to concentrate in high latitude areas. Under E-All, they concentrated in tropical and temperate regions, and increases were projected in northern areas (**Figure 4D**).

Summary

Results from the first experiment showed that alternative configurations of the ecological model had moderate effects on aggregated ecological indicators, and larger effects on species projections, even using the same physical and primary producers data (GFDL ESM2M—Historical/RCP2.6) to drive the environmental conditions. Under the simulation that combined the different ecological configurations (E-All) results showed plausible projected patterns in terms of predicted temporal changes and the distribution of biomass of aggregated ecological indicators and of species groupings (**Supplementary Figures 7–9**).

Experiment 2—Climate Impacts

Temporal Changes

Under the different scenarios of climate-change impacts using the two ESM and RCPs scenarios, without fishing and having all ecological mechanisms enabled, trajectories of ecological indicators resulted in slight to moderate differences of temporal change (**Figure 5** and **Table 2b**). Under GFDL scenarios, relative changes were positive (from +2 to +24%, depending on the indicator). Negative changes were predicted under IPSL scenarios (from −6 to −22%) (with the exception of B30 under RCP8.5). RCP2.6 scenario showed smaller increases under GFDL model and smaller declines under IPSL. Results indicated an amplification of the effect of changes in environmental conditions with larger trophic level organisms (**Table 2b**), were the moderate negative or positive impacts of aggregated ecological indicators such as TSB or TCB (**Figures 5A,B**) were larger for Bcom, B10, and B30 (with the exception of B30 under RCP8.5) (**Figures 5C,D**).

Spatial Changes

Results showed noticeable spatial variability of TCB projections under the different climate-change scenarios (**Figure 6** and **Supplementary Figure 10**), which was smaller under GFDL and RCP2.6 scenarios and larger under IPSL and RCP8.5 ones (**Supplementary Table 2**). The Indian Ocean showed small to moderate declines under all scenarios (from −0.4 to −25%), while the Atlantic regions (including the Mediterranean) and the Central Pacific showed larger declines as we moved from GFDL to IPSL models and from 2.6 to 8.5 RCPs (going from +4 to −34%). On the contrary, the South Pacific and the Antarctic Ocean showed small to moderate increases (from +1 to +30%) (**Figure 6** and **Supplementary Table 2**). TCB showed different areas of negative and positive change depending on the runs, with overall negative changes concentrated in coastal tropical and temperate areas (especially under IPSL model) and positive changes in northern regions and open sea areas (**Figure 7**), with overall larger declines projected under IPSL (**Figures 7C,D**). Similar results were recorded for TSB, Bcom, B10, and B30 (**Supplementary Table 3**).

Changes by Species Groups

Projections of biomass by species groups resulted in moderate to large temporal differences when comparing the outcomes of the different climate-change scenarios. As an example, trajectories of "Large reef fish" with time (without fishing) showed slight increases under GFDL model and important declines under IPSL one (**Figure 8A**). Similar patterns were shown for "Small reef fish" (**Figure 8B**), and "Large sharks" (**Figure 8C**), while "Small and medium sharks" only showed negative declines under IPSL and RCP8.5 simulation (**Figure 8D**).

We observed that IPSL RCP8.5 showed the strongest and most negative effects for species groups (**Figure 9** and **Supplementary Table 4**). Under climate-change impacts, marine mammals, birds, marine turtles, and elasmobranchs showed moderate to large declines in biomass (down to −43%), with the exception of small and medium sharks and rays that showed some biomass increases under GFDL simulations (**Figure 9A**). Most large pelagic and demersal fish showed large declines as well, especially under IPSL model (with maximum declines for "Large reef fish" of −66%) (**Figures 9B,C**), with the exception of "Bathydemersal large fish" (which increased from +54 to +100%). On the contrary, medium and small demersal and pelagic fish showed mixed results, with overall increases for "Medium pelagic fishes," "Bathypelagic medium fishes," and "Benthopelagic small fish" (**Figures 9B,C**). These organisms would win under climate-change conditions and no-fishing. Regarding invertebrate groupings, clear declines were projected for "Corals" (to a max. decline of −77%) and "Soft-corals and sponges" (−56%), which decreased strongly in biomass under climate change scenarios. Mixed responses were predicted for molluscs (showing increases of +9% and declines to a max. of −19%), crustaceans and other invertebrates (increases of +60% to declines of −53% depending on the groupings), and an increase of "Other megabenthos species" (with a max of +47% increase) was projected (**Figure 9D**). Noticeable changes in spatial distributions were also observed for different functional groups, were declines where most profound under IPSL model, and for GFDL RCP8.5 scenario (see example of "Large reef fish" in **Supplementary Figures 11, 12**).

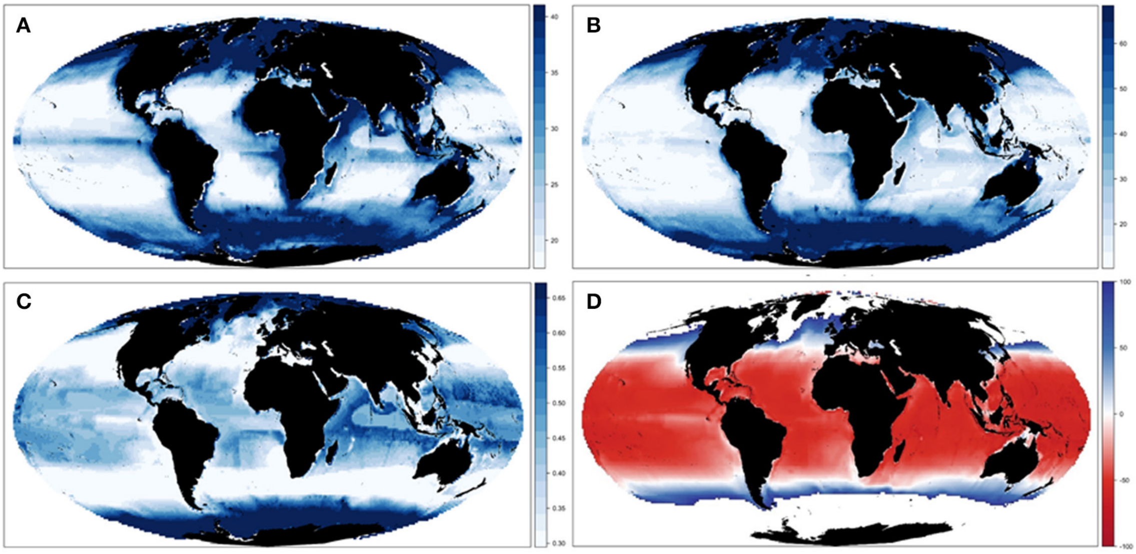

FIGURE 3 | Experiment 1 (Ecological configurations, **Table 1**)—Spatial changes of Total Consumers Biomass: **(A)** Mean spatial values across the different ecological configurations and **(B)** spatial results under configuration E-All in 2001–2005. **(C)** Coefficient of variation and **(D)** relative change across the different ecological hypotheses. For visualization purposes, maps **(A–C)** plot values between the first and third quantile.

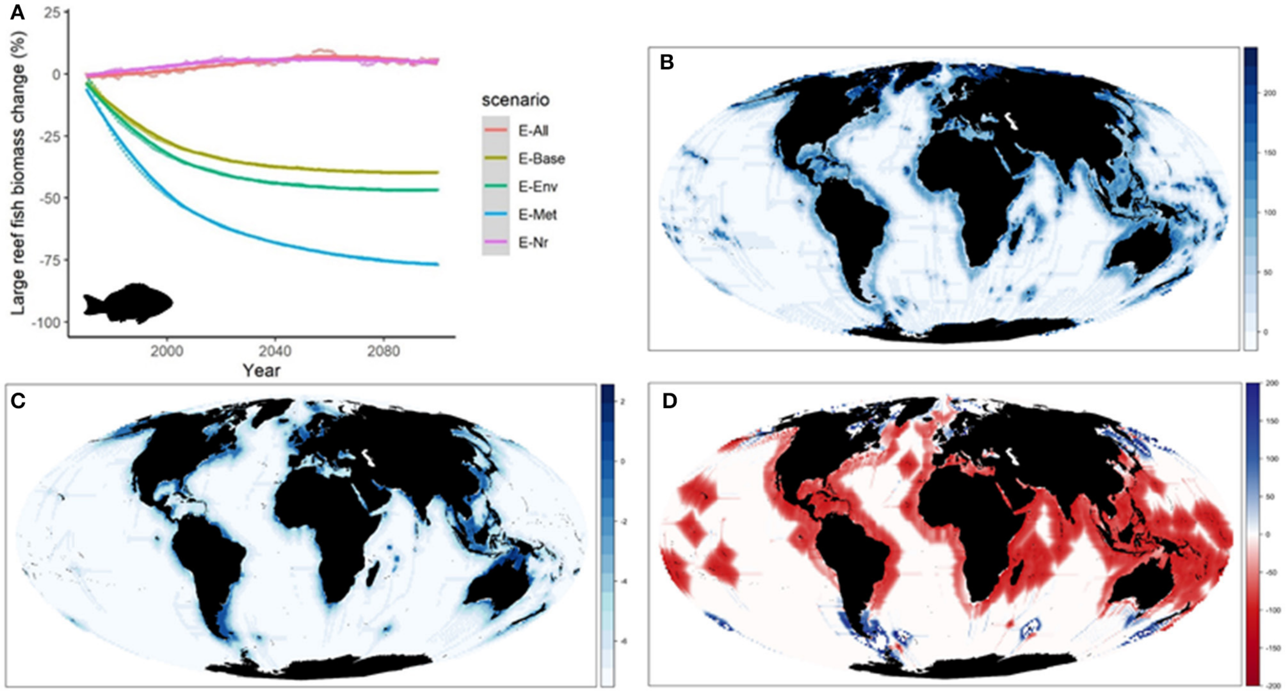

FIGURE 4 | Experiment 1 (Ecological configurations, **Table 1**)—Changes in "Large reef fish" group: **(A)** Relative temporal change of biomass (%) obtained under the different ecological configurations of the model from 1970 to 2100, **(B)** Coefficient of Variation of biomass in 2100 under the different ecological configurations, **(C)** Biomass (log10) distribution in 2100 under configuration E-All, and **(D)** Relative change (%) of biomass between 1970 and 2100 under configuration E-All (Fish images source: IAN, 2020).

Summary

Results from the second experiment showed that differences in the drivers of climate-change scenarios used under EcoOcean v2 had large impacts on ecological trajectories. The GFDL model produced, overall, less severe negative impacts than IPSL on ecological results. Climate change showed overall negative

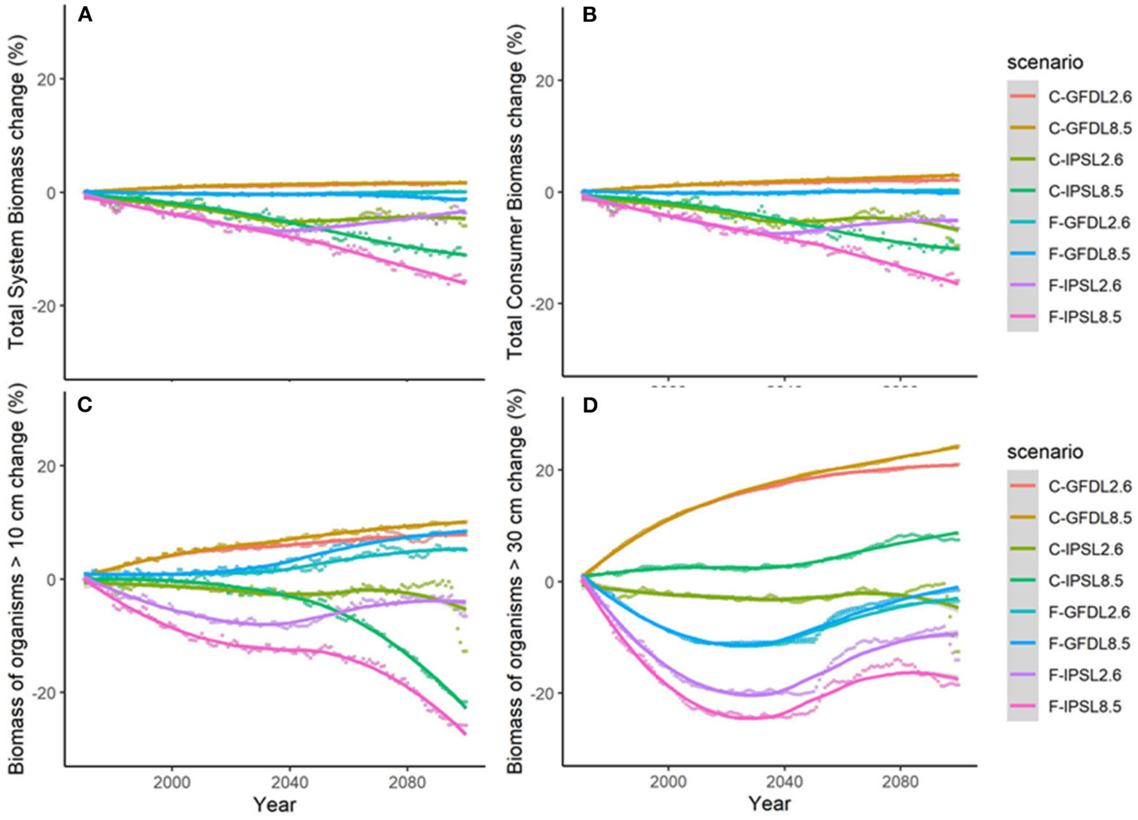

FIGURE 5 | Experiment 2 (Climate impacts) and 3 (Climate impacts and fishing impacts) (**Table 1**)—Relative temporal change of ecological indicators (%): **(A)** Total System Biomass, **(B)** Total Consumer Biomass, **(C)** Biomass of organisms >10 cm, and **(D)** Biomass of organisms >30 cm.

impacts on larger organisms, and the most pessimistic scenarios of climate impact (RCP8.5) showed the strongest negative effects. These effects were differently distributed in space, with some areas showing clear declines (Indian and Atlantic Oceans) and others showing mostly increases (Antarctic and Arctic Oceans). Climate-change impacts differently affected specific species groupings, with larger organisms showing overall negative trends and smaller organisms showing mixed or positive impacts.

Experiment 3—Climate and Fishing Impacts

Temporal Changes

Under the climate change and fishing impact experiment using the same two ESM and RCPs scenarios and including fishing, trajectories of ecological indicators resulted in smaller positive results under GFDL and larger declines under IPSL (**Figure 6**, **Table 3a**, and **Supplementary Table 5**). The exception was scenario IPSL RCP2.6, which showed the least declines for TSB, TCB, Bcom, and B10 in comparison with the non-fishing configuration.

Spatial Changes

Results showed large spatial variability of TCB trajectories under the different climate-change and fisheries runs (**Figure 10** and **Supplementary Figure 13**), which was largest under IPSL and RCP8.5 scenarios (**Table 3b** and **Supplementary Table 6**). The Central Atlantic region (including the Mediterranean) and the South Pacific showed a decline in indicators under fishing in comparison with the non-fishing configuration in all the simulations (from −0.5 to −13% and from −0.2 to −11%, respectively). This was also the case for most of the sub-regions with some exceptions under IPSL model. For example, the Antarctic regions showed larger increases of TCB under fishing when IPSL RCP2.6 was used, and the Arctic Ocean and North Atlantic when IPSL RCP2.6 and RCP8.5 were used (**Table 3b**). The average change of TCB showed different areas of negative and positive change depending on the simulation, with larger negative changes concentrated in tropical and temperate areas under IPSL, and positive changes in northern regions and open seas, and overall larger declines predicted under IPSL (**Figure 11**).

Changes by Species Groups

Trajectories of biomass by species groups resulted in moderate to large temporal differences when comparing the outcomes of the different climate-change scenarios with and without fishing (**Table 4** and **Supplementary Figure 14**). As an example, predicted changes of “Large reef fish” with time showed

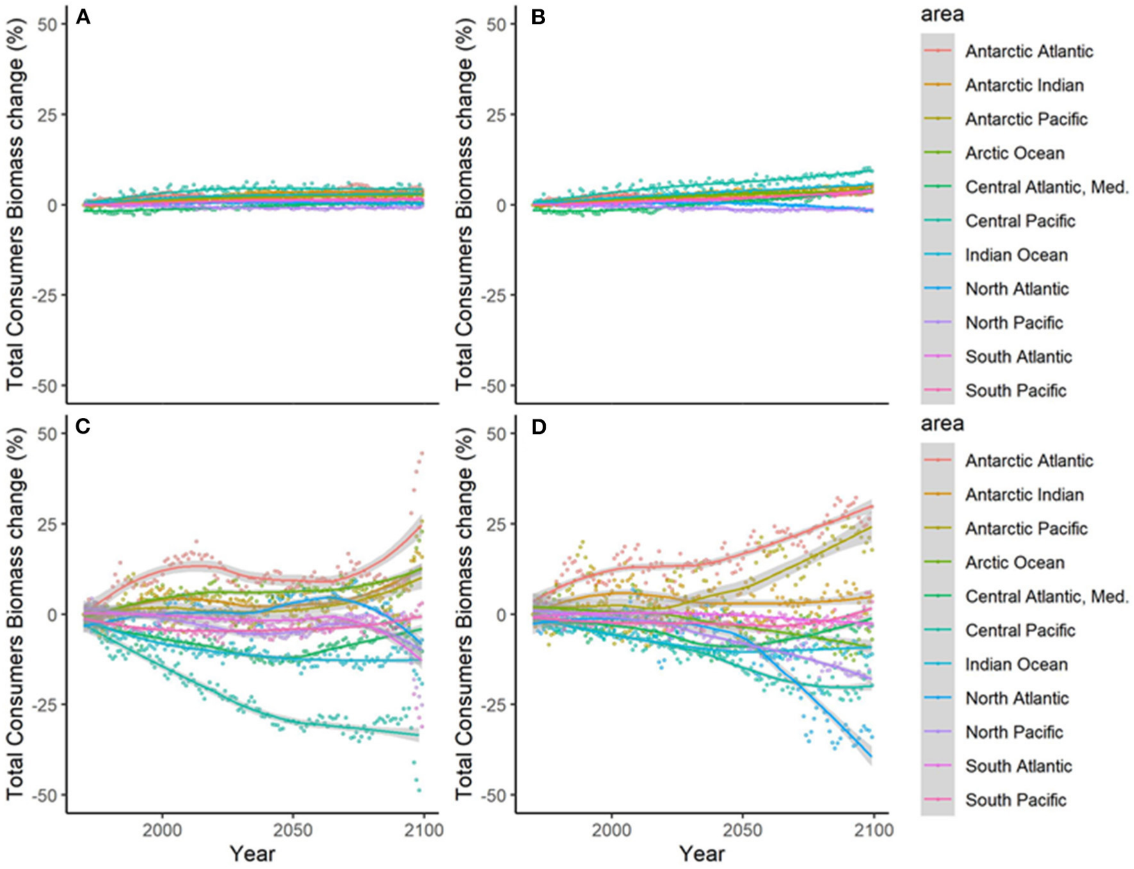

FIGURE 6 | Experiment 2 (Climate impacts, **Table 1**)—Relative temporal change of Total Consumers Biomass (%) by sub-regional oceans: **(A)** GFDL RCP2.6; **(B)** GFDL RCP8.5, **(C)** IPSL RCP2.6, and **(D)** IPSL RCP8.5.

important declines under fishing in both GFDL and IPSL models (**Figure 8A**). Similar patterns were shown for "Large sharks" (**Figure 8B**), while "Small reef fish" and "Small and medium sharks" did not show the same magnitude of declines when fishing was added, and in some cases the trends were reversed (**Figures 8C,D**).

We observed that IPSL RCP8.5 scenario showed the strongest and most negative effects for species groups (**Table 4**, **Supplementary Table 7**, and **Supplementary Figures 14, 15).** Under climate change and fisheries impacts, several species that were identified as "losers" under climate-change simulations showed higher declines. This was the case of marine mammals, birds, marine turtles, and elasmobranchs (which declined −80%), with the exception of "Small and medium sharks" under IPSL RCP2.6 (which increased +12%). Declines of biomass from pelagic and demersal fin fish were also stronger under climate change and fishing impact simulations (with declines up to −90% for "Large reef fish" and "Large pelagic fish"). In several cases, smaller species went from increasing under climate-change impacts to decreasing under the cumulative effects of climate change and fishing. This was the case of small and medium pelagic fish groups (from maximums of +7 to minimums of −40%, and max. of +68% to min. of −18%, respectively). Other species groups increased less than under climate-change impacts alone (such as "Bathypelagic medium fish" dropping from +56 to +11%, or "Bathydemersal large fish" dropping from +100 to +45%). There were a few exceptions for organisms that further benefited from fishing: this was the case of "Benthopelagic small fishes" (from −3 to +40%), which showed larger increases under the climate change and fishing simulation (**Table 4** and **Supplementary Figure 15**). Invertebrates showed a variety of mixed responses, with two groups showing clear directions of change: "Molluscs (bivalves)" showed large declines under climate change and fishing (up to −47%), and "Cephalopods" showed further increases (up to +10%) (**Supplementary Figure 14d** and **Supplementary Table 7**).

Summary

Results from the third experiment highlighted that combining climate-change and fishing impacts had mostly negative effects on both aggregated ecological indicators and the biomasses of many species groupings, especially for larger-sized species. As in the case of climate-change impact, adding fishing impacts to simulations showed similar results in terms of IPSL RCP8.5, yielding the most pessimistic results. However, some areas showed increases of biomass from a combination of climate

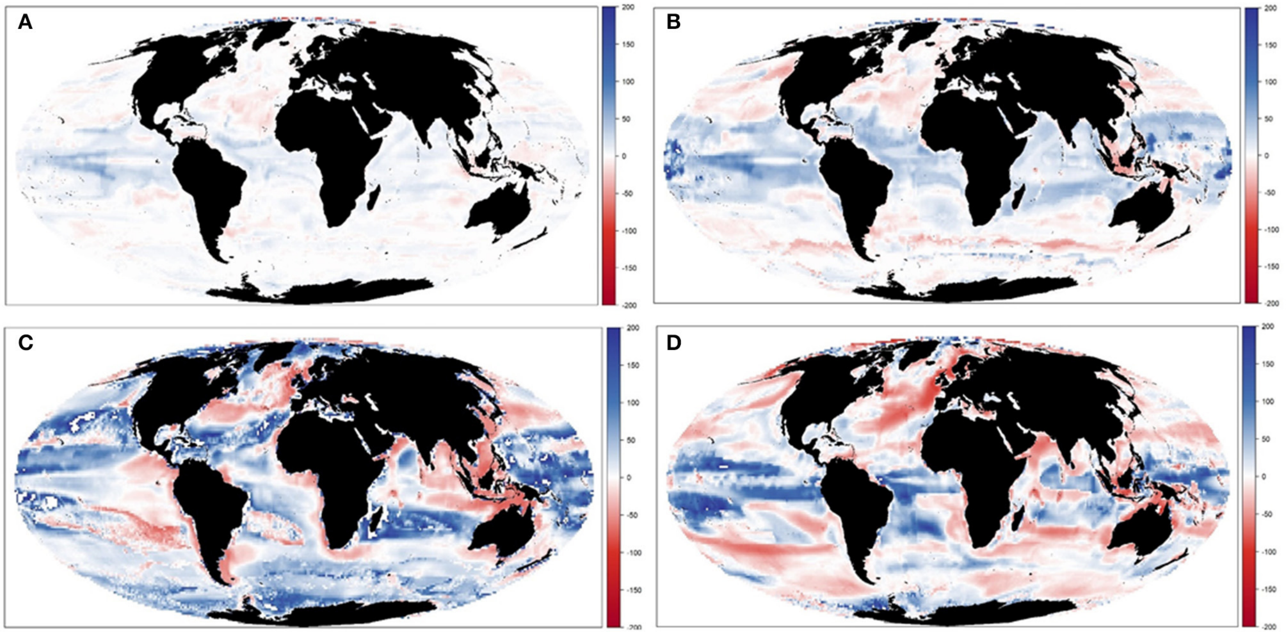

FIGURE 7 | Experiment 2 (Climate impacts, **Table 1**)—Relative spatial change of Total Consumers Biomass (%) between 1970–1979 and 2090–2099: **(A)** GFDL RCP2.6; **(B)** GFDL RCP8.5, **(C)** IPSL RCP2.6, and **(D)** IPSL RCP8.5.

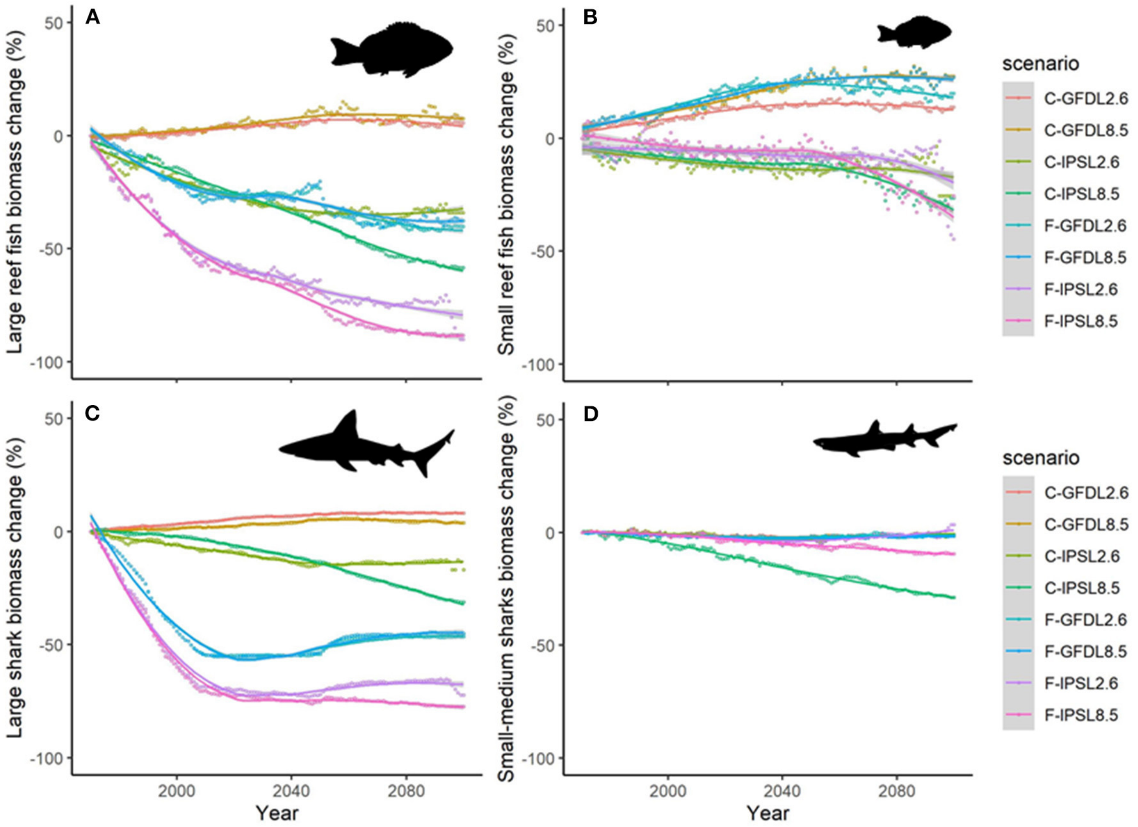

FIGURE 8 | Experiment 2 (Climate impacts) and 3 (Climate impacts and fishing impacts) (**Table 1**)—Relative temporal biomass change (%) of functional groups: **(A)** "Large reef fish", **(B)** "Small reef fish," **(C)** "Large sharks," and **(D)** "Small and medium size sharks." (Fish images source: IAN, 2020).

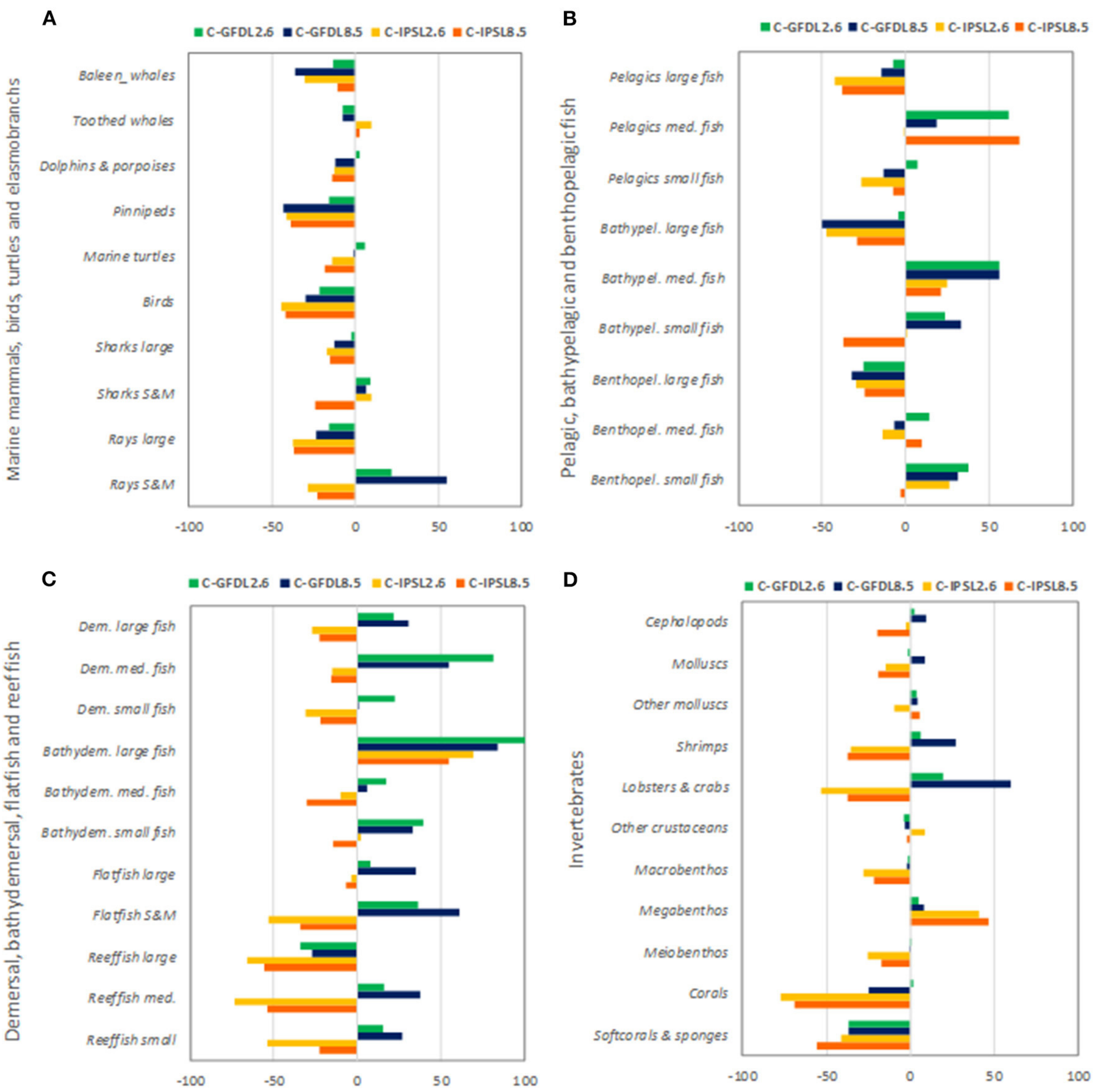

FIGURE 9 | Experiment 2 (Climate impacts, **Table 1**)—Relative temporal biomass change (%) between 1970 and 2100 by species groupings: **(A)** Marine mammals, seabirds, marine turtles, and elasmobranchs, **(B)** Pelagic, bathypelagic, and benthopelagic fish, **(C)** Demersal, bathydemersal, flatfish, and reef fish, and **(D)** Invertebrates.

change and fishing impacts (Arctic, Antarctic, and North Atlantic) and some smaller-sized organisms showed advantages, such as "Small benthopelagic fish" and "Cephalopods."

DISCUSSION

We presented a new version of the modeling complex EcoOcean to represent the global marine ecosystem. EcoOcean v2 advances marine ecosystem analyses under multiple and cumulative stressors while explicitly considering species distributions and spatial-temporal food-web dynamics.

We explored the capabilities and sensitivity of the modeling complex through three experiments. We quantified how predicted ecological indicators and species biomasses were influenced by (i) the alternative configurations of specific ecological mechanisms within the ecosystem model, (ii) alternative sets of environmental drivers of climate change accounting for variability in two ESM outputs and RCPs, and (iii) considering human impacts in the form of fishing in addition to climate change.

Our study shows that alternative configurations of the ecological model can have noticeable effects on ecological projections. They were moderate for aggregated ecological indicators such as Total System Biomass (TSB) and Total Consumers Biomass (TCB) and changes in indicators frequently showed similar direction of change. These results stress the importance of model structural uncertainty in EcoOcean v2, as has been previously illustrated for other modeling initiatives

TABLE 3 | Comparison of experiment 2 (Climate impacts) and 3 (Climate and fishing impacts) (**Table 1**)—(a) Temporal relative change (%) of ecological indicators between 1970 and 2100, and (b) of Total Consumers Biomass (TCB %) under the climate and fishing impact (**Figure 10**) compared to the climate impact simulations by sub-regional ocean (**Figure 6**).

	Change (%) 2100 vs 1970			
	GFDL2.6 with f./wo f.	GFDL8.5 with f./wo f.	IPSL2.6 with f./wo f.	IPSL8.5 with f./wo f.
a) Aggregated indicators				
TSB	-1.5	-2.9	2.3	-4.6
TCB	-1.8	-3.2	3.1	-5.7
Bcom	-2.6	-1.4	6.1	-3.9
B10	-2.6	-1.7	6.2	-4.2
B30	-24.5	-25.8	-1.5	-26.0
b) TCB by sub-ocean				
Arctic Ocean	-1.7	-1.4	12.2	11.8
North Atlantic	-1.8	-2.1	13.4	14.8
Central Atlantic, Med	-1.7	-3.8	-0.5	-13.2
South Atlantic	-1.1	-4.1	0.6	-11.8
North Pacific	0.0	-2.5	-3.6	-10.0
Indian Ocean	-1.3	-2.1	-0.6	0.5
Central Pacific	-0.9	-2.6	8.4	-36.3
South Pacific	-1.4	-5.3	-0.2	-11.2
Antarctic Atlantic	-3.0	-2.4	18.1	-11.9
Antarctic Indian	-2.2	-2.5	11.3	1.3
Antarctic Pacific	-2.1	-3.9	13.9	-12.5

TSB, Total System Biomass; TCB, Total Consumers Biomass; Bcom, Biomass of commercial species; B10, Biomass of organisms >10 cm; B30, Biomass of organisms >30 cm; With f., with fishing; wo f., without fishing. Red shade indicates decline of the indicators, while blue shade indicates an increase.

(Cheung et al., 2016a; Payne et al., 2016) and when multiple ecosystem models with different setups have been compared (Tittensor et al., 2018; Lotze et al., 2019). The use of aggregated indicators to capture ecological processes at the global level is a practical choice to limit the associated uncertainty of different working hypotheses within complex mechanistic models. These aggregated indicators have been used in recent studies under the Fish-MIP initiative to assess marine animal biomass trajectories under climate change (Tittensor et al., 2018; Lotze et al., 2019).

Effects of structural uncertainty became more evident when looking at indicators that represented larger organisms within the global food web (such as Biomass of organisms larger than 10 or 30 cm, B10 and B30, and Biomass of commercial species, Bcom), or specific species groupings. Our results suggest that informative projections to investigate changes in marine biodiversity must be accompanied by transparent statements about the ecological mechanisms behind model configurations. Community-based ensemble modeling initiatives such as Fish-MIP (Tittensor et al., 2018; Lotze et al., 2019) are designed to capture and compare structural modeling uncertainty deriving from the structural differences of participating Marine Ecosystem Models (MEMs). We believe that transparency about model configuration and ensemble approaches to scenario testing should become the norm for global ecosystem analyses such as the ones performed under IPCC and IPBES (Brondizio et al., 2019; IPCC, 2019).

For the second and third experiment, we used the "full configuration" of EcoOcean v2 in conjunction with different approaches toward climate and fishing. Enabling all ecological mechanisms allowed the model to consider species' responses to fluctuating environmental conditions in combination with affinity for more stable habitats. It also allowed the modeling complex to initialize species to their observed native ranges, from where they could move freely if nearby conditions were to become more suitable. Our first foray into Q_{10} dynamics enabled the modeling complex some measure of spatial differentiation for growth and production ratios as a function of a near-evolutionary scale average global temperatures. These combined ecological mechanisms produced results that were closer to what we should expect considering historical observations in the distribution of biomass of aggregated ecological indicators and the ecological knowledge of species groupings, while they were also comparable to projections from other modeling initiatives (Lotze et al., 2019).

Our results showed important changes in marine organism biomass distributions, and in ecosystem structure, under various scenarios of climate change. Trends of our projections were in agreement with the vast scientific literature (e.g., Hollowed et al., 2013; Barange et al., 2014; Gattuso et al., 2015; Lotze et al., 2019). Different ESMs and RCPs scenarios had notable impact on EcoOcean projections: while GFDL ESM-2M Hist&RCP scenarios produced more optimistic results, IPSL CMA5-LR Hist&RCP resulted in more pessimistic ones. Simulations under worst-case RCP8.5 emission pathways had extensive (and mostly negative) impacts on ecological properties of the marine ecosystem, while simulations under the most stringent RCP2.6 emission pathways did not experience such large negative effects. This is due to the differences in predicted trends of climate-change effects by the different ESM and RCPs, such as on temperature and phytoplankton growth, which have unique direct and indirect impacts throughout the marine food web (Lotze et al., 2019), and which are mediated by differential growth and consumption rates (Christensen and Walters, 2004). Overall, the impacts of alternative climate-change effects on ecological trajectories were similar or up to a magnitude higher than structural modeling uncertainty. This illustrates that the effect of ESM outputs is at least as important as internal model uncertainty for MEM outputs (e.g., Lotze et al., 2019).

The projected impacts of climate change were unevenly distributed: while some areas showed clear declines (such as the Indian and Atlantic Oceans), others showed increases (Antarctic Ocean). In agreement with previous data analyses and modeling studies, our results suggest that as climate change intensifies, the coastal areas around the tropics and subtropics may become less suitable for a range of species that will disappear from these areas and may be moving to cooler regions (Sunday et al., 2012; Jones and Cheung, 2015; Poloczanska et al., 2016; Bryndum-Buchholz et al., 2019; Link and Watson, 2019; Reygondeau, 2019).

Larger organisms showed overall negative trends, being identified as the "losers" of climate change. Their declines could be mostly attributed to dwindling prey and reduced environmental suitability (Pinsky et al., 2013; Poloczanska et al., 2016). On the contrary, many smaller organisms showed mixed and at times clearly positive impacts—the climate-change "winners." Some of these smaller organisms benefited from the declines of larger organisms through a reduction in predation pressure, and from density-dependent processes and competition releases as previously illustrated at regional scales (Coll et al.,

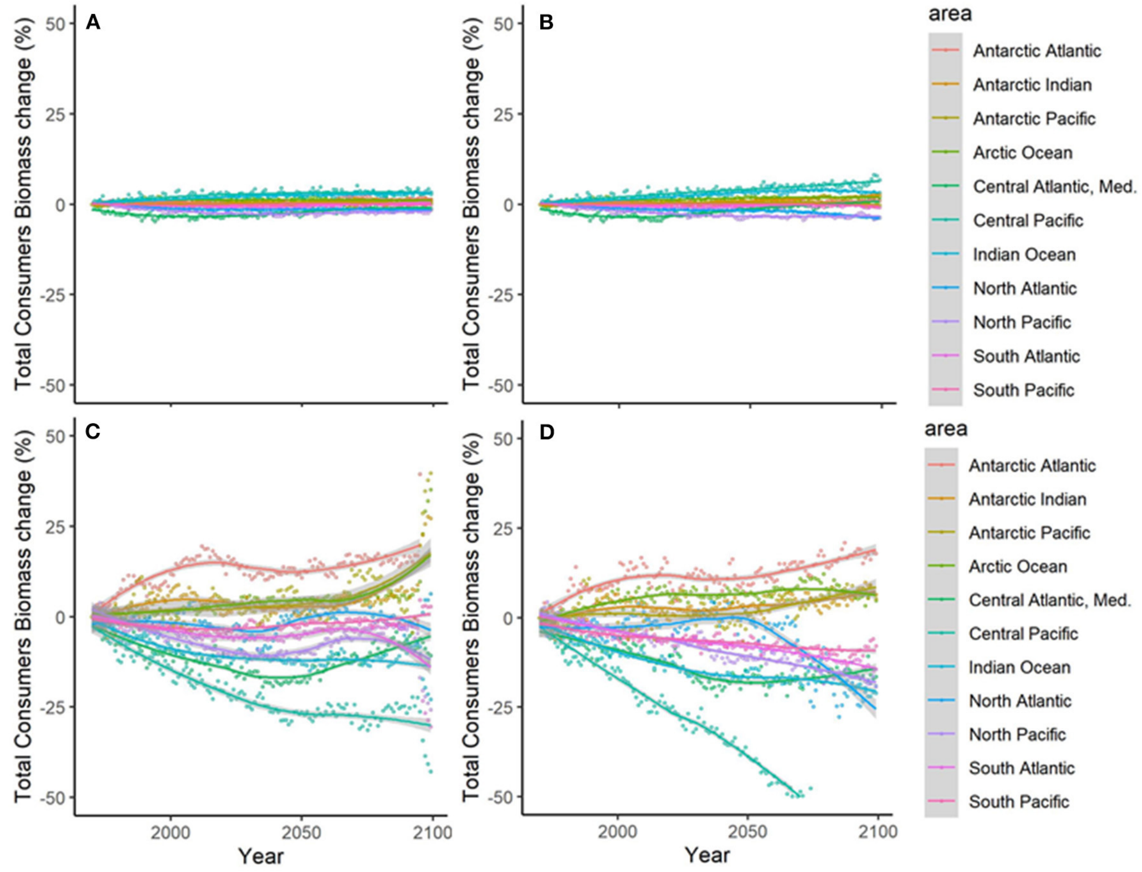

FIGURE 10 | Experiment 3 (Climate impacts and fishing impacts, **Table 1**)—Relative temporal change of Total Consumers Biomass (%) by sub-regional oceans: **(A)** GFDL RCP2.6; **(B)** GFDL RCP8.5, **(C)** IPSL RCP2.6, and **(D)** IPSL RCP8.5.

2008b; Brown et al., 2010; Fulton, 2011). These outcomes illustrate that assessment of the impacts of climate change on marine biodiversity, even in a hypothetical non-fished ocean, should include species interactions to account for non-linear and often surprising consequences (Brown et al., 2010; Fulton, 2011; Fernandes et al., 2013; Christensen et al., 2015). Our results may provide special relevant insights into climate effects on biomass dynamics of data deficient species groupings such as invertebrates (Poloczanska et al., 2016). These results can be of relevance to adapt management strategies and monitoring under a context of climate change.

Our analysis to evaluate how climate-driven responses differed between a hypothetically non-fished and a fished ocean showed that the effect of fishing was mostly negative on aggregated ecological indicators and on the biomass of many—especially larger—species groupings. Fishing generally worsened the conditions already impacted by climate change, even in the cases where climate change benefitted specific groupings of species. These findings are in line with results from a size-based modeling exercise (Blanchard et al., 2012). GFDL ESM-2M Hist&RCP scenarios consistently produced more optimistic results than IPSL CMA5-LR Hist&RCP ones, and RCP8.5 showed the most extreme and mostly negative impacts on ecological projections. Therefore, our results were in agreement with previous studies that show how fishing did not substantially alter the negative direction of climate change effects when looking at total marine animal biomass (Lotze et al., 2019). In addition, the temporal trends for aggregated indicators showed that the additional effect of fishing on climate was not always purely linear but could be non-linear, amplifying the effects of climate, as shown in regional modeling simulations (Fu et al., 2020).

When we analyzed our results by sub-oceans, a larger diversity of cumulative effects of climate change and fishing was observed. Several areas showed further declines of net animal biomass when fishing under climate-change impacts. Some areas, in contrast, showed lower declines or even (modest) gains in total system biomass. In these areas, such as the North Atlantic, fishing has historically been targeting larger organisms and their reduction could have produced a positive effect on mid and small-sized animals through reductions in predation mortality and resource competition (Mackinson et al., 2009; Planque et al., 2010). Increases in catch potential projected in areas of the North Atlantic Ocean (Barange et al., 2014; Peck and Pinnegar, 2019) coincides with our findings.

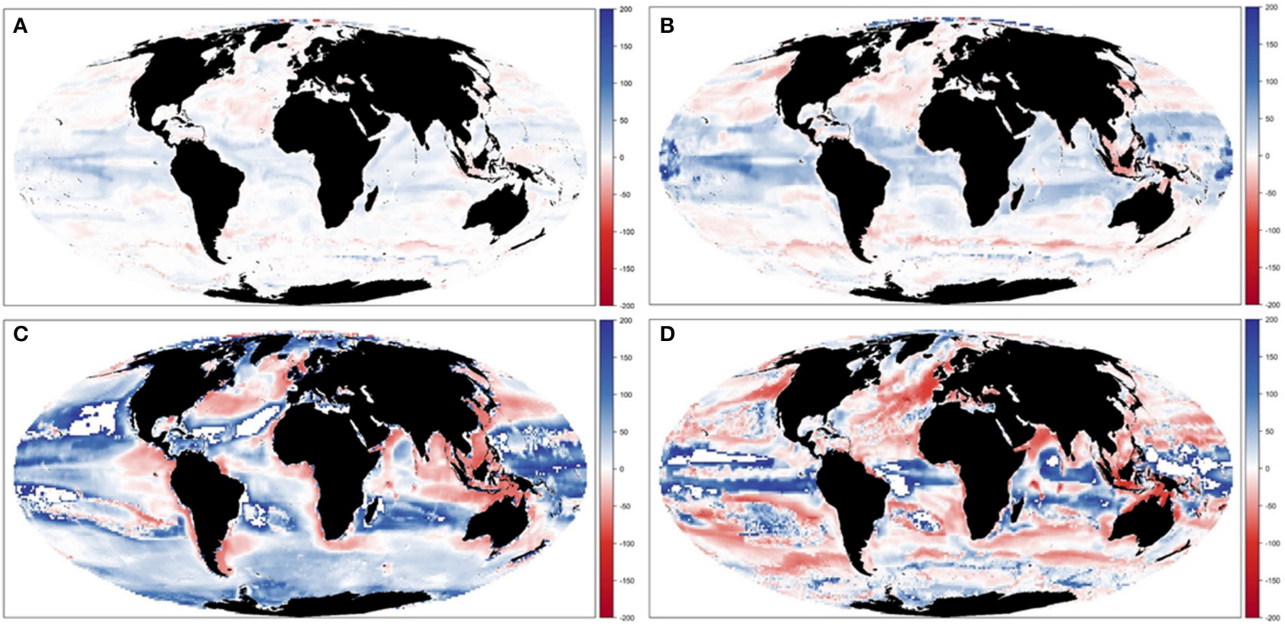

FIGURE 11 | Experiment 3 (Climate impacts and fishing impacts, **Table 1**)—Relative spatial change of Total Consumers Biomass (%) between 1970–1979 and 2090–2099: **(A)** GFDL RCP2.6; **(B)** GFDL RCP8.5, **(C)** IPSL RCP2.6, and **(D)** IPSL RCP8.5.

Species grouping also showed heterogenic responses to climate change and fishing. In essence, we identified four main population responses: (1) losers under climate change that lost more under climate and fishing ("losers that lost more"), (2) winners under climate change that won less under cumulative impacts of climate and fisheries ("winners that won less"), (3) winners under climate change that became losers under cumulative impacts ("winners that became losers"), and (4) winners under climate change that further benefited from fishing impacts ("winners that kept winning"). The "losers that lost more" were mainly large-sized organisms, which have shown historical declines due to fishing (e.g., Christensen et al., 2003; Myers and Worm, 2003). In addition, several organisms that benefited from the impact of climate effects alone "won less" or "became losers" under cumulative effects of climate and fishing. These results illustrate that global fisheries have a negative effect on marine biodiversity and ecosystems in addition to climate change (e.g., Pauly et al., 2002; Worm et al., 2006; Cury and Miserey, 2008; Christensen and Maclean, 2011; Link and Watson, 2019). This is in part related to the spatial congruence and increasing cumulative impact between multiple stressors (Halpern et al., 2015, 2019).

The groups of "Cephalopods" and "Benthopelagic small fish" species were identified to win in a warmer and exploited ecosystem ("winners that kept winning"). This result is especially relevant for monitoring and adaptive management approaches since these groups could become global indicators of cumulative effects of climate and fishing (they could be our "canaries in the environmentally changing marine coal mine"). Our results are in line with a previous global analyses of long-term trends in cephalopod abundance, which showed that cephalopods have increased consistently across taxa from 1960s to 2010 (Doubleday et al., 2016). Modeling studies at local and regional levels showed that cephalopods play a strong ecosystem role (Eddy et al., 2017). Squids, for example, are able to benefit from a general increase in fishing pressure, mainly due to predation release, and exhibit quick responses to changes triggered by the environment, and as such, are very sensitive to changes in fishing and climate change (Coll et al., 2013). Despite this projection of a global increase, cephalopods encompass a large diversity in species, with contrasting ecological strategies (Coll et al., 2013; de la Chesnais et al., 2019). Therefore, differential responses between species of the cephalopod group are expected at the local and regional level (Fulton, 2011).

Benthopelagic small fish are a highly heterogenic group of fishes that live and feed near the bottom of the ocean as well as in midwaters or near the surface and are mostly unexploited. Under climate and fishing impacts they could benefit from a large plasticity, and are able to use different resources from benthic and zooplanktonic organisms, in addition to benefitting from predation release when larger organisms decline. Hypothetically, these organisms are well-positioned to adapt to large changes in the ocean, as previously projected (Christensen et al., 2015), but still too little is known about them. Another interesting result is that "Bathypelagic small fish," where small mesopelagic fish are included, showed limited biomass increases under both climate and fishing. However, a slight decline is observed under IPSL CMA5-LR RCP8.5 scenario. These results are relevant in the light of their important biomass and key role in supporting the marine ecosystems (Irigoien et al., 2014) and the current discussion about their potential for exploitation vs. sensitivity to cumulative impacts (Hidalgo and Browman, 2019; Martin et al., 2020).

TABLE 4 | Comparison of Experiment 2 (Climate impacts) and 3 (Climate and fishing impacts) (**Table 1**)—Temporal Change (%) of biomass by functional groups obtained under the climate and fishing impact (**Supplementary Figure 14**) compared to the climate impact simulations (**Figure 9**).

	Change (%) 2100 vs 1970			
	GFDL2.6	GFDL8.5	IPSL2.6	IPSL8.5
	with f./wo f.	with f./wo f.	with f./wo f.	with f./wo f.
Baleen_whales	-28.7	-2.7	23.5	-31.7
Toothed whales	2.2	-3.0	-12.8	-19.4
Dolphins & porpoises	-14.4	-8.6	-6.6	-32.1
Pinnipeds	-15.6	-5.1	-12.8	-14.1
Marine turtles	-5.2	-1.6	-9.9	-9.9
Birds	-6.9	-7.3	-12.5	-17.2
Sharks large	-59.4	-47.9	-57.7	-64.4
Sharks S&M	-3.0	-0.5	2.3	19.7
Rays large	-28.7	-26.3	-33.9	-34.3
Rays S&M	-31.1	-39.7	-20.5	-13.4
Pelagics large adults	-66.9	-60.8	-44.8	-51.1
Pelagics med. fish	-72.4	-25.9	-13.6	-85.5
Pelagics small fish	-35.8	-13.9	-8.6	-32.0
Bathypel. large fish	-47.2	-1.0	35.4	-31.0
Bathypel. med. fish	-9.0	0.4	16.5	-10.1
Bathypel. small fish	1.2	0.3	13.7	-4.3
Benthopel. large fish	-39.1	-30.6	-39.8	-47.8
Benthopel. med. fish	-26.7	-2.1	10.8	-24.9
Benthopel. small fish	0.8	2.0	8.5	13.0
Dem. large fish	-63.6	-61.9	-46.9	-44.9
Dem. med. fish	-36.8	-27.1	-26.4	-12.2
Dem. small fish	-20.1	-16.1	-13.7	-7.0
Bathydem. large fish	-16.7	-0.1	0.5	-9.0
Bathydem. med. fish	-1.2	0.6	2.7	11.6
Bathydem. small fish	-3.1	2.0	7.2	7.4
Flatfish large	-16.1	-20.2	-39.2	-10.6
Flatfish S&M	-17.7	-19.7	-21.3	-10.8
Reeffish large	-26.9	-31.8	-24.2	-32.4
Reeffish med.	-29.3	-30.5	-11.8	-19.8
Reeffish small	4.9	0.5	12.8	-1.1
Cephalopods	1.2	-0.1	10.4	19.1
Molluscs	-33.3	-31.6	-31.9	-9.1
Other molluscs	-0.2	0.1	1.9	-4.5
Shrimps	-13.8	-15.4	-10.4	11.5
Lobsters & crabs	-2.7	-2.3	-3.0	15.3
Other crustaceans	-0.6	0.1	0.3	2.7
Macrobenthos	0.6	-0.2	-4.7	7.8
Megabenthos	2.7	0.8	16.1	-35.1
Meiobenthos	-0.4	0.1	1.9	4.8
Corals	0.7	0.1	-3.0	-3.2
Softcorals & sponges	21.6	0.0	-11.1	1.5

Red shade indicates decline of the indicators, while blue shade indicates an increase.

Overall, our results illustrate a variety of complex responses of the marine ecosystem to significant levels of climate change and fishing impacts, which will differ depending on the area and organisms' size and ecology, and can be amplified higher up in the marine food web intensifying predominantly negative impacts. Therefore, cumulative effects of climate change and fisheries can produce a mosaic of "winners," "losers" and ecological surprises due to synergies, trade-offs, and differential growth and consumption rates of species within food webs (Christensen, 1996; Fulton, 2011; Travis et al., 2014). Identifying, at the global level, which species may decline or benefit from cumulative effects of fishing and climate impacts is highly relevant for policy, although regional and local studies are needed to assess these dynamics in detail, at scales relevant to local ecological and management objectives (e.g., Fulton, 2011; Travers-Trolet et al., 2014).

Our findings underscore that under a pessimistic scenario of climate change (RCP 8.5) and with the current fishing impact projected to be maintained to the future, the majority of marine organisms will show declining trends. These results confirm the current concern about the overall unsustainable levels of global change impacts on marine ecosystems (Gattuso et al., 2015; Díaz et al., 2020) and the need for measures to ensure viable and productive fishing activities in the ocean (Barange et al., 2018). They illustrate the need to act on the implementation of sustainable management options of natural resources, and the effective mitigation and adaptation actions to balance the use and conservation of the natural capital (Duarte et al., 2020).

FUTURE WORK

With regards to the alternative configurations of EcoOcean, future studies should further investigate the effects of alternative or complementary ecological mechanisms to advance our understanding of structural model uncertainty (Planque et al., 2011; Payne et al., 2016). For example, future improvements should consider the use of multiple Q_{10} multipliers in accordance to an expanding body of work (Lefevre et al., 2017), and could incorporate hypotheses of adaptation through evolutionary processes (O'Connor et al., 2012; Miller et al., 2018) and applications of the concept to planktonic groups (Laufkötter et al., 2015). Future iterations could also consider a refinement of cell-specific responses to environmental change based on new theoretical and data analyses (Bernhardt et al., 2018; Burrows et al., 2019), or EcoOcean could drive the internal niche model with outputs from dedicated and independent niche models (Jones and Cheung, 2015; Cheung et al., 2016a; Kaschner et al., 2016; Coll et al., 2019). Last, we could improve our assumptions about species presence by connecting with modeling techniques dedicated to predicting global species distributions under scenarios of environmental change (e.g., Reygondeau, 2019).

Our assessment of climate-change impacts on the global marine ecosystem could be improved by adding additional biodiversity resolution to species groupings and explicitly consider the ecological roles that habitat forming species such as corals, seagrasses, kelp, and other macro-algae play in marine ecosystems, where they can modify direct and indirect ecological interactions (Lotze et al., 2011; Dambacher et al., 2015). The consequences of winners and losers from an ecosystem functioning point of view should be further investigated to assess if the role of species groupings may shift at the global level, as they have been observed to do at regional scales (Bates et al., 2014). In addition, the three-dimensional nature of the ocean is a key feature of the marine ecosystem (Behrenfeld et al., 2019). Our modeling complex indirectly represents the third dimension of depth by vertically stratifying species groupings, their interactions, and the flows of energy and matter. However, the vertical use of the water column may be altered by climate change and future exploitation (Brito-Morales et al., 2020; Jorda et al., 2020; Martin et al., 2020). As new insights into these still underexplored deep-sea habitats become available, future iterations of our work may have to revisit the representation of processes that take place in the water column.

Future iterations of this modeling exercise should include additional physical changes in the ocean to better represent localized stressors such as change in ice cover at high latitude areas that can profoundly affect both the lowest and highest trophic levels of the food web (Stroeve et al., 2012; Wang and Overland, 2012); changes in hypoxic or oxygen-minimum zones and their expansions, which is especially relevant for the tropics (Schmidtko et al., 2017; Breitburg et al., 2018); and changes in ocean pH that can be of special relevance to areas such as the North Atlantic (Peck and Pinnegar, 2019). We should also consider the additional range of mitigation targets after the release of the Shared Socioeconomic Pathways, SSPs (Rogelj et al., 2018), namely RCP1.9, RCP3.4, and RCP7.0., and new outputs of ESMs under CMIP6 (Eyring et al., 2016). Especially relevant is the evaluation of the more ambitious target of RCP 1.9 as the new pathway that focusses on limiting global warming below 1.5°C, the goal of the Paris Agreement (Cheung et al., 2016b; IPCC, 2018).

Future iterations of EcoOcean v2 should also be subjected to rigorous model skill assessments (Olsen et al., 2016). This is still a general Achilles heel of spatial-temporal MEMs, where compounding factors such as their complex parameterization, long run times, and limited access to distributed computing facilities and observational data mean that full uncertainty assessments are rarely undertaken (Hollowed et al., 2013; Fulton et al., 2019; Heymans et al., 2020).

A strength of EcoOcean is that the fishing component is explicitly modeled through fishing fleet dynamics that include the interactions between bio-economics of fishing and the abundance and accessibility to marine resources (Walters et al., 1999). Future interactions of this study will invest in revisiting and complementing the fisheries model. For example, we will update to new versions of catch and fishing effort datasets (Watson, 2017; Watson and Tidd, 2018), new data on illegal, unreported, and unregulated catches, global demands and impacts of marine aquaculture (Pauly and Zeller, 2016; Davies et al., 2019; FAO, 2020) and projections of seafood demand (e.g., Maury et al., 2017; FishMIP—ISIMIP, 2020). Future studies can include the further characterization of ecosystem overfishing at the global level (Coll et al., 2008a; Link and Watson, 2019) and the exploration of alternative pathways to reduce it and avoid it. Our modeling complex could be further complemented with additional anthropogenic impacts such as habitat loss due to the degradation of the deep sea (Mengerink et al., 2014) and marine pollution and eutrophication (Halpern et al., 2015). Past and current spatial-temporal management tools can be now explicitly incorporated in the simulations at any time due to the new management model (**Figure 1**).

In addition to enhancing the predictive capabilities of EcoOcean v2, and of MEMs in general, the main degradation patterns highlighted by studies such as ours show that the scientific community needs to move toward deploying MEMs to test future scenarios of management and evaluate plausible ecosystem responses. EcoOcean v2 is ready to be used to test alternative plausible actions toward protection, mitigation and adaptation actions (e.g., Gownaris et al., 2019; Jones et al., 2020), and eventually, inform about combined effects of plausible ocean-based solutions to global change (Gattuso et al., 2018).

DATA AVAILABILITY STATEMENT

All data inputs to EcoOcean v2 are either freely available as online databases or available under request from data providers. Results from the 13 runs of EcoOcean v2 presented in this study are available upon request to the lead author. The source code of EcoOcean is available under request to the lead author within a collaborative framework.

AUTHOR CONTRIBUTIONS

MC, JS, VC, and CW designed research. MC, JS, MP, and VC performed research and analyzed data. All authors wrote the paper.

FUNDING

This study received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 817578 (TRIATLAS project). Additional financial support was provided by the German Federal Ministry of Education and Research through the Inter-Sectorial Impact Model Intercomparison Project (ISIMIP, Grant 01LS1201A1). HL further acknowledges funding by the Natural Sciences and Engineering Research Council (NSERC) of Canada (RGPIN-2014-04491). DT acknowledges support from the Jarislowsky Foundation. VC received support from the Natural Sciences and Engineering Research Council of Canada (NSERC), Discovery Grant RGPIN-2019-04901.

ACKNOWLEDGMENTS

The authors acknowledge the key contribution of the Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP) from the Inter-Sectorial Impact Model Intercomparison Project (ISIMIP). Specifically, they would like to thank L. Bopp, J. Dunne, C. Stock, and T. Roy for providing ESM outputs, and M. Büchner, J. Volkholz, and J. Schewe for technical support. They also thank Mary O'Connor for discussions about scaling due to temperature effects, and Cristina Garilao for assistance with AquaMaps modeling.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.567877/full#supplementary-material

REFERENCES

Abson, D. J., Fischer, J., Leventon, J., Newig, J., Schomerus, T., Vilsmaier, U., et al. (2017). Leverage points for sustainability transformation. *Ambio* 46, 30–39. doi: 10.1007/s13280-016-0800-y

Ahrens, R. N. M., Walters, C. J., and Christensen, V. (2012). Foraging arena theory. *Fish Fisher.* 13, 41–59. doi: 10.1111/j.1467-2979.2011.00432.x

Alder, J., Guénette, S., Beblow, J., Cheung, W., and Christensen, V. (2007). Ecosystem-based global fishing policy scenarios. *Fisher. Centre Res. Rep.* 15:93. doi: 10.14288/1.0074764

Anticamara, J., Watson, R., A, G., and Pauly, D. (2011). Global fishing effort (1950-2010): trends, gaps, and implications. *Fisher. Res.* 107, 131–136. doi: 10.1016/j.fishres.2010.10.016

Barange, M., Bahri, T., Beveridge, M. C., Cochrane, K. L., Funge-Smith, S., and Poulain, F. (2018). "Impacts of climate change on fisheries and aquaculture. Synthesis of current knowledge, adaptation and mitigation options," in *FAO Fisheries and Aquaculture Technical Paper No. 627.* (Rome: FAO), 628.

Barange, M., Merino, G., Blanchard, J., Scholtens, J., Harle, J., Allison, E., et al. (2014). Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nat. Clim. Chang.* 4, 211–216. doi: 10.1038/nclimate2119

Barraclough, T. G. (2015). How do species interactions affect evolutionary dynamics across whole communities? *Annu. Rev. Ecol. Evol. Syst.* 46, 25–48. doi: 10.1146/annurev-ecolsys-112414-054030

Bates, A. E., Barrett, N. S., Stuart-Smith, R. D., Holbrook, N. J., Thompson, P. A., and Edgar, G. J. (2014). Resilience and signatures of tropicalization in protected reef fish communities. *Nat. Clim. Chang.* 4, 62–67. doi: 10.1038/nclimate2062

Beaugrand, G., and Kirby, R. R. (2018). How do pelagic species respond to climate change? Theories and observations. *Ann. Rev. Mar. Sci.* 10, 169–197. doi: 10.1146/annurev-marine-121916-063304

Behrenfeld, M. J., Gaube, P., Della Penna, A., O'Malley, R. T., Burt, W. J., Hu, Y., et al. (2019). Global satellite-observed daily vertical migrations of ocean animals. *Nature* 576, 257–261. doi: 10.1038/s41586-019-1796-9

Bernhardt, J. R., Sunday, J. M., Thompson, P. L., and O'Connor, M. I. (2018). Nonlinear averaging of thermal experience predicts population growth rates in a thermally variable environment. *Proc. R Soc. B Biol. Sci.* 285:20181076. doi: 10.1101/247908

Bivand, R., Lewin-Koh, N., Pebesma, E., Archer, E., Baddeley, A., Bearman, N., et al. (2020). *Package 'maptools'*. Available online at: https://cranr-projectorg/web/packages/maptools/maptoolspdf

Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., et al. (2012). Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Phil. Trans. R Soc. B Biol. Sci.* 367, 2979–2989. doi: 10.1098/rstb.2012.0231

Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., and Finnegan, S. (2013). Climate change and the past, present, and future of biotic interactions. *Science* 341, 499–504. doi: 10.1126/science.1237184

Bonan, G. B., and Doney, S. C. (2018). Climate, ecosystems, and planetary futures: The challenge to predict life in Earth system models. *Science* 359:eaam8328. doi: 10.1126/science.aam8328

Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., et al. (2013). Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences* 10, 6225–6245. doi: 10.5194/bg-10-6225-2013

Bradbury, I. R., Laurel, B., Snelgrove, P. V. R., Bentzen, P., and Campana, S. E. (2008). Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proc. Biol. Sci.* 275, 1803–1809. doi: 10.1098/rspb.2008.0216

Brander, K. (2015). Improving the reliability of fishery predictions under climate change. *Curr. Clim. Change Rep.* 1, 40–48. doi: 10.1007/s40641-015-0005-7

Breitburg, D. L., Levin, L. A., Oschlies, A., Grégoire, M., Chavez, F. P., Conley, D. G., et al. (2018). Declining oxygen in the global ocean and coastal waters. *Science* 359:eaam7240. doi: 10.1126/science.aam7240

Brito-Morales, I., Schoeman, D. S., Garcia Molinos, J., Burrowns, M. T., Klein, C. J., Arafeh-Dalmau, N., et al. (2020). Climate velocity reveals increasing exposure of deep-ocean biodiversity to future warming. *Nat. Clim. Chang.* 10, 576–581. doi: 10.1038/s41558-020-0773-5

Brondizio, E., Settele, J., Díaz, S., and Ngo, H. (2019). *Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.* Bonn: IPBES Secretariat.

Brown, C. J., Fulton, E. A., Hobday, A. J., Matear, R. J., Possingham, H. P., Bulman, C., et al. (2010). Effects of climate driven primary production change on marine food webs: implications for fisheries and conservation. *Glob. Chang. Biol.* 16, 1194–1212. doi: 10.1111/j.1365-2486.2009.02046.x

Bryndum-Buchholz, A., Tittensor, D., Blanchard, J., Cheung, W., Coll, M., Galbraith, E. D., et al. (2019). 21st century climate change impacts on marine animal biomass and ecosystem structure across ocean basins. *Glob. Chang. Biol.* 25, 459–472. doi: 10.1111/gcb.14512

Burrows, M. T., Bates, A. E., Costello, M. J., Edwards, M., Edgar, G. J., Fox, C. J., et al. (2019). Ocean community warming responses explained by thermal affinities and temperature gradients. *Nat. Clim. Chang.* 9, 959–963. doi: 10.1038/s41558-019-0631-5

CBD (2013). *Convention on Biological Diversity.* Available online at: http://www.cbd.int (accessed August 1, 2020).

Cheung, W. W., Jones, M. C., Reygondeau, G., Stock, C. A., Lam, V. W., and Frölicher, T. L. (2016a). Structural uncertainty in projecting global fisheries catches under climate change. *Ecol. Model.* 325, 57–66. doi: 10.1016/j.ecolmodel.2015.12.018

Cheung, W. W., Reygondeau, G., and Frölicher, T. L. (2016b). Large benefits to marine fisheries of meeting the 1.5 C global warming target. *Science* 354, 1591–1594. doi: 10.1126/science.aag2331

Christensen, V. (1996). Managing fisheries involving predator and prey species. *Rev. Fish Biol. Fish* 6, 417–442. doi: 10.1007/BF00164324

Christensen, V., Coll, M., Buszowski, J., Cheung, W., Frölicher, T., Steenbeek, J., et al. (2015). The global ocean is an ecosystem: Simulating marine life and fisheries. *Glob. Ecol. Biogeogr.* 24 507–517. doi: 10.1111/geb.12281

Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., and Walters, C. J. (2014). Representing variable habitat quality in a spatial food web model. *Ecosystems* 17, 1397–1412. doi: 10.1007/s10021-014-9803-3

Christensen, V., Guenette, S., Heymans, J. J., Walters, C., Watson, R., Zeller, D., et al. (2003). Hundred-year decline of North Atlantic predatory fishes. *Fish Fisher.*4, 1–24. doi: 10.1046/j.1467-2979.2003.00103.x

Christensen, V., and Maclean, J. (2011). *Ecosystem Approaches to Fisheries: A Global Perspective*. Cambridge: Cambridge University Press.

Christensen, V., and Walters, C. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model.* 72, 109–139. doi: 10.1016/j.ecolmodel.2003.09.003

Christensen, V., Walters, C. J., Ahrens, R., Alder, J., Buszowski, J., Christensen, L. B., et al. (2009). Database-driven models of the world's large Marine ecosystems. *Ecol. Model.* 220, 1984–1996. doi: 10.1016/j.ecolmodel.2009.04.041

Claudet, J., Bopp, L., Cheung, W. W., Devillers, R., Escobar-Briones, E., Haugan, P., et al. (2020). A roadmap for using the UN decade of ocean science for sustainable development in support of science, policy, and action. One *Earth* 2, 34–42. doi: 10.1016/j.oneear.2019.10.012

Coll, M., Libralato, S., Tudela, S., Palomera, I., and Pranovi, F. (2008a). Ecosystem overfishing in the Ocean. *PLoS ONE* 3:e3881. doi: 10.1371/journal.pone.0003881

Coll, M., Navarro, J., Olson, R., and Christensen, V. (2013). Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. *Deep Sea Res. II Top. Stud. Oceanogr.* 95, 21–36. doi: 10.1016/j.dsr2.2012.08.020

Coll, M., Palomera, I., Tudela, S., and Dowd, M. (2008b). Food-web dynamics in the South Catalan Sea ecosystem (NW Mediterranean) for 1978-2003. *Ecol. Model.* 217, 95–116. doi: 10.1016/j.ecolmodel.2008.06.013

Coll, M., Pennino, M. G., Sole, J., Steenbeek, J., and Bellido, J. M. (2019). Predicting marine species distributions: complementarity of food-web and Bayesian hierarchical modelling approaches. *Ecol. Model.* 405, 86–101. doi: 10.1016/j.ecolmodel.2019.05.005

Coll, M., Steenbeek, J., Sole, J., Palomera, I., and Christensen, V. (2016). Modelling the cumulative spatial-temporal effects of environmental factors and fishing in a NW Mediterranean marine ecosystem. *Ecol. Model.* 331, 100–114. doi: 10.1016/j.ecolmodel.2016.03.020

Colloff, M. J., Lavorel, S., Kerkhoff, L. E., Wyborn, C. A., Fazey, I., Gorddard, R., et al. (2017). Transforming conservation science and practice for a postnormal world. *Conserv. Biol.* 31, 1008–1017. doi: 10.1111/cobi.12912

Cury, P., and Miserey, Y. (2008). *Une mer Sans Poissons.* Paris: Calmann-Lévy.

Dambacher, J. M., Rothlisberg, P. C., and Loneragan, N. R. (2015). Qualitative mathematical models to support ecosystem-based management of Australia's Northern prawn fishery. *Ecol. Appl.* 25, 278–298. doi: 10.1890/13-2030.1

Davies, I. P., Carranza, V., Froehlich, H. E., Gentry, R. R., Kareiva, P., and Halpern, B. S. (2019). Governance of marine aquaculture: pitfalls, potential, and pathways forward. *Marine Policy* 104, 29–36. doi: 10.1016/j.marpol.2019.02.054

de la Chesnais, T., Fulton, E. A., Tracey, S. R., and Pecl, G. T. (2019). The ecological role of cephalopods and their representation in ecosystem models. *Rev. Fish Biol. Fish.* 29, 313–334. doi: 10.1007/s11160-019-09554-2

Díaz, S., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., et al. (2020). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Bonn: IPBES secretariat. doi: 10.5281/zenodo3553579

Doubleday, Z. A., Prowse, T. A., Arkhipkin, A., Pierce, G. J., Semmens, J., Steer, M., et al. (2016). Global proliferation of cephalopods. *Curr. Biol.* 26, R406–R407. doi: 10.1016/j.cub.2016.04.002

Drakou, E. G., Pendleton, L., Effron, M., Ingram, J. C., and Teneva, L. (2017). When ecosystems and their services are not co-located: oceans and coasts. *ICES J. Marine Sci.* 74, 1531–1539. doi: 10.1093/icesjms/fsx026

Duarte, C. M., Agusti, S., Barbier, E., Britten, G. L., Castilla, J. C., Gattuso, J.-P., et al. (2020). Rebuilding marine life. *Nature* 580, 39–51.

du Pontavice, H., Gascuel, D., Reygondeau, G., Maureaud, A., and Cheung, W. W. L. (2020). Climate change undermines the global functioning of marine food webs. *Glob. Change Biol.* 26, 1306–1318. doi: 10.1111/gcb.14944

Eddy, T. D., Lotze, H. K., Fulton, E., Coll, M., Ainsworth, C. H., Neves de Araújo, J., et al. (2017). Ecosystem effects of invertebrate fisheries. *Fish Fish.* 18, 40–53. doi: 10.1111/faf.12165

Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J., et al. (2016). Overview of the coupled model intercomparison project phase 6 (CMIP6) experimental design and organization. *Geosci. Model Dev.* 9, 1937–1958. doi: 10.5194/gmd-9-1937-2016

FAO (2019). "Report of the expert meeting on other effective area-based conservation measures in the marine capture fishery sector," in *FAO Fisheries and Aquaculture Report No.* 1301 (Rome), 74.

FAO (2020). *The State of World Fisheries and Aquaculture*. Rome.

Fernandes, J. A., Cheung, W. W., Jennings, S., Butenschön, M., Mora, L., Frölicher, T. L., et al. (2013). Modelling the effects of climate change on the distribution and production of marine fishes: accounting for trophic interactions in a dynamic bioclimate envelope model. *Glob. Chang. Biol.* 19, 2596–2607. doi: 10.1111/gcb.12231

Fernandes, J. A., Kay, S., Hossain, M. A., Ahmed, M., Cheung, W. W., Lazar, A. N., et al. (2015). Projecting marine fish production and catch potential in Bangladesh in the 21st century under long-term environmental change and management scenarios. *ICES J. Marine Sci.* 73, 1357–1369. doi: 10.1093/icesjms/fsv217

FishMIP—ISIMIP (2020). *Fisheries and Marine Ecosystem Model Intercomparison Project.* Available online at: https://www.isimip.org/about/marine-ecosystems-fisheries/ (accessed August 1, 2020).

Fu, C., Xu, Y., Grüss, A., Bundy, A., Shannon, J. L., Heymans, J. J., et al. (2020). Responses of ecological indicators to fishing pressure under environmental change: exploring nonlinearity and threshold. *ICES J Marine Sci.* 77, 1516–1531. doi: 10.1093/icesjms/fsz182

Fulton, B., Blanchard, J., Melbourne-Thomas, J., Plagányi, E. E., and Tulloch, V. J. D. (2019). Where the ecological gaps remain, a modelers' perspective. *Front. Ecol. Evol.* 7:424. doi: 10.3389/fevo.2019.00424

Fulton, E. (2011). Interesting times: winners, losers, and system shifts under climate change around Australia. *ICES J. Marine Sci.* 68, 1329–1342. doi: 10.1093/icesjms/fsr032

Fulton, E. A. (2010). Approaches to end-to-end ecosystem models. *J. Marine Syst.* 81, 171–183. doi: 10.1016/j.jmarsys.2009.12.012

Fulton, E. A., Boschetti, F., Sporcic, M., Jones, T., Little, L. R., Dambacher, J. M., et al. (2015). A multi-model approach to engaging stakeholder and modellers in complex environmental problems. *Environ. Sci. Policy* 48, 44–56. doi: 10.1016/j.envsci.2014.12.006

Galbraith, E., Carozza, D., and Bianchi, D. (2017). A coupled human-Earth model perspective on long-term trends in the global marine fishery. *Nat. Commun.* 8:14884. doi: 10.1038/ncomms14884

Gattuso, J.-P., Magnan, A., Billé, R., Cheung, W. W., Howes, E. L., Joos, F., et al. (2015). Contrasting futures for ocean and society from different anthropogenic CO_2 emissions scenarios. *Science* 349:aac4722. doi: 10.1126/science.aac4722

Gattuso, J.-P., Magnan, A. K., Bopp, L., Cheung, W. W., Duarte, C. M., Hinkel, J., et al. (2018). Ocean solutions to address climate change and its effects on marine ecosystems. *Front. Marine Sci.* 5:337. doi: 10.3389/fmars.2018.00337

Gownaris, N. J., Santora, C. M., Davis, J. B., and Pikitch, E. (2019). Gaps in protection of important ocean areas: a spatial meta-analysis of ten global mapping initiatives. *Front. Marine Sci.* 6:650. doi: 10.3389/fmars.2019.00650

Halpern, B. S., Frazier, M., Afflerbach, J., Lowndes, J. S., Micheli, F., O'Hara, C., et al. (2019). Recent pace of change in human impact on the world's ocean. *Sci. Rep.* 9:11609. doi: 10.1038/s41598-019-47201-9

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., et al. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nat. Commun.* 6:7615. doi: 10.1038/ncomms8615

Heymans, J. J., Bundy, A., Christensen, V., Coll, M., de Mutsert, K., Fulton, E., et al. (2020). The ocean decade: a true ecosystem modelling challenge. *Front. Mar. Sci.* 554573. doi: 10.3389/fmars.2020.554573

Hidalgo, M., and Browman, H. I. (2019). Developing the knowledge base needed to sustainably manage mesopelagic resources. *ICES Journal of Marine Science* 7, 609–615. doi: 10.1093/icesjms/fsz067

Hijmans, R. J., Van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A., et al. (2015). *Package 'raster'*. R package 734. Available online at: https://cran.r-project.org/web/packages/raster/raster.pdf

Hoegh-Guldberg, O., and Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science* 328, 1523–1528. doi: 10.1126/science.1189930

Hoegh-Guldberg, O., Northrop, E., and Lubchenco, J. (2019). The ocean is key to achieving climate and societal goals. *Science* 365, 1372–1374. doi: 10.1126/science.aaz4390

Hollowed, A. B., Barange, M., Beamish, R. J., Brander, K., Cochrane, K., Drinkwater, K., et al. (2013). Projected impacts of climate change on marine fish and fisheries. *ICES J. Marine Sci.* 70, 1023–1037. doi: 10.1093/icesjms/fst081

IAN(2020). *IAN Symbol Libraries*. Available online at: https://ian.umces.edu/symbols/ (accessed August 1, 2020).

IPCC (2018). *Global Warming of 1.5° C: An IPCC Special Report on the Impacts of Global Warming of 1.5°C Above Pre-Industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty*. Intergovernmental Panel on Climate Change. Available online at: https://www.ipcc.ch/site/assets/uploads/sites/2/2019/06/SR15_Full_Report_Low_Res.pdf

IPCC (2019). "IPCC special report on the ocean and cryosphere in a changing climate," in *Working Group II Technical Support Unit Intergovernmental Panel on Climate Change*, eds H.- O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, M. Nicolai, A. Okem, J. Petzold, B. Rama, and N. Weyer. Available online at: https://www.ipcc.ch/site/assets/uploads/sites/3/2019/12/SROCC_FullReport_FINAL.pdf

Irigoien, X., Klevjer, T. A., Røstad, A., Martinez, U., Boyra, G., Acuña, J., et al. (2014). Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nat. Commun.* 5:4271. doi: 10.1038/ncomms4271

Jennings, S., and Collingridge, K. (2015). Predicting consumer biomass, size-structure, production, catch potential, responses to fishing and associated uncertainties in the world's marine ecosystems. *PLoS ONE* 10:e0133794. doi: 10.1371/journal.pone.0133794

Jones, K. R., Klein, C. J., Grantham, H. S., Possingham, H. P., Halpern, B. S., Burgess, N. D., et al. (2020). Area requirements to safeguard Earth's marine species. One *Earth* 2, 188–196. doi: 10.1016/j.oneear.2020.01.010

Jones, M. C., and Cheung, W. W. (2015). Multi-model ensemble projections of climate change effects on global marine biodiversity. *ICES J. Marine Sci.* 72, 741–752. doi: 10.1093/icesjms/fsu172

Jorda, G., Marbà, N., Bennett, S., Santana-Garcon, J., Agusti, S., and Duarte, C. M. (2020). Ocean warming compresses the three-dimensional habitat of marine life. *Nat. Ecol. Evol.* 4, 109–114. doi: 10.1038/s41559-019-1058-0

Kaschner, K., Kesner-Reyes, K., Garilao, C., Rius-Barile, J., Rees, T., and Froese, R. (2016). *AquaMaps: Predicted Range Maps for Aquatic Species.* World Wide Web Electronic Publication. Available online at: www.aquamaps.org, (accessed August 1, 2020).

Koenigstein, S., Mark, F. C., Gößling-Reisemann, S., Reuter, H., and Poertner, H. O. (2016). Modelling climate change impacts on marine fish populations: process-based integration of ocean warming, acidification and other environmental drivers. *Fish Fish.* 17, 972–1004. doi: 10.1111/faf.12155

Kroodsma, D. A., Mayorga, J., Hochberg, T., Miller, N. A., Boerder, K., Ferretti, F., et al. (2018). Tracking the global footprint of fisheries. *Science* 359, 904–908. doi: 10.1126/science.aao5646

Laufkötter, C., Vogt, M., Gruber, N., Aita-Noguchi, M., Aumont, O., Bopp, L., et al. (2015). Drivers and uncertainties of future global marine primary production in marine ecosystem models. *Biogeosciences* 12, 6955–6984. doi: 10.5194/bg-12-6955-2015

Lavergne, S., Mouquet, N., Thuiller, W., and Ronce, O. (2010). Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annu. Rev. Ecol. Evol. Syst.* 41, 321–350. doi: 10.1146/annurev-ecolsys-102209-144628

Lefevre, S. (2016). Are global warming and ocean acidification conspiring against marine ectotherms? A meta-analysis of the respiratory effects of elevated temperature, high CO2 and their interaction. *Conserv. Physiol.* 4:ow009. doi: 10.1093/conphys/cow009

Lefevre, S., McKenzie, D. J., and Nilsson, G. E. (2017). Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. *Glob. Chang. Biol.* 23, 3449–3459. doi: 10.1111/gcb.13652

Levin, L., and Le Bris, N. (2015). The deep ocean under climate change. *Science* 350, 766–768. doi: 10.1126/science.aad0126

Link, J., and Watson, R. A. (2019). Global ecosystem overfishing: clear delineation within real limits to production. *Sci. Adv.* 5:eaav0474. doi: 10.1126/sciadv.aav0474

Link, J. S., Pranovi, F., Libralato, S., Coll, M., Christensen, V., Solidoro, C., et al. (2015). Emergent properties delineate marine ecosystem perturbation and recovery. *Trends Ecol. Evol.* 30, 649–661. doi: 10.1016/j.tree.2015.08.011

Lotze, H. K., Coll, M., Magera, M. A., Ward-Paige, C., and Airoldi, L. (2011). Recovery of marine animal populations and ecosystems. *Trends Ecol. Evol.* 26, 595–605. doi: 10.1016/j.tree.2011.07.008

Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. L., Galbraith, E. D., et al. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc. Natl. Acad. Sci. U.S.A.* 116, 12907–12912. doi: 10.1073/pnas.1900194116

Lubchenco, J., and Grorud-Colvert, K. (2015). Making waves: the science and politics of ocean protection. *Science* 350, 382–383. doi: 10.1126/science.aad5443

Mackinson, S., Daskalov, G., Heymans, J. J., Neira, S., Arancibia, H., Zetina-Rejón, M., et al. (2009). Which forcing factors fit? Using ecosystem models to investigate the relative influence of fishing and changes in primary productivity on the dynamics of marine ecosystems. *Ecol. Model.* 220, 2972–2987. doi: 10.1016/j.ecolmodel.2008.10.021

Martell, S. J., Essington, T. E., Lessard, B., Kitchell, J. F., Walters, C. J., and Boggs, C. H. (2005). Interactions of productivity, predation risk, and fishing effort in the efficacy of marine protected areas for the central Pacific. *Can. J. Fish. Aquat. Sci.* 62, 1320–1336. doi: 10.1139/f05-114

Martin, A., Boyd, P., Buesseler, K., Cetinic, I., Claustre, H., Giering, S., et al. (2020). The oceans' twilight zone must be studied now, before it is too late. *Nature* 580, 26–28. doi: 10.1038/d41586-020-00915-7

Maury, O. (2010). An overview of APECOSM, a spatialized mass balanced "Apex Predators ECOSystem Model" to study physiologically structured tuna population dynamics in their ecosystem. *Prog. Oceanogr.* 84, 113–117. doi: 10.1016/j.pocean.2009.09.013

Maury, O., Camplingc, L., Arrizabalaga, H., Aumont, O., Bopp, L., Merino, G., et al. (2017). From shared socio-economic pathways (SSPs) to oceanic system pathways (OSPs): building policy-relevant scenarios for global oceanic ecosystems and fisheries. *Glob. Environ. Change* 45, 203–216. doi: 10.1016/j.gloenvcha.2017.06.007

McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., and Warner, R. R. (2015). Marine defaunation: animal loss in the global ocean. *Science* 347, 247–256. doi: 10.1126/science.1255641

Mengerink, K., Van Dover, C., Ardron, J., Baker, M., Escobar-Briones, E., Gjerde, K., et al. (2014). A call for deep-ocean stewardship. *Science* 344, 696–698. doi: 10.1126/science.1251458

Miller, D. D., Ota, Y., Sumaila, U. R., Cisneros-Montemayor, A. M., and Cheung, W. W. (2018). Adaptation strategies to climate change in marine systems. *Glob. Chang. Biol.* 24, e1–e14. doi: 10.1111/gcb.13829

Myers, R. A., and Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283. doi: 10.1038/nature01610

Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. A., and Loeuille, N. (2012). Eco-evolutionary responses of biodiversity to climate change. *Nat. Clim. Chang.* 2, 747–751. doi: 10.1038/nclimate1588

O'Connor, M. I., Holding, J. M., Kappel, C. V., Duarte, C. M., Brander, K., Brown, C. J., et al. (2015). Strengthening confidence in climate change impact science. *Glob. Ecol. Biogeogr.* 24, 64–76. doi: 10.1111/geb.12218

O'Connor, M. I., Selig, E. R., Pinsky, M. L., and Altermatt, F. (2012). Toward a conceptual synthesis for climate change responses. *Glob. Ecol. Biogeogr.* 21, 693–703. doi: 10.1111/j.1466-8238.2011.00713.x

Olsen, E., Fay, G., Gaichas, S., Gamble, R., Lucey, S., and Link, J. S. (2016). Ecosystem model skill assessment. Yes we can! *PLoS ONE* 11:e0146467. doi: 10.1371/journal.pone.0146467

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37, 637–669. doi: 10.1146/annurev.ecolsys.37.091305.110100

Pauly, D., Christensen, V., Guenette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., et al. (2002). Towards sustainability in world fisheries. *Nature* 418, 689–695. doi: 10.1038/nature01017

Pauly, D., and Palomares, M. L. D. (2010). An empirical equation to predict annual increases in fishing efficiency. *Fisheries Centre Working Paper Series Book 07* (Vancouver, BC).

Pauly, D., and Zeller, D. (2016). Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat. Commun.* 7:10244. doi: 10.1038/ncomms10244

Payne, M. R., Barange, M., Cheung, W. W., MacKenzie, B. R., Batchelder, H. P., Cormon, X., et al. (2016). Uncertainties in projecting climate-change impacts in marine ecosystems. *ICES J. Marine Sci.* 73, 1272–1282. doi: 10.1093/icesjms/fsv231

Peck, M., and Pinnegar, J. K. (2019). "Chapter 5: Climate change impacts, vulnerabilities and adaptations: North Atlantic and Atlantic Arctic marine fisheries," in *Impacts of Climate Change on Fisheries and Aquaculture*, eds M. Barange, T. Bahri, M. Beveridge, K. Cochrane, S. Funge-Smith, and F. Poulain (Rome: FAO).

Peck, M. A., Arvanitidis, C., Butenschön, M., Canu, D. M., Chatzinikolaou, E., Cucco, A., et al. (2016). *Projecting Changes in the Distribution and Productivity of Living Marine Resources: A Critical Review of the Suite of Modelling Approaches Used in the Large European Project Vectors.* Estuarine: Coastal and Shelf Science.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., et al. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355:eaai9214. doi: 10.1126/science.aai9214

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science* 308, 1912–1915. doi: 10.1126/science.1111322

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., and Levin, S. A. (2013). Marine taxa track local climate velocities. *Science* 341, 1239–1242. doi: 10.1126/science.1239352

Planque, B., Bellier, E., and Loots, C. (2011). Uncertainties in projecting spatial distributions of marine populations. *ICES J. Marine Sci.* 68, 1045–1050. doi: 10.1093/icesjms/fsr007

Planque, B., Fromentin, J. M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., et al. (2010). How does fishing alter marine populations and ecosystems sensitivity to climate? *J. Marine Syst.* 79, 403–417. doi: 10.1016/j.jmarsys.2008.12.018

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., et al. (2013). Global imprint of climate change on marine life. *Nat. Clim. Chang.* 3, 919–925. doi: 10.1038/nclimate1958

Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., et al. (2016). Responses of marine organisms to climate change across oceans. *Front. Marine Sci.* 3:62. doi: 10.3389/fmars.2016.00062

Polovina, J. J. (1984). Model of a coral-reef ecosystem 1. The ecopath model and its application to French Frigate Shoals. *Coral Reefs* 3, 1–11. doi: 10.1007/BF00306135

Rao, K. P., and Bullock, T. H. (1954). Q10 as a function of size and habitat temperature in poikilotherms. *Am. Nat.* 88, 33–44. doi: 10.1086/281806

Reygondeau, G. (2019). "Chapter 9: Current and future biogeography of exploited marine exploited groups under climate change," in *Predicting Future Oceans: Sustainability of Ocean and Human Systems Amidst Global Environmental Change,* eds A. Cisneros-Montemayor, W. L. Cheung, and Y. Ota (Cambridge, MA: Elsevier).

Roberts, C. M., O'Leary, B. C., McCauley, D. J., Cury, P. M., Duarte, C. M., Lubchenco, J., et al. (2017). Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl. Acad. Sci. U.S.A.* 114, 6167–6175. doi: 10.1073/pnas.1701262114

Rogelj, J., Popp, A., Calvin, K. V., Luderer, G., Emmerling, J., Gernaat, D., et al. (2018). Scenarios towards limiting global mean temperature increase below 1.5 C. *Nat. Clim. Chang.* 8, 325. doi: 10.1038/s41558-018-0091-3

Rousseau, Y., Watson, R. A., Blanchard, J. L., and Fulton, E. A. (2019). Evolution of global marine fishing fleets and the response of fished resources. *Proc. Natl. Acad. Sci. U.S.A.* 116, 12238–12243. doi: 10.1073/pnas.1820344116

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., et al. (2000). Biodiversity - global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774. doi: 10.1126/science.287.5459.1770

Scheffers, B. R., De Meester, L., Bridge, T. C., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., et al. (2016). The broad footprint of climate change from genes to biomes to people. *Science* 354: aaf7671. doi: 10.1126/science.aaf7671

Schmidtko, S., Stramma, L., and Visbeck, M. (2017). Decline in global oceanic oxygen content during the past five decades. *Nature* 542, 335–339. doi: 10.1038/nature21399

Steenbeek, J., Buszowski, J., Christensen, V., Akoglu, E., Aydin, K., Ellis, N., et al. (2016). Ecopath with Ecosim as a model-building toolbox: source code capabilities, extensions, and variations. *Ecol. Model.* 319, 178–189. doi: 10.1016/j.ecolmodel.2015.06.031

Steenbeek, J., Coll, M., Gurney, L., Melin, F., Hoepffner, N., Buszowski, J., et al. (2013). Bridging the gap between ecosystem modeling tools and geographic information systems: driving a food web model with external spatial–temporal data. *Ecol. Model.* 263, 139–151. doi: 10.1016/j.ecolmodel.2013.04.027

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S., and Lima, M. (2002). Ecological effects of climate fluctuations. *Science* 297, 1292–1296. doi: 10.1126/science.1071281

Stock, C. A., Dunne, J. P., and John, J. G. (2014). Global-scale carbon and energy flows through the marine planktonic food web: an analysis with a coupled physical–biological model. *Prog. Oceanogr* 120, 1–28. doi: 10.1016/j.pocean.2013.07.001

Stroeve, J. C., Serreze, M. C., Holland, M. M., Kay, J. E., Malanik, J., and Barrett, A. P. (2012). The Arctic's rapidly shrinking sea ice cover: a research synthesis. *Clim. Change.* 110, 1005–1027. doi: 10.1007/s10584-011-0101-1

Sumaila, U. R., Marsden, A. D., Watson, R., and Pauly, D. (2007). A global ex-vessel fish price database: construction and applications. *J. Bioecon.* 9, 39–51. doi: 10.1007/s10818-007-9015-4

Sunday, J. M., Bates, A. E., and Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nat. Clim. Chang.* 2, 686–690. doi: 10.1038/nclimate1539

Tittensor, D. P., Eddy, T. D., Lotze, H. K., Galbraith, E. D., Cheung, W., Barange, M., et al. (2018). A protocol for the intercomparison of marine fishery and ecosystem models: fish-MIP v1.0. *Geosci. Model Dev.* 11, 1421–1442. doi: 10.5194/gmd-11-1421-2018

Toonen, R. J., Wilhelm, T. A., Maxwell, S. M., Wagner, D., Bowen, B. W., Sheppard, C. R., et al. (2013). One size does not fit all: the emerging frontier in large-scale marine conservation. *Mar. Pollut. Bull.* 77, 7–10. doi: 10.1016/j.marpolbul.2013.10.039

Travers, M., Shin, Y.-J., Jennings, S., Machu, E., Huggett, J., Field, J., et al. (2009). Two-way coupling versus one-way forcing of plankton and fish models to predict ecosystem changes in the Benguela. *Ecol. Model.* 220, 3089–3099. doi: 10.1016/j.ecolmodel.2009.08.016

Travers-Trolet, M., Shin, Y.-J., Shannon, L. J., Moloney, C. L., and Field, J. G. (2014). Combined fishing and climate forcing in the southern Benguela upwelling ecosystem: an end-to-end modelling approach reveals dampened effects. *PLoS ONE* 9:e94286. doi: 10.1371/journal.pone.0094286

Travis, J., Coleman, F. C., Auster, P. J., Cury, P. M., Estes, J. A., Orensanz, J., et al. (2014). Integrating the invisible fabric of nature into fisheries management. *Proc. Natl. Acad. Sci. U.S.A.* 111, 581–584. doi: 10.1073/pnas.1305853111

Trisos, C. H., Merow, C., and Pigot, A. L. (2020). The projected timing of abrupt ecological disruption from climate change. *Nature* 580, 496–501. doi: 10.1038/s41586-020-2189-9

UN (2020). *The UN Sustainable Developmement Goals.* Available online at: http://www.un.org/sustainabledevelopment/sustainable-development-goals/ (accessed August 1, 2020).

Urban, M., Bocedi, G., Hendry, A., Mihoub, J.-B., Pe'er, G., Singer, A., et al. (2016). Improving the forecast for biodiversity under climate change. *Science* 353:aad8466. doi: 10.1126/science.aad8466

Visbeck, M. (2018). Ocean science research is key for a sustainable future. *Nat. Commun.* 9:690. doi: 10.1038/s41467-018-03158-3

Walters, C., Christensen, V., and Pauly, D. (1997). Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fish.* 7, 139–172. doi: 10.1023/A:1018479526149

Walters, C., Pauly, D., and Christensen, V. (1999). Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2, 539–554. doi: 10.1007/s100219900101

Walters, C. J., and Juanes, F. (1993). Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Can. J. Fish. Aquat. Sci.* 50, 2058–2070. doi: 10.1139/f93-229

Walters, C., Christensen, V., Walters, W., and Rose, K. (2010). Representation of multistanza life histories in Ecospace models for spatial organization of ecosystem trophic interaction patterns. *Bull. Mar. Sci.* 86, 439–459.

Wang, M., and Overland, J. E. (2012). A sea ice free summer Arctic within 30 years: an update from CMIP5 models. *Geophys. Res. Lett.* 39. doi: 10.1029/2012GL052868

Watson, R. A. (2017). A database of global marine commercial, small-scale, illegal and unreported fisheries catch 1950–2014. *Sci. Data* 4:170039. doi: 10.1038/sdata.2017.39

Watson, R. A., Cheung, W. W. L., Anticamara, J. A., Sumaila, R. U., Zeller, D., and Pauly, D. (2013). Global marine yield halved as fishing intensity redoubles. *Fish Fisher.* 14, 493–503. doi: 10.1111/j.1467-2979.2012.00483.x

Watson, R. A., and Tidd, A. (2018). Mapping nearly a century and a half of global marine fishing: 1869–2015. *Marine Policy* 93, 171–177. doi: 10.1016/j.marpol.2018.04.023

White, C. R., Phillips, N. F., and Seymour, R. S. (2005). The scaling and temperature dependence of vertebrate metabolism. *Biol. Lett.* 2, 125–127. doi: 10.1098/rsbl.2005.0378

Wickham, H., Chang, W., and Wickham, M. H. (2016). Package 'ggplot2'. Create Elegant Data Visualisations Using the Grammar of Graphics. Ver 2, 1–189. Available online at: https://cran.r-project.org/web/packages/ggplot2/index.html

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., et al. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science* 314, 787–790. doi: 10.1126/science.1132294

Conflict of Interest: JB was employed by Mountainsoft.

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 27 October 2020
doi: 10.3389/fmars.2020.578014

Who You Speak to Matters: Information Sharing and the Management of a Small-Scale Fishery

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OPEN ACCESS

Edited by:
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Specialty section:
This article was submitted to
Marine Fisheries, Aquaculture
and Living Resources,
a section of the journal
Frontiers in Marine Science

Received: 30 June 2020
Accepted: 21 August 2020
Published: 27 October 2020

Citation:
Obregón C, Admiraal R,
van Putten I, Hughes M, Tweedley JR
and Loneragan NR (2020) Who You
Speak to Matters: Information Sharing
and the Management of a
Small-Scale Fishery.
Front. Mar. Sci. 7:578014.
doi: 10.3389/fmars.2020.578014

Sustainable natural resource management requires collaboration, adaptability and coordination between science, policy and stakeholders. Communication of scientific information through social networks is integral to effective governance. This study employed social network analysis to investigate information flow between stakeholders associated with the blue swimmer crab (*Portunus armatus*) fishery in the Peel-Harvey Estuary, south-western Australia. Although the fishery received Marine Stewardship Council certification in 2016, a preliminary study conducted between 2017 and 2018 revealed that fishers were concerned about its status and management. Consequently, 85 face-to-face interviews were conducted with commercial and recreational fishers, academics, government bodies, representatives of fishing organizations, non-governmental organizations, and tourism operators to understand the flow of information and the influence on perceptions of sustainability. The results showed that: (i) few individuals were key for sharing information within and between different organizations forming the fishery network and only two of the six groups (government bodies and the commercial fishing sector) were highly connected and appeared as key for information sharing; (ii) after the public awareness and tourism groups, academic groups were the second-least connected, despite having actively researched the Peel-Harvey Estuary and the *P. armatus* fishery for over 40 years; (iii) recreational fishers exchanged information mainly with other fishers and the state fisheries department; (iv) modes of communication used with the recreational fishing sector differed greatly between the fisheries department (i.e., mainly via phone/email) and the recreational fishing organization (i.e., strong online presence, social media, and phone/email); (v) issues of inclusiveness and representativeness were highlighted for some of the groups and organizations. This is the first study looking at information-sharing patterns through an Australian fishery network. Through this research we have identified logistical and institutional challenges to communicating information regarding the science, management and environmental issues related to a small-scale crab fishery and made suggestions to enhance information flow in the network.

Keywords: Australia, crab, commercial fishing, human dimensions, recreational fishing, social network

INTRODUCTION

Fisheries are a classic example of natural resources that are vulnerable to management conflict (Hardin, 1968). Interactions between human populations and natural resources (such as a fishery) form complex adaptive social-ecological systems (SES), defined by uncertainties, natural variations and nuanced dynamics that can be challenging to manage effectively (Berkes et al., 2000). Effective management of SES ideally requires the inclusion of human dimensions such as stakeholder perceptions and knowledge (Bodin and Crona, 2009). Hence, calls for a transition from traditional fisheries management to a transdisciplinary and inclusive approach (i.e., incorporating human dimensions) are gaining support. In the last two decades, the concept of ecosystem-based fisheries management (EBFM) has been increasingly used globally and appears to be the main stated approach to guiding regulation and exploitation of natural aquatic resources in developed countries (Pitcher et al., 2009), although implementation remains limited (Link and Marshak, 2019).

The challenge of EBFM is deepened further by the existing pressures resulting from climate change. Predictions for temperate, south-western Australia suggest that this region will have reduced winter rainfall (25–72% reduction according to different global climate models), and that sea level will increase by 20 to 84 cm above its current level by the end of 2100 (Hallett et al., 2018). The combination of increased air temperature, sea level rise and reduced rainfall is expected to result in increased salinity and residence time of water in closed or semi-closed environments, such as estuaries. Furthermore, reduced water exchange and salinity stratification would be expected to increase the frequency and severity of algal blooms, hypoxia and fish kill events (Gillanders et al., 2011). As a result, ecosystems are anticipated to undergo shifts in their community structure and function which will affect the abundance of species targeted by fishers (Caputi et al., 2014). More marine conditions in estuaries will result in greater occurrence of marine species, and this might encourage a greater use of these systems by fishers (Valesini et al., 2019). If an increase in fishing pressure occurred, estuarine fisheries, such as the blue swimmer crab (BSC, *Portunus armatus*) in Western Australia, which is the focus of this paper, will require new and adaptive management approaches.

Despite the acknowledgment that a transition toward EBFM is needed, in practice, the ecological and human dimensions of fisheries are rarely considered equally, particularly the social, cultural, and institutional aspects, which are often overlooked (Barclay, 2012). The inclusion of stakeholders in the management process (i.e., co-management), along with the study of social networks is fundamental when assessing fishery management approaches. One way to integrate the study of social networks in fisheries research is by better understanding information-sharing within the network and how the structure of the network influences this exchange (Leonard et al., 2011). Information exchange often depends on making and maintaining positive interactions with key individuals and organizations. Thus, understanding the structural pattern of interactions between social network actors, particularly how information is shared, provides insight into the key elements that facilitate and impede efficient communication within the network.

Social network theory derives from graph theory, a mathematical approach used to represent complex systems. Social network analysis (SNA) is a commonly used method to analyze and graphically represent the exchange of resources, such as information and behavioral patterns, amongst individuals, groups, or organizations (Rogers, 1995). This method is increasingly recognized as an interdisciplinary tool with potential to clarify the implications of network properties for natural resource management (Turner et al., 2014). In social networks, interactions between actors can affect individuals' views, decisions, and behaviors. The structure of the social network of fishers and managers, such as the engagement or disengagement of local users and all stakeholders in the design and implementation of management regulations, can influence the effectiveness and efficiency of both adaptive management and EBFM (Bodin and Norberg, 2005). Understanding these networks and the connections within them provides a key to understanding the reasons behind the success of management and governance of a fishery (Cárcamo et al., 2014).

Social networks can influence the resilience of local communities as well as their capacity to adapt to ecosystem change. Indeed, previous research has demonstrated that social network structure greatly influences the potential for collective action (Bodin and Norberg, 2005). It has also shown the importance of collaboration and information sharing (Cohen et al., 2012), as well as the significance of particular organizations, partnerships (Berdej and Armitage, 2016) and individuals (Gutiérrez et al., 2011) for successfully managing natural resources, such as fisheries. Effective information flow between stakeholders is a key element for the success of fisheries management worldwide as well as for setting realistic management objectives at a regional or local scale (Barnes-Mauthe et al., 2015). To our knowledge, however, no studies have investigated the patterns of information-sharing through an Australian fishery network.

The BSC fishery is one of the most important fisheries in south-western Australia, both from a recreational and a commercial perspective, particularly in the Peel-Harvey Estuary. Both sectors of the Peel-Harvey BSC fishery (hereafter PHBSC) were certified in 2016 as sustainable by the Marine Stewardship Council (MSC), in a world first joint certification (Morison et al., 2015). Information sharing between individuals and organizations participating in the PHBSC fishery network is a major element to facilitate an efficient management of this resource. Despite the fishery's sustainability certification, a previous study that analyzed fishers' perceptions on current management approaches, revealed that fishers were concerned about the fishery's status and management (Obregón et al., 2020). Consequently, this study used social network analysis to empirically investigate information-sharing patterns among actors in the SES of the PHBSC fishery. We explored three different network configurations: (i) relations based on information sharing between individual stakeholders actively involved in the management and the study of the fishery (i.e., not including recreational fishers); (ii) relations based on information sharing between organizations, and (iii) relations based on information exchange between recreational fishers and some organizations belonging to the PHBSC fishery network. The analysis of this small-scale fishery network in south-western Australia provided insight into specific points of intervention and ways forward to help enhance innovative and adaptive management of regional fisheries (Ernoul and Wardell-Johnson, 2013).

MATERIALS AND METHODS

Study Area and Target Species

Fishing is an important activity in Western Australia (WA), both culturally and commercially. It is estimated that ∼700,000 Western Australians fish recreationally (Ryan et al., 2019), representing a significant proportion (∼27%) of the state's total population of 2.6 million people. Commercial fishing in WA contributes around AUD 1 billion and provides direct employment to over 5,000 people (WAFIC, 2020). The BSC fishery comprises a significant component of the WA recreational fishery catch. For example, in 2017/2018, recreational boat fishers were estimated to have caught ∼660,000 crabs in WA (Ryan et al., 2019). Additionally, a significant number are caught by shore-based fishers in estuaries and coastal embayments. Events organized to celebrate the catch of crabs in WA, such as the annual "Crabfest" celebration in Mandurah, reflect the cultural importance of blue swimmer crabs in this region. This species is also targeted by the commercial sector, which employs more than 80 people directly and is valued at ∼AUD 3.5 million per year (Department of Primary Industries and Regional Development, 2018). The commercial catch in WA was 518.2 t in 2017 (Fletcher et al., 2017).

Commercial fishing for BSC in WA is managed mainly by restrictions on fishing vessels, fishing traps and enforcing a minimum size limit (MSL) of 127 mm carapace width. Daily time limits and a closed fishing season also apply (Fletcher et al., 2017). Recreational catches are mainly regulated through bag limits and size restrictions (i.e., a maximum of 10 crabs per person when fishing from the shore, or a maximum of 20 per boat provided that there are at least two people in the boat, and MSL of 127 mm carapace width). A fishing license is also needed for recreational fishers using a boat. Shore-based recreational fishers are exempt from this license. In 2019, new management measures were introduced for both fishing sectors in south-western Australia. These include a seasonal closure for all waters from Perth (WA capital city) to Manjimup Beach (200 km south of Perth) from September to November, a reduction of bag limits for regional systems, and a buy-out of commercial fishing licenses in the Peel-Harvey Estuary (Department of Primary Industries and Regional Development, 2018).

Located about 80 km south of Perth, the Peel-Harvey Estuary is the largest estuary in south-western Australia (area ∼130 km^2, **Figure 1**) it is also one of the most popular locations for BSC fishing, and is part of the Ramsar-listed Peel-Yalgorup wetland system (Valesini et al., 2019). The City of Mandurah (population ∼80,000) is located at the mouth of the estuary and is the fastest growing city in the state and second fastest growing regional city in Australia (Peel Development Commision [PDC], 2019). The estuary's importance as a major natural asset and the population growth in the region create challenges for managing the natural resources depending on this environment.

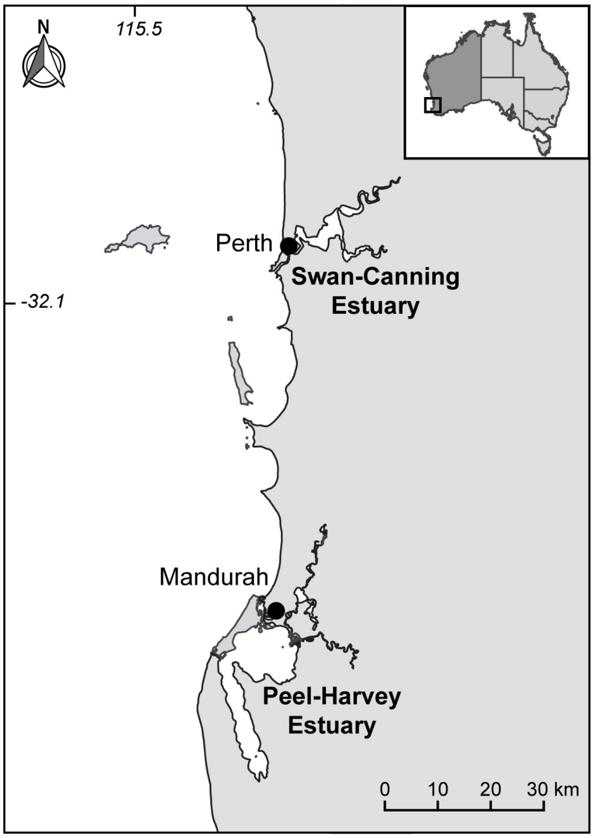

FIGURE 1 | Map of Western Australia (Australia), showing the location of the Peel-Harvey Estuary and the cities of Mandurah and Perth.

To achieve certification of the PHBSC fishery by the MSC, fishery stakeholders were required to demonstrate its sustainability. The certification process required pooling data from various groups (e.g., government bodies, fishing sectors and other organizations) on the status of the fishery and its environment, as well as its management and other elements related to decision making (Marine Stewardship Council, 2019). Consequently, as part of the certification process much information was shared between individuals and organizations participating in the PHBSC fishery network. Both fishery sectors were required to engage in providing pre-certification information and contribute to annual audits. The information shared among the network of stakeholders was a key element in this process.

Data Collection

The target population for the social network analysis was the PHBSC fishery network, which includes a diverse range of stakeholders, such as non-governmental organization

(NGO) representatives, government bodies, academics, and fishing sectors representatives (**Table 1**). Potential survey participants from each organization were identified in a three-step process, which included a preliminary identification of primary participants who were known to the researchers and who were actively involved in the fishery. These 33 primary participants were contacted via email, and 23 agreed to be interviewed. Snowball sampling was used to identify and survey other stakeholders (secondary participants) (Maiolo et al., 1992). To be invited to participate in the survey, secondary participants had to be nominated by at least two primary participants. This process continued for three waves (i.e., three interview sets where, if survey participants named new stakeholders twice or more, these people were contacted and invited to participate in

TABLE 1 | Organisations forming the PHBSC fishery network and acronyms used for each organisation, groups they are affiliated with, description of each organisation and total individuals mentioned (*N* = 112) and individuals interviewed (*n* = 35) for each organisation.

Group	Organization	Acronym	*N*	*n*	Description of each organization
Commercial fishing sector	Commercial fishers	MLFA	10	2	Commercial fishers representing the Mandurah licensed Fishermen Association (MLFA)
	Southern Seafood Producers of WA	SSPWA	1	1	Association for professional seafood producers in south-western Australia
	WA Fishing Industry Council	WAFIC	6	2	Main organisation representing commercial fishing in the state of WA
Recreational sector	Recfishwest	RFW	5	5	Main organisation representing recreational fishing in the state of WA
	Recreational fishers	Rec. fishers	6	0	Recreational fishers actively involved in the discussions on the management of the fishery
	Mandurah offshore fishing and sailing club	MOFSC	1	0	Recreational fishing club in Mandurah
Government body	City of Mandurah	CoM	4	1	Council for Mandurah
	Department of Biodiversity, Conservation and Attractions	DBCA	2	0	State government department for the management of WA's environment and its conservation
	Department of Primary Industries and Regional Development	DPIRD	38	17	State government department for WA fisheries management
	Department of Water and Environmental Regulations	DWER	5	1	State government department for water regulations in WA
	Fisheries Research and Development Corporation	FRDC	1	0	National body for research, development and extension of fisheries and aquaculture sectors
	Peel Development Commission	PDC	2	1	Regional commission for the Peel region (including the Peel-Harvey Estuary)
	Politicians	–	2	0	Local politicians
Academics	Murdoch researchers	–	12	2	Post-graduate students and established academics involved in BSC research
	University of Western Australia researchers	–	1	0	Established academics involved in BSC research
NGOs, Conservation groups	Birdlife Australia	–	1	0	Non-profit, non-governmental organisation (NGO) for the conservation of Australian birds
	Marine Stewardship Council	MSC	1	1	Non-profit NGO providing a certification scheme of sustainable seafood
	Peel-Harvey Catchment Council	PHCC	6	1	Non-profit NGO community based organization for the management of natural resources in the Peel-Harvey Estuary Catchment
	Scientific Certification Systems	SCS	1	1	Third-party organization providing independent assessment of sustainability
Public awareness, Tourism	Dolphin Watch	–	1	0	Partnership between DBCA, Murdoch and Curtin Universities for the conservation of dolphins in the region
	General public	–	2	0	General public (not necessarily fishers) actively involved in the discussions on the management of the fishery
	Mandurah Cruises	–	1	0	Tour operator doing river and coastal cruises, based in Mandurah
	Mandurah Times	–	1	0	Local newspaper, based in Mandurah
	Peel Bright Minds	–	1	0	Community-based organization promoting events and regional activities in the Peel region
	Western Angler Magazine	WAM	1	0	WA recreational fishing magazine

the survey). Despite some recreational fishers being mentioned during these interviews (**Table 1**), no individuals were mentioned by two or more participants, and therefore recreational fishers were not invited to participate in the survey. Recreational fishers were therefore interviewed separately.

The approach used to interview recreational fishers differed from the method used with the rest of respondents. While individual meetings were arranged with non-recreational fisher respondents, recreational fishers were randomly selected at popular fishing spots throughout the summer season (peak time for BSC fishing in the region) and invited to be interviewed.

A total of 85 semi-structured interviews were conducted between November 2018 and November 2019, during daylight hours to collect network data, respondents' attitudes and perceptions toward information sharing efficiency, and individuals' demographics. Note that more recently, monitoring by DPIRD has found a significant number of recreational fishers fishing throughout the evening (Taylor et al., 2018). No interviews were carried out at during the night and therefore we have no information on whether the night fishers represent a different group to those interviewed during the day.

Relations which involved information-sharing were elicited by asking stakeholders (i) to name up to 10 individuals with whom they exchanged information on the BSC fishery; (ii) how frequently information-sharing interactions occurred; and (iii) their perceptions of the utility of the information shared. Recreational fishers refused to provide individual names of the people they shared information with, as they considered this to be a breach of their privacy. Consequently, the survey for recreational fishers was adapted to not require mentioning individual names. Instead, recreational fishers were asked to identify the organizations they had been or were in contact with (rather than naming individual stakeholders) from a list of key organizations (including an "other" option) that had been produced based on the fishery network. This difference in the data collected required a separate data analysis for the individual recreational fishers included in the network, as the recreational fishers provided information on organizations, whereas the non-recreational fisher stakeholders identified and provided information on individuals.

The network data collected included a description of the relations/edges (i.e., interactions between actors), directionality of information-sharing (i.e., who shared the information and who received it), mode of communication used (e.g., face-to-face, telephone, and e-mail), topic discussed (i.e., fishery science, management, or environment), frequency of interaction, length of the relationship between the two individuals, and the perceived quality of interaction, defined as the quality of the information received and the perceived efficiency of the interaction, quantified on a three-point scale (1 = low, 2 = medium, and 3 = high). Data from each respondent/node were also recorded, including the name, affiliation, age and level of seniority (as represented by role) in the organization. To preserve respondent privacy, names of respondents were replaced with a unique identifier code, and organization names were categorized into six broad groups [i.e., commercial sector, recreational sector (formed by organizations representing and managing the recreational fishing sector only), government body, academics, NGOs and conservation groups, public awareness and tourism] according to the general purpose of each organization (**Table 1**). Individual recreational fishers were not included in the recreational fishing sector group as these responded to a different survey and therefore were analyzed separately.

Qualitative data were also collected to provide context regarding the information-sharing relations. These included questions about personal satisfaction with their own information sharing, perceived fishers' satisfaction on the management of the fishery by other stakeholders and public events where information on the BSC fishery was shared.

Network and Data Analyses

Social network analysis was used to describe, analyze, and map how individuals, organizations, and stakeholder groups interacted and shared information. We considered three forms of networks based on the different types of data, as follows:

(1) An egocentric network of non-recreational fisher stakeholders (hereafter "egocentric network of stakeholders") and only their direct information sharing relations.
(2) A full network of the previously described closed population (hereafter "closed population network") and all information sharing relations among respondents who were part of this closed population. We also considered a network of organizations and relations among these organizations corresponding to this closed population.
(3) A bipartite network of surveyed recreational fishers and the organizations with which they shared or received information (hereafter "bipartite network of recreational fishers and organizations").

These networks are described in more detail below.

The statistical analysis of these networks was carried out in R using the 'sna' (Butts, 2019), 'network' (Butts et al., 2019), 'statnet' (Handcock et al., 2019), and 'igraph' (Csardi, 2019) packages. This included calculating descriptive statistics, such as various measures of centrality [relating to out-ties or sharing of information, see **Table 2** for a description of these measures, and prestige (relating to in-ties or reception of information)]. Eigenvector centrality and prestige were considered, although we do not present measures of these forms of centrality and prestige, as these did not provide any additional insights to those obtained from the analysis of degree centrality, betweenness centrality and degree prestige. When applied to a network of organizational relations, measures were weighted by the number of relations between organizations (or groups). In addition to measures of centrality and prestige, we also examined attribute-based mixing [i.e., cross-tabulations of relations between actors based on certain attributes for both actors involved in the relation and fit statistical models for networks, specifically exponential random graph models (ERGMs)].

Egocentric Network of Stakeholders

The egocentric network of stakeholders examined only the local networks of primary survey participants (i.e., the respondents and those with whom they directly shared or

TABLE 2 | Individual and organisational level network metrics of centrality, definitions, and descriptions.

Centrality measure	Definition	Description
Degree centrality	Count of number of outgoing edges to the node. We present normalized degree centrality to account for network size.	Actors with a high degree centrality have a greater capacity to share information and have a greater information-sharing power.
Betweenness centrality	Calculations of betweenness for a particular actor are based on the quantity of shortest paths between other nodes that go through that particular node. We present normalized betweenness centrality to account for network size.	This measure gives information on which nodes (i.e., actors) receive information more frequently. They are important for controlling the flow of information between nodes. The more 'in between' an agent is, the more that agent will be able to receive and share different types of information among others.
Degree prestige	Count of number of incoming edges to one node/actor. We present normalized degree prestige to account for network size.	Actors with high degree prestige potentially have a greater influence in the network and have a greater information-sharing power.

received information). These included individuals surveyed from the PHBSC organizations representing different stakeholder groups but excluded recreational fishers since, as previously described, recreational fishers provided a different type on information of the network, and therefore were analyzed separately, as a bipartite network (see section below for more details).

An examination of attribute-based mixing for age, gender, education level and organizational affiliation elucidated whether there was a tendency for homophily (i.e., individuals preferring information sharing relations with others who were similar to themselves) or heterophily (i.e., individuals preferring to share information with others who were different than themselves). Attribute-based mixing is important because it has implications for information diffusion between different groups and opportunities for new information to enter a network (Peel et al., 2018).

Closed Population Network

The closed population network included only individuals who had been interviewed by the researchers and their information sharing relations between each other (i.e., it excluded relations with people outside of this closed network). We examined this network at two levels: (i) an actor-level scale where individuals and their relations were considered, and (ii) an organization-level scale where organizations and interactions between organizations were considered. For confidentiality reasons, in the actor-level network we report organizations according to the previously described groups relating to the purpose of the organization (**Table 1**). In the organization-level, on the other hand, we present results according to the individual organizations.

Bipartite Network of Recreational Fishers and Organizations

Data extracted from the recreational fishers questionnaire were used to produce a network of recreational fishers and the organizations from which they received or with whom they shared information (e.g., if they needed to report something related to the BSC fishery). Thus, the network for the PHBSC recreational fishery was considered a bipartite (i.e., two-mode) network, as it describes interactions between two disjoint entities in the community—individuals and organizations (Chizinski et al., 2018). We treated this bipartite network as undirected (i.e., interest was simply in terms of which organizations recreational fishers interacted with). We considered degree centrality with a focus on organizations (i.e., identifying the organizations with which recreational fishers most commonly interact) and perceived quality of information from each organization in contact with recreational fishers.

Qualitative Data Analysis

Qualitative data, other than demographics, were analyzed separately for non-fisher stakeholders and recreational fishers. Summary statistics were used to describe stakeholder perceptions (fishers and non-fishers), sources available to obtain information on the fishery and its management, as well as fishers' satisfaction with the fishery management (rated on a three-point scale).

RESULTS

We describe the structure of the closed population network where we focus on the individual and organization level. First, we describe the bipartite network of recreational fishers and organizations, discussing the modes of communication used to share information and the perceived quality of the information shared. Then we use qualitative data to help understand gaps and impediments in the process of information sharing. Finally, we discuss potential implications for the management of the PHBSC fishery.

Demographics

In total, 85 individuals from 13 different organizations were interviewed, including 74 face-to-face interviews and 11 conducted by phone. A total of 50 recreational fishers and 35 non-recreational fisher stakeholders (related to government organizations, the commercial sector, etc.) were interviewed (see section "Materials and Methods").

Most survey participants were male (76%) and ranged in age from 18 to 65+ years with the largest portion of participants (30%) between 45 and 54 years of age. The highest level of education completed by most interviewees (51%) was a higher degree education (i.e., technical certificates, diplomas, and/or University studies), while 39% had completed secondary education.

PHBSC Fishery Stakeholders

A total of 194 stakeholders from 28 different organizations and 571 information sharing relations were identified for the PHBSC fishery network. Overall, 377 relations related to the management of the fishery, 199 relations focused on information related to the scientific research on BSC populations, and 63 relations related to the broader environment of the Peel-Harvey Estuary. Note that some information sharing relations involved multiple topics.

The consistency of respondents' reports on information sharing for relations was checked where both respondents were interviewed. This consistency was necessarily restricted to a closed population network consisting only of those people who were sampled and the relations/edges between them. Respondents agreed on the presence and directionality (i.e., who shared information with whom) for only 25.1% of the reported information sharing relations. When ignoring directionality (i.e., simply focusing on whether there is some form of information sharing between two people), still only 38.7% of relations between primary respondents were reported by both parties.

Egocentric Network of Stakeholders

The egocentric network of stakeholders was comprised of 35 non-recreational fisher stakeholders and their 458 direct information sharing relations with other stakeholders. These direct information sharing relations involved a total of 113 unique individuals. Of these information sharing relations, 264 related to the management of the fishery, 199 focused on the scientific research of BSC populations, and 63 related to the environment of the Peel-Harvey Estuary. Note that some of the relations related to more than one topic.

Centrality and Prestige of Stakeholders

Certain stakeholders in the egocentric network were identified as more important for information flow in terms of information sharing relations (**Table 3**). The individual with highest degree centrality (i.e., direct information sharing relations) and highest degree prestige (i.e., direct information receiving relations), normalized for unique individuals identified in the network, was affiliated with the commercial fishing sector (ID: 33, degree centrality = 0.295, degree prestige = 0.214) (**Table 3**). These measures of degree centrality and degree prestige reflect that this individual shared information with 29.5% and received information from 21.4% of the 113 unique stakeholders identified in the egocentric network. Two individuals affiliated with a government body (IDs 6 and 12, degree centrality = 0.268 and 0.214, degree prestige = 0.205 and 0.188, respectively) and one affiliated with the recreational fishing sector (ID: 32, degree centrality = 0.170, degree prestige = 0.188) were also identified as important. The top five ranked individuals included more representatives of primary users (i.e., recreational and commercial fishing sectors) than government body representatives (**Table 3**).

TABLE 3 | Individual identifier (ID) for the 10 stakeholders with highest degree centrality and degree prestige metrics forming the egocentric PHBSC fishery network and the groups they belong to.

Individual ID	Group	Degree centrality	Degree prestige
33	Commercial sector	0.295	0.214
6	Government body	0.268	0.205
12	Government body	0.214	0.188
32	Recreational sector	0.170	0.188
34	Commercial sector	0.161	0.152
18	NGO, Conservation groups	0.152	0.143
22	Government body	0.152	0.116
9	Government body	0.134	0.098
28	Government body	0.134	0.054
2	Government body	0.125	0.125

Individuals are ranked according to their degree centrality (i.e., out-degree) and degree prestige (i.e., in-degree).

TABLE 4 | Exponential random graph model (ERGM) results for attribute-based mixing for individual stakeholders (n = 35) forming the egocentric PHBSC fishery network.

Attribute	*p*-value
Gender	0.134
Seniority	<0.001*
Age	<0.001*
Organization	<0.001*
Group	0.1366

*See **Supplementary Tables S1–S5** for more details. The symbol '*' denotes the presence of significant differences ($p < 0.001$).*

Attribute-Based Mixing

To assess whether people in the network tended to share information within their own groups or with those who were similar to them, we examined attribute-based mixing for organizational affiliation, seniority level in the organization, age group, and gender of individuals using an ERGM (**Table 4**). Examining each of these attributes, we found evidence of homophily (i.e., preference for those with similar attributes beyond what would be expected under random selection) for those who were more senior in their organizations (e.g., directors, senior research scientists, and professors) and based on organization. For example, the highest number of information relations occurred between individuals from DPIRD (129 relations), with this number being significantly higher than what would be expected if there was no clear preference to share information with people from particular organizations ($p = 0.042$; **Supplementary Tables S1, S2**).

When looking at age groups, there is evidence of homophily with individuals in the age groups of 45–54 years and older sharing information with each other more frequently than would be expected if there was no preference for relations based on age ($p = 0.0001$; **Supplementary Table S3**). This is likely to be related to the homophily observed for higher seniority levels, where individuals in higher seniority levels exchanged information more frequently with individuals of a similar seniority level than would be expected if information sharing was not related to seniority level. At the same time, those aged 45–54 years old shared information with others in the age group of 25–34 years more frequently than would be expected ($p = 0.001$; see **Supplementary Table S3**), and these younger individuals also tended to establish information-sharing relations with those 45–54 years and older more frequently than would be expected if there was no preference for relations based on age ($p = 0.010$; see **Supplementary Table S3**), evidence of heterophily.

Closed Population Network

The closed population network was comprised of 35 non-recreational fisher stakeholders and 242 information sharing relations among these individuals. We examined this network in terms of the importance of various individuals (for an actor-based network) and organizations (for an organization-based network) for information flow.

Actor-Based Network

To assess the importance of individuals for information flow, we considered degree centrality and degree prestige (as above), and also considered betweenness centrality, which provides a measure of the number (or proportion, when normalized) of shortest paths between individuals that go through a given actor (Barnes-Mauthe et al., 2015).

The two individuals with highest degree centrality and degree prestige when considering the egocentric network (IDs 33 and 6) also had the highest degree centrality and degree prestige when considering the closed population network (**Table 5** and **Figure 2**). Here, however, their relative rankings were swapped (**Tables 3**, **5**). Given that the closed population network includes only those relations between members of the closed population (i.e., individuals who were surveyed) whereas the egocentric network considers all direct ties for an individual (i.e., both individuals who were and were not surveyed), this means that a significant number of ties for individual 33 are with individuals with whom other members of the closed population do not have contact. Considering that individual 33 is one of the few representatives from the commercial fishing sector, this is not terribly surprising and indicates that this person has a number of ties outside the key stakeholder groups (e.g., to other commercial or recreational fishers) and could be a central liaison between these key stakeholder groups and other groups that are less represented in the network. Individuals 6 and 33 also have the highest measures of betweenness centrality for the closed population network. This suggests that these individuals are not only high-volume sharers and recipients of information directly to and from others in the network, but also that they are important "gatekeepers" for the indirect

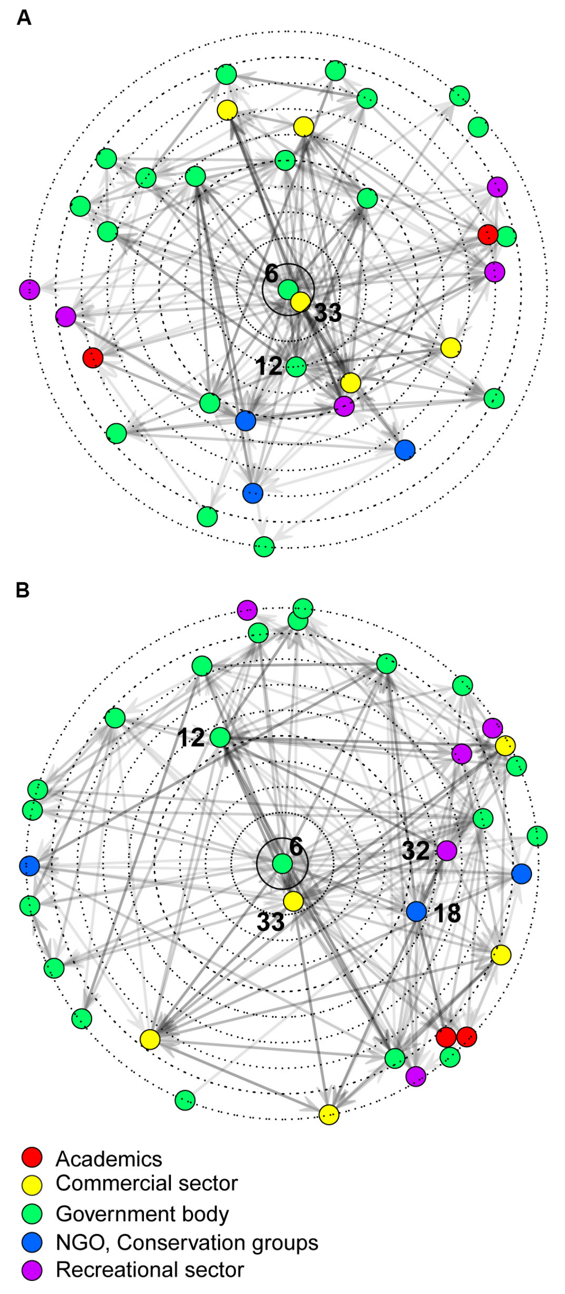

FIGURE 2 | Target plot of degree centrality **(A)** and betweenness centrality **(B)** for individuals forming the closed population network. Numbers indicate individuals with higher centrality and betweenness, These appear near the center of the plot.

TABLE 5 | Results showing individuals with highest degree centrality and prestige metrics forming the closed population network and the organizations they belong to.

ID	Group	Degree centrality	Degree prestige	Betweenness centrality
6	Government body	0.882	0.647	0.198
33	Commercial sector	0.824	0.706	0.168
12	Government body	0.618	0.559	0.089
34	Commercial sector	0.500	0.471	0.028
22	Government body	0.471	0.382	0.024
32	Recreational sector	0.441	0.588	0.071
9	Government body	0.441	0.294	0.039
18	NGO, Conservation groups	0.412	0.441	0.088
28	Government body	0.412	0.176	0.033
2	Government body	0.382	0.382	0.024

transmission of information between individuals. Note, however, that neither of these individuals had formal information-sharing roles, but were taking responsibility for sharing information in an unofficial capacity.

When examining those individuals with the highest measures of degree centrality for the closed population network and egocentric network, we note that the same people comprise the top 10 most central actors, although their relative rankings have changed with those associated with government bodies being more central in the closed population network (**Tables 3**, **5**). The largest drops in relative ranking were for those associated with the recreational fishing sector (ID 32) and an NGO or conservation organization (ID 18), which would be consistent with these individuals from groups with low representation (in terms of numbers) in our study having a number of key information-sharing relations outside the key stakeholder groups and potentially being important for the transmission of information to the recreational sector, the general public and other NGOs or conservation organizations, respectively.

When considering degree prestige, the five highest ranked individuals belonged to the commercial fishing sector (IDs 33 and 34), government bodies (IDs 6 and 12), and the recreational fishing sector (ID 32) (**Table 5**). Both commercial fishers maintained (ID 33) or increased (in the case of ID 34) their relative rankings in terms of degree prestige from the egocentric network to the closed population, indicating that most of those who are reported to share information with these individuals come from central stakeholder groups. This suggests that relevant government agencies and BSC fishery bodies are ensuring that the commercial sector is well-informed.

Organization-Based Network

The 35 individuals comprising the closed population network represented 10 organizations. We considered the network of information sharing relations between these organizations, restricted to the relations within the closed population. For this network, directed relations/edges between organizations were weighted by the frequency with which they occurred in the closed population, and measures of centrality and prestige for this network accounted for edge weights. Additionally, self-ties (i.e., relations within the organization) were permitted to reflect information sharing within an organization. **Figure 3** shows the structure of this network with edge widths reflecting the frequency of directed relations between organizations and node sizes reflecting degree centrality (**Figure 3A**) and betweenness centrality for organizations (**Figure 3B**). Self-ties are represented by loops.

When considering degree centrality, the analysis of the closed population network based on organizations presented DPIRD and MLFA as the organizations with highest scores (degree centrality = 0.727 for both). The Peel-Harvey Catchment Council (PHCC) appeared as the third organization in the ranking (degree centrality = 0.636). These are the organizations sharing most often information to others in the network, and since these are affiliated to three different groups, information sharing relations will take into account a diversity of topics, including the management of the commercial and recreational fishing sectors and the environment of the estuary. For example, the topic of discussions started by PHCC focused mainly on environmental and management topics (45% for both) and less so on the fishery science (10%), whereas DPIRD and MLFA talked mainly about management (47.1 and 69.2%, respectively) as well as the fishery (47.1 and 23.1%), with little information exchange focusing on the environment of the estuary (5.78 and 7.7%, respectively).

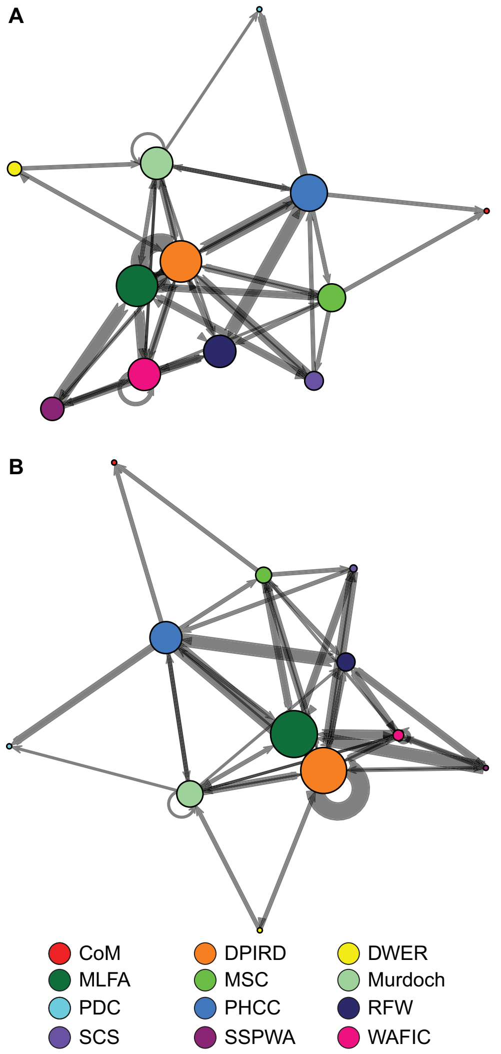

FIGURE 3 | Plots of the network of organizations represented in the closed population network with edge widths representing the frequency of relations between organizations and node sizes representing weighted degree centrality **(A)** and betweenness centrality **(B)** for organizations.

When considering degree prestige, the analysis of the closed population network based on organizations presented again DPIRD and MLFA as the organizations receiving most information (degree prestige = 0.818 and 0.727, respectively). Recfishwest (RFW) appeared as the third organization in the ranking (degree prestige = 0.636). These are the organizations receiving most often information from others in the network. This is not surprising as these organizations represent the main

TABLE 6 | Results showing centrality and prestige measures for organizations represented in the closed population network, (*n* = 35).

Organization	Degree centrality	Degree prestige	Betweenness centrality
Department of Primary Industries and Regional Development	0.727	0.818	0.135
Mandurah licensed Fishermen Association	0.727	0.727	0.138
Peel-Harvey Catchment Council	0.636	0.364	0.089
Recfishwest	0.545	0.636	0.043
Murdoch	0.545	0.455	0.071
WA Fishing Industry Council	0.545	0.455	0.019
Marine Stewardship Council	0.455	0.364	0.036
Southern Seafood Producers of WA	0.364	0.364	0
Scientific Certification Systems	0.273	0.364	0.007
Department of Water and Environmental Regulation	0.182	0.091	0

managing bodies and the primary users of the fishery, which are expected to receive and share information with each other.

Finally, when looking at the bridging capacity (i.e., betweenness centrality) of these organizations, DPIRD, MLFA, and PHCC had betweenness centrality scores considerably higher than the rest (betweenness centrality = 0.135, 0.138, 0.089, respectively; **Table 6** and **Figure 3**). These organizations belonged to three different groups (government body, commercial fishing sector and NGOs and conservation organizations). Having access potentially to different types of information, these organizations have the highest capacity to share it among other organizations that otherwise might not receive it. Despite having greater measures of degree centrality and degree prestige, RFW bridging capacity was lower than Murdoch University's (betweenness centrality = 0.043). Murdoch University was the fourth ranked organization when looking at its bridging capacity (betweenness = 0.067). This is interesting as no individuals from the group of academics, to which this organization is affiliated to, had appeared in previous analyses (**Tables 3**, **5** and **Figures 2**, **3**), suggesting that despite the individuals having low connectivity, the organization is seen as key gatekeeper of information and has an influence in information sharing between groups that otherwise would not be connected to each other.

Bipartite Network of Recreational Fishers and Organizations

In surveys of recreational fishers, respondents mentioned sharing with or receiving information from nine organizations or sources. Of these, four were identified only by recreational fishers and not by other stakeholders. Three of these organizations (i.e., a local fishing club, an angling magazine, and a journalist) do not focus solely on the BSC fishery, but rather aim to share general information on local recreational fisheries with the general public. For this component of the study "recreational fishers" were defined as an organization, as many recreational fishers exchanged information on the PHBSC fishery.

An undirected bipartite network (i.e., a two-mode network) was used to map information exchange between two classes of actors (i.e., recreational fishers and the organizations with which they exchanged information). Analysis of centrality measures for each organization forming the bipartite network highlighted that the recreational fishers mostly exchanged information with four organizations or groups: (i) Other recreational fishers (degree centrality = 0.402); (ii) MLFA (degree centrality = 0.196); (iii) DPIRD (degree centrality = 0.188); and (iv) RFW (degree centrality = 0.161) (**Table 7**). This highlights that the primary sources of information are other fishers instead of the organizations responsible for the management of the fishery. The network map highlights recreational fishers as being the main source of information for other recreational fishers (**Figure 4**, and further analysis below).

The perceived quality of information received by recreational fishers differed significantly among organizations (from low = 1,

TABLE 7 | Results showing the organisations mentioned by recreational fishers and their degree metrics.

Organization	Degree centrality
Recreational fishers	0.402
Mandurah licensed Fishermen Association	0.196
Department of Primary Industries and Regional Development	0.188
Recfishwest	0.161
Journalist	0.018
Western Angler Magazine	0.018
Local Fishing Club	0.018
Peel-Harvey Catchment Council	0.009

Organisations are ranked according to their degree centrality. Refer to ***Table 1*** *for information on which acronym corresponds to each organisation, (n = 50).*

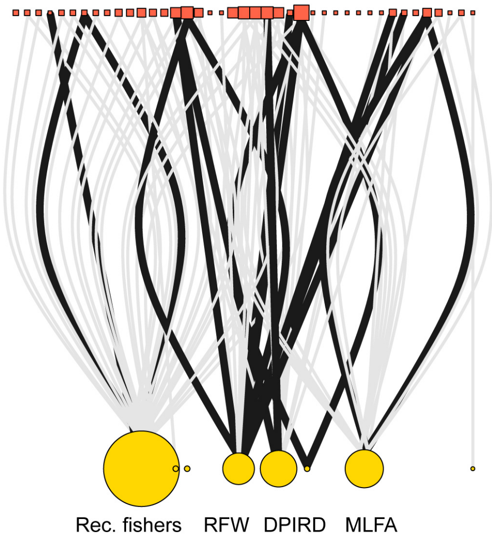

FIGURE 4 | Bipartite network of recreational fishers network and the organizations (i.e., nodes) with which they exchange information. Recreational fishers are denoted by red squares, while organizations are represented by yellow circles. Organizations with degree centralities exceeding 0.1 are labeled, and node size reflects the degree centrality. Edges that are wider and black highlight information exchanges that are perceived by recreational fishers to be of low quality. Refer to **Table 1** for information on which acronym corresponds to each organisation.

to high = 3). Recreational fishers perceived information quality they received from RFW (median quality = 1; mean quality = 1.73) to be significantly lower quality than the information received from DPIRD (median quality = 3; mean quality = 2.82), MLFA fishers (median quality = 3; mean quality = 2.78), and other recreational fishers (median quality = 3; mean quality = 2.76) (Kruskal–Wallis test; p = 0.029, 0.044, and 0.036, respectively). Recreational fishers considered the information from DPIRD as of the highest quality. When looking at the information shared by recreational fishers to organizations, no significant differences in the perceived quality of information were found.

There was also considerable variation in terms of the mode of communication used in information exchange between recreational fishers and different organizations (**Figure 5**). Most information exchange with DPIRD was via email or website updates, while information exchange between recreational fishers was primarily face-to-face, though they also used social media, and to a lesser degree, email and phone or official websites to share and receive information (**Figure 5**). Commercial fishers used only face-to-face communication when exchanging information with the recreational fishing sector. Recfishwest used social media and their website to share information more than other organizations, along with email subscriptions and phone calls, although a small number of exchanges were done face-to-face with recreational fishers. Information from DPIRD was mainly sourced via phone and email by recreational fishers, and rarely available from face-to-face meetings, social media or their website. This highlights a mismatch between the way information is exchanged among fishers and other stakeholders.

Finally, qualitative data analysis provided insight into various elements of fishers' satisfaction with the fishery, fishers' perceptions on information sharing, and public events available. Non-recreational fisher stakeholders' satisfaction with how they shared information with other stakeholders was also recorded. On a five-point Likert scale (with 1 being the lowest rating, and 5 the highest), non-recreational fisher stakeholders seemed largely satisfied with how they shared information with others (mean = 4).

Non-recreational fisher stakeholders also reported on public events for fishers to receive information on the management and science of the fishery. In total, seven events perceived as useful for sharing information on the fishery, were mentioned by 31 of the 35 non-recreational fisher stakeholders interviewed. These included Crabfest (37.2%); the annual management meetings organized for the peak bodies representing the fishery stakeholders (AMMS, 34.8%); events organized by the MSC (11.6%); community presentations at PHCC (6.9%); the annual boatshow (4.6%); seafood week (2.3%), and public forums (2.3%). When asked if they found these events useful to share information on the management and the science of the fishery, 45.1% of non-recreational fisher stakeholders reported these events to be useful, 38.7% reported these to be somewhat useful, and 16.1% reported that they were not useful.

The qualitative data as reported by recreational fisher stakeholders showed that six of the 50 recreational fishers interviewed were aware of two of the seven events that were available to recreational fishers. Both, Crabfest and the annual boatshow were cited by different fishers. The rest of the participants (86.9%) reported that they were unaware of events providing information on the management and science of the PHBSC fishery. When asked if they would consider informative events to be beneficial in the future, 70% were supportive of this, whereas 26.7% were not. The fact that a quarter of the interviewees perceived public events as not beneficial could be due to a lack of interest in the information itself or that the information was not presented in a useful manner.

DISCUSSION

Our study demonstrated the value of empirical research in understanding stakeholder connections and information flow processes for informing the management of fisheries. We provide an empirical basis for identifying the suite of individuals and range of organizations involved in the Peel-Harvey blue swimmer crab (PHBSC) fishery network, representing NGOs, governmental bodies, tourism operators, commercial and recreational fishing sectors, academic groups, and community-based organizations. We examined the fishery through the lens of (i) an egocentric network of non-recreational fisher stakeholders; (ii) a closed population network of non-recreational fisher stakeholders (both individual- and organization-based analysis); and (iii) a bipartite network of recreational fishers and

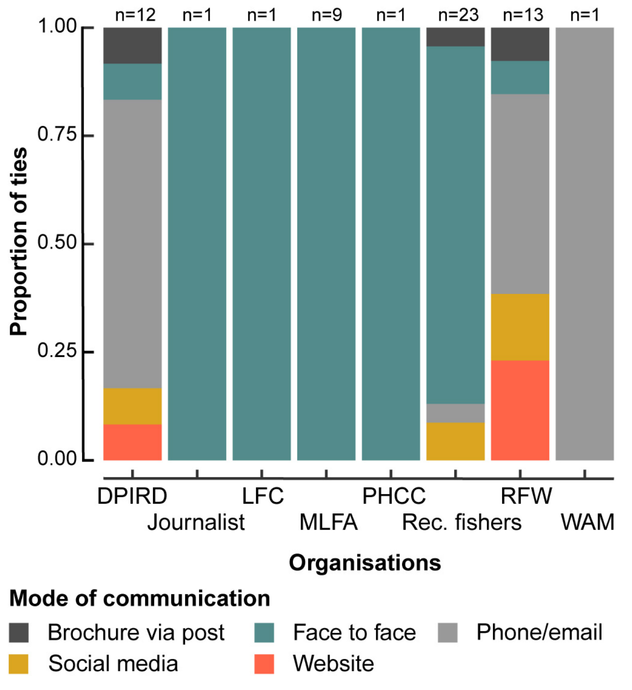

FIGURE 5 | The proportion of information exchanges between recreational fishers and organizations involving various modes of communication, as reported by recreational fishers. Sample sizes (n) on which these proportions are estimated are also presented. Refer to **Table 1** for information on which acronym corresponds to each organisation.

organizations. To our knowledge, this is the first study looking at information sharing in an Australian fishery social network and one of the few network studies looking at information sharing between small-scale fishery stakeholders globally (Bodin and Norberg, 2005; Leonard et al., 2011; Turner et al., 2014).

The PHBSC Fishery Network

Of the 28 organizations identified in the PHBSC network, two were most prominent in terms of measures of centrality and prestige: the government body responsible for the management of the fishery (DPIRD) and commercial fishers (MLFA). This is evidence of a high engagement of the MLFA fishers in information-sharing and is potentially a way for the commercial fishing sector to be included and directly involved in discussions related to the fishery's management, instead of being involved in these discussions only through the organization representing the commercial fishing sector in WA (i.e., WAFIC). This is consistent with previous studies showing how the inclusion of fisher-knowledge in management discussions can benefit adaptive management decision making, as fishers adapt their methods and their learning with environmental changes and uncertainty (Grant and Berkes, 2007). Stakeholders from both the commercial and recreational fishing sector figured prominently in the network in terms of measures of centrality and prestige. Increases in degree prestige and decreases in degree centrality for commercial and recreational fishers, relative to other stakeholders for the closed population network, is consistent with commercial and recreational PHBSC fishing representatives largely receiving information from key government bodies, community-based organizations, NGOs, etc., but then disseminating that information outside of those groups, to others involved in BSC fishing.

The PHBSC fishery network showed a tendency for individuals to form significantly more ties with similar individuals (homophily). Individuals within the Department of Primary Industries and Regional Development (DPIRD) were more likely to share information with others affiliated to DPIRD, and individuals in the network with a senior role were more likely to interact with others at a similar level in the hierarchy of the organization. This tendency has previously been reported in fishery networks. For example, commercial fishers in Hawaii share information with other commercial fishers of their same ethnic background, rather than other backgrounds (Barnes-Mauthe et al., 2015). Homophily generally limits interactions between individuals from different organizations and hinders the inclusion of new knowledge among the individuals of the network (McPherson et al., 2001; Bodin and Crona, 2009). Overall, homophily has the potential to reduce the efficiency of resource management and therefore reduce the capacity to adapt management if change occurs (Bodin and Norberg, 2005; Turner et al., 2014). Heterophily, the preference for establishing relations with different types of individuals, was also present in the PHBSC fishery network, particularly among different age groups. Younger and less experienced people across all the groups tended to exchange information with older and more experienced stakeholders in the network more often than expected by chance. These results are consistent with previous studies that described less experienced individual fishers seeking advice from more experienced fishers (Mueller et al., 2008; Turner et al., 2014).

Discrepancies in actors' reports on shared relations are common due to poor memory recall, the manner in which relational information is elicited, or bias in reporting (Admiraal and Handock, 2015). Although, the relatively low level of agreement between actors found in our study may be partially due to the fact that participants were asked to name a maximum of 10 people with whom they interacted rather than all people with whom they exchanged information, forcing respondents to select the individuals they interacted with the most. In so doing, we assume that inconsistencies between respondents are not due to errors or bias in reporting but rather to restrictions on the number of reported information-sharing relations and incomplete memory recall. We also observed inconsistencies in the reported mode of communication, frequency of communication, and duration of the information-sharing relations. The percentage of relations for which there were such inconsistencies were 31.1, 37.7, and 41%, respectively. The highest level of inconsistency was observed for the topic of the information exchanged (41%). Inconsistencies can occur for a variety of reasons, including confusion about the topic's definition (particularly between the topics 'fishery' and 'management,' as these can overlap), an incomplete reporting of modes of communication, or miscalculating the frequency or duration of communication. These inconsistencies can result in changes for some edge attributes (i.e., the details of an interaction), but they do not influence the overall network structure.

The Peel-Harvey Catchment Council (PHCC), a community-based non-governmental organization (NGO) that promotes an integrated approach to protecting, restoring and generally managing the Peel-Harvey catchment, and Recfishwest (RFW), the main NGO and advocate for recreational fishing in WA, were the two other organizations most highly connected, after DPIRD and MLFA. RFW, was one of the most connected organizations in the network. Unlike commercial fishers, it is common for recreational fishers to be represented by a broad recreational fishing organization, as they are often not affiliated to one group or association (Kearney, 2002). The high degree prestige of this organization suggests that most information received is sourced from government bodies and other groups responsible for the management of the fishery. Though a decrease in the degree centrality, combined with a relatively low betweenness centrality suggests that this organization is sharing information with other stakeholders outside these groups, and not so much within it. The PHCC is the only organization that is not directly involved in the fishery, research on BSC or its management. This organization had a high degree centrality compared to its degree prestige, suggesting that it shared information with the main organizations forming the PHBSC fishery network (included in the closed population network), though it received information from other stakeholders outside these groups. Its bridging capacity was the third highest in the PHBSC closed population network, suggesting that through sharing information with stakeholders within and outside the PHBSC network, this organization connects groups that otherwise would be disconnected, making it a key bridging organization in the PHBSC network. A greater inclusion of PHCC in the fishery management network would enable new information coming into the network to be disseminated and facilitate information-exchange in the network.

The above four organizations (i.e., DPIRD, MLFA, RFW, and PHCC) represent stakeholders with different objectives for the development and the protection of the natural resources of the Peel-Harvey Estuary. The strong degree centrality, degree prestige and/or betweenness centrality of these four groups enable the inclusion of management, science and environmental topics and issues as part of the main discussions between stakeholders. However, most discussions focused on the management of the fishery and its science, and a reduced focus was put on the environment of the estuary.

Organizations such as the Western Australian Fishing Industries Council (WAFIC), representing commercial fishers in WA, and the Marine Stewardship Council (MSC), one of the main certification bodies for sustainable seafood globally, had low measures of degree and betweenness centrality and degree prestige in the BSC fishery network. The low centrality and prestige metrics of MSC could be due to having only one representative in WA, who is responsible for managing the certifications for all WA fisheries. The low measures of degree centrality and degree prestige for WAFIC may relate to the strong connectivity of the MLFA in the network. MLFA is a member of WAFIC, and through the commercial fishers being highly engaged in information exchange in the network, it is potentially not necessary for WAFIC to be highly connected too.

Our study found that the connectivity of academics, particularly from Murdoch University, was low despite a 40-year history of research on fish and invertebrate biology and ecology in the Peel-Harvey Estuary (e.g., Potter et al., 1983). This issue is quite common as scientists, and particularly academics (Cvitanovic et al., 2018), are usually sources of high-quality information yet, have traditionally mainly shared their knowledge with their peers (i.e., other academics and scientists) and to a lesser degree with relevant organizations such as key stakeholders in the field of study (Fullwood and Rowley, 2017). Restricting knowledge exchange within an organization or group impedes the diffusion of information outside the entity and can create clusters or silos of high-quality information that is not shared across the network. As an organization, Murdoch's bridging capacity was among the five highest of all organizations, and mainly shared information with DPIRD and RFW, and less so with groups such as the PHCC or WAFIC. This high bridging capacity highlights that despite having relatively fewer interactions with others, the established interactions are with different organizations or groups, and suggests that Murdoch could play a more important role connecting groups that otherwise would be disconnected through information sharing.

Network of Recreational Fishers

The bipartite network analysis highlighted that recreational fishers were mostly connected with their peers, such as family or friends that also fish or other fishers they meet at fishing spots. Other studies have previously described the value of information-sharing relationships among different fishers, and the different strategies used for information sharing, for example commercial lobster fishers in Maine, United States, exchange information on fishing sites and catch (Palmer, 1991). Interestingly, our results showed that while mainly interacting with other recreational fishers, this sector also commonly exchanged information with commercial fishers, mainly on fishing spots, catches, bait used and shared opinions on the catches during the season. This is probably a result of sharing the same fishing locations and launching their boats from the same boat ramps. Though these discussions are very informal, they are relevant for the social acceptability (or social license to operate) of the commercial sector in the region. In fact, social license to operate is an increasingly important issue for commercial fishers throughout Australia, as the recreational sector grows, and the commercial sector is pushed out of some fisheries (Cullen-Knox et al., 2017). Conflict between recreational and commercial fishers over a resource has often been reported worldwide (Voyer et al., 2017). Previous studies have demonstrated the importance of communication between stakeholders for achieving understanding between groups, reaching consensus and gaining a social license to operate for commercial resource users (Voyer et al., 2015). Commercial fishers in WA have previously reported that gaining an enhanced social license to operate was a key reason for initiating the certification process of the PHBSC fishery with the Marine Stewardship Council (van Putten et al., 2020).

It has been reported previously that bridging organizations face difficulties in fully representing the views of large numbers of constituents (Berdej and Armitage, 2016). Recreational fishers' perceptions of the quality of information provided by various organizations showed a contrast between how they viewed information related to the BSC fishery from DPIRD (rated as highest quality) and that from RFW (lower quality). Individual perceptions are strongly linked to prior beliefs and/or expectations (Ajzen, 1991; Stern et al., 1999), and while understanding the elements that could potentially influence perceptions was beyond the scope of this study, the perceived lower quality of the information provided by RFW as well as its lower centrality in the bipartite network of recreational fishers and organizations, could be related to the diverse views of thousands of BSC recreational fishers. It should be noted that the lower perceived quality of information described here is specific to the blue swimmer crab fishery, and therefore it does not necessarily apply to RFW's communication strategy for other recreational fisheries in WA.

Impediments to Information Flow in the Network

The current modes of communication used within the PHBSC recreational fishery network could potentially be an impediment for sharing information effectively with the recreational fishing sector, thus reducing the capacity for sharing high-quality information. Though, both DPIRD and

RFW rarely shared information using a face-to-face approach, RFW used a greater diversity of communication modes to recreational fishers DPIRD. This is an important element as the recreational fishing sector is composed of individuals of different social groups with different cultural and socio-economic backgrounds. Previous research has demonstrated that different social groups might access information differently. For example, younger individuals are likely to use social media more extensively than older individuals (Correa et al., 2010). Thus, a greater diversity of modes of communication will facilitate the diffusion of information through the social network. The diversity of communication modes used by RFW means that the perceived lower quality information is potentially more accessible to others in the network, than information shared through DPIRD, which is perceived as of higher quality.

Our study found a mismatch between the public events available with a focus on the fishery and their potential to share information among resource users. While at least seven public events that shared information on the management and science of the fishery occurred over the course of this study, only a minority of the recreational fishers (12%) were aware of them. Furthermore, those who were aware of the events could only identify at most two of the seven, suggesting that the promotion of public events among the PHBSC fishery resource users and, subsequently, the effectiveness of sharing information through these events, is poor. These events could greatly enhance the communication of high-quality information as both non-fisher and fisher stakeholders considered them useful and supported having more public events promoting the fishery and sharing information on its status and management. This study shows that resource users and the general public, who have low degree centrality and degree prestige and, were not present in the closed population network, are highly dependent on bridging organizations to receive information from government bodies and other organizations responsible for the management of the fishery. The PHCC and RFW, could potentially enhance the promotion of these events by sharing the information with groups that are not central in the fishery network. This aligns with the organizations' strategic plans. The utilization of effective modes of communication, such as having a strong presence online, as well as face-to-face interaction would also benefit the promotion of such events.

CONCLUSION

In general, very little is known about how information is shared through a fishery social network or about the influence of network structure on information sharing and its consequences for fisheries management (Alexander et al., 2015). Social network analysis can disentangle some of these questions using an interdisciplinary approach with an emphasis on the human dimensions of fisheries. Our study demonstrated empirically that (i) a few individuals were key for sharing information within and between different organizations forming the fishery network and only two of six stakeholder groups appeared as key for information sharing (a Government body and the commercial fishing sector); (ii) academic groups were the least connected despite having actively researched the Peel-Harvey Estuary, including research on the biology of *P. armatus* for over 40 years; (iii) recreational fishers exchanged information mainly with other fishers and the regional fisheries department, and less with the organization representing this sector, highlighting a potential impediment to sharing information on the status and management of the fishery; (v) issues of inclusiveness and representation were highlighted for some of the groups and organizations. From these, we have identified logistical and institutional impediments to communicating information on the science, management and environmental issues related to a small-scale crab fishery. The findings provide managers and other stakeholders with a pathway to action to enhance resource management. In terms of small-scale fishery networks this study demonstrated the importance of: (i) communication modes including face-to-face interactions with fishers, and the use of online resources such as social media; (ii) effective integration of bridging organizations in the network who do not necessarily have primary responsibility for fisheries research and management; and (iii) the need for academics to actively create connections with other stakeholders in the network.

The sustainability of fisheries management requires an understanding of the different elements composing a fishery system. Each stakeholder group is required to provide information available on the fishery to enable the assessment of the fishery status. Understanding information-sharing pathways and assessing their performance is fundamental to sustainable fisheries management, as information might be incorrectly interpreted or even overlooked. This could potentially affect the fishery's social license to operate, reducing acceptance within the local community. Reduced community acceptance could even lead to conflict and failure of effective management and implementation. The results from this study also illustrate the value of empirical research in understanding stakeholder connections and information flow processes for informing the management of fisheries.

DATA AVAILABILITY STATEMENT

The datasets generated in this article are not readily available because of the significantly increased risk that individuals may be more easily identifiable and therefore breach confidentially of the data required by the Human Research Ethics approval conditions. Requests to access the datasets should be directed to clara.obregon@murdoch.edu.au.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Murdoch University Human Research Ethics Committee. All work was conducted in accordance with Murdoch University Human Ethics Permit 2017/129.

The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

CO, MH, NL, and JT conceived and devised the presented idea. CO, IP, and MH designed the surveys. CO and IP classified the data collected and determined planned potential outlines that could be obtained from the results. CO and RA performed the network analysis and structured the manuscript. RA aided in interpreting the results. All authors contributed to writing and reviewing of the manuscript.

FUNDING

This study was supported by funding from the FRDC (FRDC 2016/034) on behalf of the Australian Government, the Recreational Fishing Initiatives Fund and Murdoch University.

ACKNOWLEDGMENTS

Stakeholders from the Peel-Harvey blue swimmer crab fishery, in particular, the commercial and recreational fishers, are thanked for their time and participation in the surveys. Dr. Emily Ogier from the Human Dimension Research subprogram of the Fisheries Research and Development Corporation of Australia (FRDC) and DPIRD staff are thanked for their useful input. The writing of this paper was helped by a research visit to CSIRO in Hobart, and the support of this institution is greatly acknowledged. We also thank the two reviewers, as well as the editor, whose input and feedback greatly improved the clarity and overall quality of the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.578014/full#supplementary-material

REFERENCES

Admiraal, R., and Handock, M. S. (2015). A log-linear modelling approach to assessing the consistency of ego reports of dyadic outcomes with applications to fertility and sexual partnerships. *J. R. Stat. Soc. Ser. A Stat. Soc.* 178, 363–382. doi: 10.1111/rssa.12067

Ajzen, I. (1991). The theory of planned behavior. *Organ. Behav. Hum. Decis. Process.* 50, 179–211. doi: 10.1016/0749-5978(91)90020-T

Alexander, S. M., Armitage, D., and Charles, A. (2015). Social networks and transitions to co-management in jamaican marine reserves and small-scale fisheries. *Glob. Environ. Change* 35, 213–225. doi: 10.1016/j.gloenvcha.2015.09.001

Barclay, K. (2012). The social in assessing for sustainability. Fisheries in Australia. *Cosmopol. Civil Soc. Interdiscip. J.* 4, 38–53. doi: 10.5130/ccs.v4i3.2655

Barnes-Mauthe, M., Allen Gray, S., Arita, S., Lynham, J., and Leung, P. (2015). What determines social capital in a socialecological system? Insights from a network perspective. *Environ. Manag.* 55, 392–410. doi: 10.1007/s00267-014-0395-7

Berdej, S. M., and Armitage, D. R. (2016). Bridging organizations drive effective governance outcomes for conservation of Indonesia's marine systems. *PLoS One* 11:e0147142. doi: 10.1371/journal.pone.0147142

Berkes, F., Folke, C., and Colding, J. (2000). *Linking Social and Ecological Systems: Management Practices and Social Mechanisms for Building Resilience*. Cambridge, MA: Cambridge University Press.

Bodin, O., and Crona, B. I. (2009). The role of social networks in natural resource governance: what relational patterns make a difference? *Glob. Environ. Change* 19, 366–374. doi: 10.1016/j.gloenvcha.2009.05.002

Bodin, O., and Norberg, J. (2005). Information network topologies for enhanced local adaptive management. *Environ. Manag.* 35, 175–193. doi: 10.1007/s00267-004-0036-7

Butts, C. T. (2019). *Sna. R package version 4.0.2.* Available online at: https://cran.r-project.org/web/packages/sna/index.html

Butts, C. T., Hunter, D. R., Handcock, M. S., Bender-deMoll, S., Homer, J., and Wang, L. (2019). *"Package 'Network"'. R package version 4.0.2.* Available online at: https://cran.r-project.org/web/packages/network/index.html

Caputi, N., Jackson, G., and Pearce, A. (2014). *The Marine Heat Wave Off Western Australia During the Summer of 2010/11: 2 Years on*. Fisheries Research Report No 250. Western Australia: Department of Fisheries.

Cárcamo, P. F., Garay-Flühmann, R., and Gaymer, C. F. (2014). Collaboration and knowledge networks in coastal resources management: how critical stakeholders interact for multiple-use marine protected area implementation. *Ocean Coast. Manag.* 91, 5–16. doi: 10.1016/j.ocecoaman.2014.01.007

Chizinski, C. J., Martin, D. R., Shizuka, D., and Pope, K. L. (2018). Bipartite networks improve understanding of effects of waterbody size and angling method on anglerfish interactions. *Can. J. Fish. Aquat. Sci.* 75, 72–81. doi: 10.1139/cjfas-2016-0176

Cohen, P. J., Evans, L. S., and Mills, M. (2012). Social networks supporting governance of coastal ecosystems in solomon islands: social networks for ecosystem governance. *Conserv. Lett.* 5, 376–386. doi: 10.1111/j.1755-263X.2012.00255.x

Correa, T., Hinsley, A. W., and Gil de Zúñiga, H. (2010). Who interacts on the web?: the intersection of users' personality and social media use. *Comput. Hum. Behav.* 26, 247–253. doi: 10.1016/j.chb.2009.09.003

Csardi, G. (2019). *Igraph. R package version 4.0.2.* Available online at: https://cran.r-project.org/web/packages/igraph/index.html

Cullen-Knox, C., Haward, M., Jabour, J., Ogier, E., and Tracey, S. R. (2017). The social licence to operate and its role in marine governance: insights from Australia. *Mar. Policy* 79, 70–77. doi: 10.1016/j.marpol.2017.02.013

Cvitanovic, C., van Putten, E. I., Hobday, A. J., Mackay, M., Kelly, R., McDonald, J., et al. (2018). Building trust among marine protected area managers and community members through scientific research: insights from the Ningaloo Marine Park, Australia. *Mar. Policy* 93, 195–206. doi: 10.1016/j.marpol.2018.04.010

Department of Primary Industries, and Regional Development [DPIRD] (2018). *Protecting Breeding Stock Levels of the Blue Swimmer Crab Resource in the South West*. Fisheries Management Paper No. 288. Western Australia: Department of Primary Industries and Regional Development.

Ernoul, L., and Wardell-Johnson, A. (2013). Governance in integrated coastal zone management: a social networks analysis of cross-scale collaboration. *Environ. Conserv.* 40, 231–240. doi: 10.1017/S0376892913000106

Fletcher, W. J., Mumme, M. D., and Webster, F. J. (2017). *Status Reports of the Fisheries and Aquatic Resources of Western Australia 2015/2016: The State of the Fisheries*. Western Australia: Department of Fisheries.

Fullwood, R., and Rowley, J. (2017). An investigation of factors affecting knowledge sharing amongst UK academics. *J. Knowl. Manag.* 21:38. doi: 10.1108/JKM-07-2016-0274

Grant, S., and Berkes, F. (2007). Fisher knowledge as expert system: a case from the longline fishery of Grenada, the Eastern Caribbean. *Fish. Res.* 84, 162–170. doi: 10.1016/j.fishres.2006.10.012

Gutiérrez, N. L., Hilborn, R., and Defeo, O. (2011). Leadership, social capital and incentives promote successful fisheries. *Nature* 470, 386–389. doi: 10.1038/nature09689

Hallett, C. S., Hobday, A. L., Tweedley, J. R., Thompson, P. A., McMahon, K., and Valesini, F. J. (2018). Observed and predicted impacts of climate change on the estuaries of South-Western Australia, a mediterranean climate region. *Region. Environ. Change* 18, 1357–1373. doi: 10.1007/s10113-017-1264-8

Handcock, M. S., Hunter, D. R., Butts, C. T., Goodreau, S. T., Krivitsky, P. N., Bender-deMoll, S., et al. (2019). *Statnet. R package version 4.0.2*. Available online at: https://cran.r-project.org/web/packages/statnet/index.html

Hardin, G. (1968). The tragedy of the commons. *Science* 162, 1243–1248. doi: 10.1126/science.162.3859.1243

Kearney, R. E. (2002). Co-management: the resolution of conflict between commercial and recreational fishers in victoria, Australia. *Ocean Coast. Manag.* 45, 201–214. doi: 10.1016/S0964-5691(02)00055-8

Leonard, N. J., Taylor, W. W., Goddard, C. I., Frank, K. A., Krause, A. E., and Schechter, M. S. (2011). Information flow within the social network structure of a joint strategic plan for management of great lakes fisheries. *N. Am. J. Fish. Manag.* 31, 629–655. doi: 10.1080/02755947.2011.603651

Link, J. S., and Marshak, A. R. (2019). Characterizing and comparing marine fisheries ecosystems in the united states: determinants of success in moving toward ecosystem-based fisheries management. *Rev. Fish Biol. Fish.* 29, 23–70. doi: 10.1007/s11160-018-9544-z

Maiolo, J. R., Johnson, J., and Griffith, D. (1992). Applications of social science theory to fisheries management: three examples. *Soc. Nat. Resourc.* 5, 391–407. doi: 10.1080/08941929209380801

Marine Stewardship Council [MSC] (2019). *Get Certified. Your Guide to the MSC Fishery Assessment Process*. London: Marine Stewardship Council.

McPherson, M., Smith-Lovin, L., and Cook, J. M. (2001). Birds of a feather: homophily in social networks. *Annu. Rev. Sociol.* 27, 415–444. doi: 10.1146/annurev.soc.27.1.415

Morison, A., Daume, S., Gardner, C., and Lack, M. (2015). *Western Australia Peel-Harvey Estuarine Fishery MSC Full Assessment Final Report*. Victoria: SCS Global Services Report.

Mueller, K. B., Taylor, W. W., Frank, K. A., Robertson, J. M., and Grinold, D. L. (2008). Social networks and fisheries: the relationship between a charter fishing network, social capital, and catch dynamics. *N. Am. J. Fish. Manag.* 28, 447–462. doi: 10.1577/M07-016.1

Obregón, C., Tweedley, J. R., Loneragan, N. R., and Hughes, M. (2020). Different but not opposed: perceptions between fishing sectors on the status and management of a crab fishery. *ICES J. Mar. Sci.* 2019:fsz225. doi: 10.1093/icesjms/fsz225

Peel Development Commision [PDC] (2019). *Our Region - Fastest Growing Region in Western Australia*. Mandurah: Peel Development Commision.

Pitcher, T. J., Kalikoski, D., Short, K., Varkey, D., and Pramod, G. (2009). An evaluation of progress in implementing ecosystem-based management of fisheries in 33 countries. *Mar. Policy* 33, 223–232. doi: 10.1016/j.marpol.2008.06.002

Potter, I. C., Chrystal, P. J., and Loneragan, N. R. (1983). The biology of the blue manna crab *Portunus pelagicus* in an Australian Estuary. *Mar. Biol.* 78, 75–85. doi: 10.1007/BF00392974

Rogers, E. M. (1995). *Diffusion of Innovations*, 5th Edn. New York, NY: Free Press.

Ryan, K. L., Hall, N. G., Lai, E. K., Smallwood, C. B., Tate, A., Taylor, S. M., et al. (2019). *Statewide Survey of Boat-Based Recreational Fishing in Western Australia 2017/18*. Fisheries Research Report No. 297. Western Australia: Department of Primary Industries and Regional Development.

Stern, P. C., Dietz, T., Abel, T., Guagnano, G. A., and Kalof, L. (1999). A value-belief-norm theory of support for social movements: the case of environmentalism. *Hum. Ecol. Rev.* 6, 81–97.

Taylor, S. M., Blight, S. J., Desfosses, C. J., Steffe, A. S., Ryan, K. L., Denham, A. M., et al. (2018). Thermographic cameras reveal high levels of crepuscular and nocturnal shore-based recreational fishing effort in an Australian estuary. *ICES J. Mar. Sci.* 75, 2107–2116. doi: 10.1093/icesjms/fsy066

Turner, R. A., Polunin, N. V. C., and Stead, S. M. (2014). Social networks and fishers' behavior: exploring the links between information flow and fishing success in the northumberland lobster fishery. *Ecol. Soc.* 19:38. doi: 10.5751/ES-06456-190238

Valesini, F. J., Hallett, C. S., Hipsey, M. R., Kilminster, K. L., Huang, P., and Hennig, K. (2019). "Peel-harvey estuary, Western Australia," in *Coasts and Estuaries*, eds E. Wolanski, J. W. Day, M. Elliott and R. Ramesh (Amsterdam: Elsevier), 103–120. doi: 10.1016/b978-0-12-814003-1.00007-1

van Putten, I., Longo, C., Arton, A., Watson, M., Anderson, C. M., Himes-Cornell, A., et al. (2020). Shifting focus: the impacts of sustainable seafood certification. *PLoS One* 15:e0233237. doi: 10.1371/journal.pone.0233237

von Heland, F., Crona, B., and Fidelman, P. (2014). Mediating science and action across multiple boundaries in the coral triangle. *Glob. Environ. Change* 29, 53–64. doi: 10.1016/j.gloenvcha.2014.08.003

Voyer, M., Gladstone, W., and Goodall, H. (2015). Obtaining a social licence for MPAs influences on social acceptability. *Mar. Policy* 51, 260–266. doi: 10.1016/j.marpol.2014.09.004

WAFIC (2020). *Who We Are – Our members*. Fremantle: Western Australian Fishing Industry Council Inc.

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 30 October 2020
doi: 10.3389/fmars.2020.577964

Contrasting Futures for Australia's Fisheries Stocks Under IPCC RCP8.5 Emissions – A Multi-Ecosystem Model Approach

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Specialty section:
This article was submitted to
Marine Fisheries, Aquaculture
and Living Resources,
a section of the journal
Frontiers in Marine Science

Received: 30 June 2020
Accepted: 17 September 2020
Published: 30 October 2020

Citation:
Pethybridge HR, Fulton EA, Hobday AJ, Blanchard J, Bulman CM, Cheung WWL, Dutra LXC, Gorton R, Hutton T, Matear R, Lozano-Montes H, Plagányi EE, Villanueva C, Zhang X and Butler IR (2020) Contrasting Futures for Australia's Fisheries Stocks Under IPCC RCP8.5 Emissions – A Multi-Ecosystem Model Approach. Front. Mar. Sci. 7:577964. doi: 10.3389/fmars.2020.577964

Climate-driven trends in ocean temperature and primary productivity are projected to differ greatly across the globe, triggering variable levels of concern for marine biota and ecosystems. Quantifying these changes, and the complex ways in which resource-dependent communities will need to respond, is inherently difficult. Existing uncertainty about the structure, function and responses of marine ecosystems, means that a multi-model or ensemble model approach is the most prudent means of assessing the potential ecosystem responses to climate change. In this study, climate-ecological projections of 13 marine ecosystem models for regions around Australia were evaluated. Model types included dynamic food web, spatial whole of ecosystem, intermediate complexity, species distribution, and size spectrum models and were all forced by high-resolution ocean model data. Each Australian region and fishery will face its own challenges in terms of ecosystem shifts and fisheries management responses over the next 30 years. Across regions, demersal systems appear to be more strongly affected by climate change than pelagic systems, with invertebrate species in shallow waters likely to respond first and to a larger degree. With the assistance of qualitative confidence evaluations, the multi-model approach was useful for identifying the likely state of concern for each functional group and thus adaptive management and research priorities. Largest model discrepancies were found between the regional ecosystem models that represent trophic interactions and the species distribution models, with implications for future assessments and adaption planning. Study results highlight that fisheries and their management will need to foster pro-active and flexible adaptation options to make the most of coming opportunities and to minimize risks or negative outcomes.

Keywords: forecasting, climate change, model uncertainty, fisheries management, adaptive management, ensemble modeling

INTRODUCTION

Globally, marine ecosystems are in a period of rapid change with predicted climate effects reducing our confidence in the outcomes from continued existing management actions. There is substantial evidence of climate change affecting the distribution, abundance and size of both target and non-target species around the globe in tropical, temperate and polar environments (Hobday and Pecl, 2014) and at time scales relevant to current management and strategic planning (Allison and Bassett, 2015; Busch et al., 2016; Sheaves et al., 2016). While some species or populations will be highly sensitive to ocean warming, others will be much more tolerant and adaptive, meaning there will be winners, losers, and potential surprises (Fulton, 2011; Dutkiewicz et al., 2013). Changes at the sub-population level can modify communities and ecosystems, which in turn feedback to affect individuals of many species. Therefore, industries and managers will need to be strategic and structured in their approach to adaptive planning in ways that will minimize losses and maximize opportunities that might arise from climate change (Norman-López et al., 2011; Pecl et al., 2017). Ideally this would involve taking a climate-informed, ecosystem approach to fisheries management (EAFM), which encourages conservation and sustainable use of the whole ecosystem (Heenan et al., 2015).

Marine ecosystem and multi-species models attempt to represent links between species, either through feeding or habitat use, as well as human activities and natural variability influencing the system. These models are particularly useful tools for synthesizing and extending scientific understanding of how the ecosystems function. The models also offer a strategic tool for managers of natural resources where they can explore the potential consequences of human or environmental impacts and test potential solutions. Increasingly, ecosystem models are used to distinguish the effects of climate change and fishing on entire ecosystems as well as on individual species or groups of species (Plagányi et al., 2011). Global model simulations of direct and indirect effects of climate change suggest that over a large spatial scale, bulk fisheries yields will be reduced (Cheung et al., 2010; Sumaila et al., 2011; Blanchard et al., 2012; Free et al., 2019).

Best practice for utilizing ecosystem models in support of EAFM is suggested as a multi-model (or ensemble) approach where at least two models, developed independently and that use different frameworks, are compared to make sure underlying process biases or structural assumptions are not skewing model results (Spence et al., 2018). Direct comparisons across many regional and global models are inherently difficult due to the way that different models are structured and function (Payne et al., 2016). However, the multi-model approach has proven useful to demonstrate the potential range in outcomes and the level of confidence that is associated with each of the different model projections (Cheung et al., 2016a; Barange et al., 2018; Hollowed et al., 2020). Close agreement between model outputs offers enhanced confidence in model outcomes while disagreement can be used to flag the need for more targeted information. Within a climate context, most effort to date around ensemble projections has been in terms of bulk (total system-level) changes in biomasses, though more is being done through the Fisheries Inter-Model Comparison Project (Fish-MIP) in terms of functional group and species level effects at the global (Tittensor et al., 2018; Lotze et al., 2019) and ocean basin (Bryndum-Buchholz et al., 2019) scales. Within both Fish-MIP and national agencies, there are also a growing number of studies, particularly in the Northern hemisphere, being undertaken using the multi-model approach to project local or regional-scale climate driven changes at the species or functional level (e.g. Pacific sardine in the California current; Kaplan et al., 2019).

Australia's marine environment encompasses sub-polar to tropical zones. Two of the world's most rapidly warming ocean areas are located in the south-east and south-west, and even outside these regions, the tropical waters of Australia are warming at almost twice the global average (Lough and Hobday, 2011; Hobday and Pecl, 2014). Australia has a rich history of ecosystem modeling and many ecosystem models, using various modeling platforms, have been developed over the last two decades such that they collectively cover most of the Australian coastline (**Figure 1**). These models were built for varying purposes but are being increasingly used to provide information in support of EAFM (Brown et al., 2010; Fulton et al., 2011a; Smith et al., 2017). Key examples include the use of a spatial whole of ecosystem model (Atlantis) as a tool for evaluating alternative management strategies for the Southern and Eastern Scalefish and Shark Fishery (SESSF), where model projections were used to restructure the fisheries (Fulton et al., 2014). Dynamic food web models (using the Ecopath with Ecosim (EwE) framework) of the Northern Prawn Fishery have been used to evaluate spatial management options for the Marine Stewardship Certified high value fishery (Dichmont et al., 2013). Lastly, statistical fit bespoke Models of Intermediate Complexity of Ecosystems (MICE) are being used to inform strategic thinking about management of tropical beche-de-mer, prawn and lobster fisheries (Plagányi et al., 2014, 2019).

The aim of this study was to use 13 different ecosystem models to assess the likely state of concern for Australia's fisheries stocks under projected climate change and to report the level of confidence in our ecosystem projections. To achieve this, we run ecosystem projections to 2050 using ocean model projections for the Australian region and the Commonwealth fisheries and explored the single and combined effects of climate change and fisheries. Commonwealth fisheries are those managed at a federal Australia wide level, (typically) from three nautical miles offshore to the boundary of the Australian Fishing Zone (200 nautical miles offshore), as well as Australian boats fishing on the high seas. A novel framework was developed to assess confidence in the robustness of climate-mediated biomass projections by accounting for uncertainty from multiple sources (the ocean model, ecosystem model, and data). We focus on ecological projections over the short to medium term (between 2020 and 2050) as this is the scale most relevant to industry and climate-risk management and adaptation planning. It is also a period for which a high degree of overlap occurs in the various greenhouse gas emissions scenarios used in future climate projection such as the Coupled Model Intercomparison Project (CMIP5 IPCC; Van Vuuren et al., 2011). The information generated from this study is of relevance to Australian and international fishers

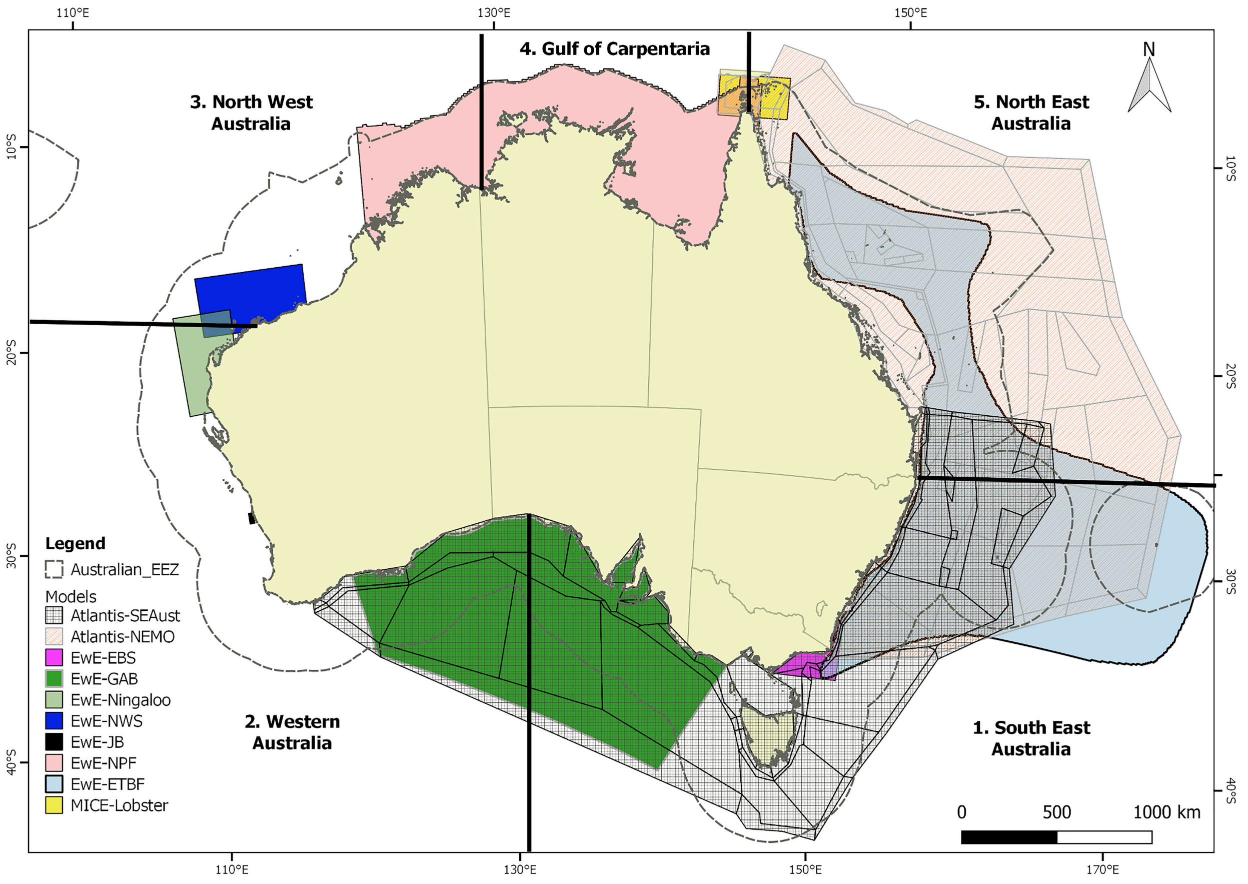

FIGURE 1 | Map showing the regional ecosystem model domains and the 5 assessment regions. The two global modeling platforms are not shown on the map though extracted outputs for each assessment region within the Australian Economic Exclusion Zone (EEZ).

and fisheries managers looking to incorporate climate change adaptation measures and strategies into existing plans.

MATERIALS AND METHODS

Ecosystem Modeling Platforms

We used thirteen extant ecosystem models across five published and validated modeling platforms to provide a wide coverage of the Australian Exclusive Economic Zone (EEZ) (**Table 1**). This set included five different modeling platforms and approaches: a dynamic and spatially explicit whole of ecosystem model, Atlantis (Fulton et al., 2011b; Audzijonyte et al., 2019), a dynamic mass-balanced EwE model (Christensen and Walters, 2004; Colléter et al., 2015), a statistically data-fitted MICE (Plagányi et al., 2014), a community size spectrum model (Blanchard et al., 2012), and an ensemble of species-based distribution models called dynamic bioclimate envelope models (DBEM, Cheung et al., 2009). Greater details of these modeling approaches are provided in **Supplementary Material 1**. These modeling platforms vary greatly in their assumptions, structure (number of functional groups, size or age classes represented) and the level of spatio-temporal and ecological complexity (**Table 2**). Each of these models was originally designed for a specific question or purpose and as such often focuses on particular components of the ecosystem.

Regional models, using the Atlantis, EwE or MICE platforms, have been implemented for specific Australian marine ecosystems (**Figure 1** and **Table 2**), with the combined set covering much of Australia's coastline: Great Barrier Reef, Coral Sea, Gulf of Carpentaria, Northwest Shelf, Ningaloo Reef (Gascoyne coast), southwest Australia (Jurien Bay), North east Australia (Torres Strait), Great Australian Bight, and the entire southeast Australia. This geographic extent also spans all of Australia's major marine continental ecosystem types from sub-polar to tropical.

Outputs from two global models, which contributed global-scale climate simulations to the Fisheries Inter-Model Comparison Project (Fish-MIP; Tittensor et al., 2018), were obtained for the Australian EEZ. Mean outputs from the global models were extracted for each of the 5 assessment regions: (1) South East Australia, (2) Western Australia; (3) North West Australia, (4) Gulf of Carpentaria; and (5) North East Australia (**Figure 1**).

Four hundred and sixty five species or functional groups were assessed from the 11 regional ecosystem models around

TABLE 1 | Summary of the main differences between the five model frameworks used to examine ecosystem responses to climate and fishing management drivers.

Model framework	**Main assumption**	**Key processes considered**	**Climate drivers**	**Level of complexity**			**Attributes tracked**	**Calibration method**	**Scale suitability**
				Spatial	**Temporal**	**Taxa**			
Atlantis	Deterministic, species-based and size/age structured, whole system model	Biogeochemical cycles, animal movements (including migrations), life-history, habitat dependency, environmental tolerance and physiologically mediated responses, trophic interactions	Temp, Salinity	High (3D, multiple spatial boxes - vertical layers)	High (12 h)	Moderate (groups)	Biomass, body size, condition, distribution, phenology, fisheries yields	Pattern-oriented simultaneous but heuristic calibration to produce plausible spatiotemporal dynamics or fit to observations; uses a data pedigree approach to tune most uncertain parameters	Ecosystem-level, regional-level, fisheries species (ideally for data-rich species, but can be extended to data poor using general ecological principles)
Ecopath with Ecosim (EwE)	Mass-balanced, species-based food web model	Trophic interactions, energy flow	PP	Low (whole domain)	Moderate (seasonal)	Moderate (groups)	Biomass, fisheries yields	Fitting to biomass, catches by tuning predator vulnerabilities based on data pedigree	Ecosystem-level, regional-level, fisheries (data-rich species)
Models of Intermediate Complexity of Ecosystems (MICE)	Statistically fitted species-based model	Population dynamics, focus on key species-specific processes such as trophic interactions and environmental drivers	Temp	Low (whole domain)	Low (annual)	High (species)	Biomass, numbers-at-age, fisheries yields	Statistically fitted to data	Regional-level, fisheries (data poor and preferably rich species)
Size spectrum model (dynamic benthic-pelagic)	Mechanistic, coupled benthic-pelagic community size spectrum	Body size scaling, coupled trophic interactions between pelagic and benthic pathways	Temp, PP	High (10°grid- no vertical)	Low (annual)	Low (3 groups, 1 biomass pool)	Biomass density	Based on empirical-ecological relationships and parameters. Previously verified against ecological theory and global fisheries catches at country scale.	System-level
Species distribution or dynamic bioclimate envelope	Mechanistic, statistical fitted, species-based model	Spatial ranges, habitat dependency, environmental tolerance and physiology mediated responses	Temp	High (10°grid- no vertical)	Low (annual)	High (species)	Relative abundance, distribution, body size	Statistical correlative relationships	Global-level, fisheries (data-rich species)

Temp, temperature; PP, primary productivity.

TABLE 2 | Summary of the regional and global ecosystem models used in this project to examine ecosystem responses to climate change and fisheries. NA indicates that fishing was not directly included.

Model framework	Model name	Model domain	Region	Main purpose	Fishing effort	Functional groups	Fished groups	Key references
Atlantis	SEAust	South East Australia	1	F, E	Constant, Dynamic	64	36	Fulton et al., 2011a; Fulton and Gorton, 2014; Fulton et al., 2016
	NEMO	Great Barrier Reef	5	E	Constant	62	29	Hutton et al., 2017
EwE	EBS	Eastern Bass Strait	1	E, F	Constant	59	46	Bulman et al., 2002
	GAB	Great Australian Bight	2	R, E	Constant	75	44	Fulton et al., 2018b
	Ningaloo	Ningaloo	2	R	Constant	53	40	Fulton et al., 2011b
	NWS	North West Shelf	3	E	Constant	36	26	Bulman, 2006, 2008
	JB	Jurien Bay Marine Park	2	E	Constant	82	33	Lozano-Montes et al., 2011, 2013
	NPF	Gulf of Carpentaria	4	F	Constant	53	42	Bustamante et al., 2011
	ETBF	Eastern Tuna & Billfish Fishery	5	F	Constant	41	30	Griffiths et al., 2010
Size spectrum	DBPM	Global; Australian EEZ box	1–5	E, F	Constant	6	NA	Blanchard et al., 2012
Species distribution	DBEM-(IPSL, MPIMR, GFDL)	Global; Australian EEZ	1–5	E	Constant	138	NA	Cheung et al., 2009
MICE	Lobster subcomponent	Torres Strait	4	F	Constant, Dynamic	1	1	Plagányi et al., 2014, 2019

E, Ecological understanding; F, fisheries management scenarios; R, Other resource management (including industry).

Australia. This equates to representing in total 294 harvested groups and 52 threatened, endangered and protected species (TEPs), and a significant proportion of non-target bycatch species. A further 6 trophic size-based and system level groups were assessed using the output from the global benthic-pelagic size spectrum model and 138 species were assessed by the ensemble of dynamic bioclimate envelope models. While the complete set of species represented (either individually or within functional groups) is well short of the more than 600 species that interact with Australian fisheries, it incorporates the major target species and the interactions between them either individually or within ecological functional groups.

Fisheries Data and Forcing

The regional ecosystem models were updated and re-calibrated with fisheries data on catches, discards and effort obtained from both State and Commonwealth fisheries for the 2006 to 2016 period. In all regional models, fishing fleets were distinguished by gear-type and target species and projections were made using constant fishing mortality or effort of 2016. All harvested groups or species were assigned according to nine Australian Commonwealth fisheries including the SESSF, Small Pelagic Fishery (SPF), Northern Prawn Fishery (NPF), Eastern and Western Tuna and Billfish Fishery (ETBF and WTBF), Southern Bluefin Tuna Fishery (SBTF), Torres Strait Rock Lobster Fisheries (TSRLF), and Bass Strait Central Zone Scallop Fishery (BSCZSF).

For the global benthic-pelagic size spectrum model (DBPM) fishing was not included and therefore the model outputs reported here represent relative changes in the unexploited biomass of pelagic and benthic consumers under climate forcing only. Previously, DBPM was calibrated for the North Sea (Blanchard et al., 2009) and globally using regional shelf sea models with fishing mortality rates of 0.2 year^{-1} producing catches in broad agreement with empirical time-averaged country-level EEZ estimates from the Sea Around Us Project (Blanchard et al., 2012). Size-dependent growth rates were consistent with the empirical estimates by Pauly (1980) (Blanchard et al., 2012). DBPM produced relative biomass change close to the multi-model mean of (Lotze et al., 2019) which were shown to be consistent with the temperature-dependent hindcasts of Maximum Sustainable Yield for 235 assessed fish stocks after controlling for fishing effects (Free et al., 2019; Lotze et al., 2019).

For the dynamic bioclimate envelope model, global fisheries catch data from the *Sea Around Us* project (Pauly et al., 2020) contributed to the determination of the baseline biogeography of the exploited marine species. Moreover, simulated maximum catch potential for historical time period from the model was shown to be significantly correlated with the reported fisheries catch data, providing additional confidence on the model outputs (Cheung et al., 2009, 2016c).

Climate Model Projections

The climate projection used to force the environmental conditions for each regional model was derived from the Ocean Forecasting Australia Model version 3 (OFAM-v3) downscaling simulations which used the IPCC RCP8.5 high emissions or "no mitigation" greenhouse gas emission scenarios. The atmospheric forcing of the ocean model comes from the multi-model mean of the CMIP5 climate projections under the RCP8.5 scenario (Feng et al., 2017; Zhang et al., 2017). The OFAM-v3 model was coupled to a biogeochemical model representing nutrient flows and plankton components of the ocean food web to produce patterns of primary productivity, nutrient cycling and carbon fluxes that are consistent with observations. The OFAM-v3 simulations provided high-resolution (10 km, 0.1°) projection of the future ocean state with outputs that resolved important oceanographic features (e.g. eddies) and ocean state variables including sea surface temperature (°C), sea surface salinity (PSU), phytoplankton (mmol N m^{-3}), primary productivity (mmol C m^{-2}), phosphate (nmol m^{-3}), base oxygen levels, aragonite saturation, and current flows. For this study, we used two different atmospheric forcings of OFAM-v3 over the 2006 to 2101 period: (1) a high "no mitigation" emission scenario (RCP8.5) where the atmospheric forcings are derived from the CMIP5 multi-model mean, and (2) a control scenario where the atmospheric forcings are based on present-day conditions (Zhang et al., 2017). We used the difference between the RCP8.5 and control scenarios to determine the future climate change. Monthly climate data with spatial resolution of 0.1° (∼10 km) was stored for use in forcing the ecosystem models.

The two global ecosystem models were not forced by the OFAM-v3 model, instead they were forced by climate simulations generated from the ensemble of global Earth system models used within the CMIP5 (Taylor et al., 2012) under the framework of the Fisheries and Marine Ecosystems Impact Models Intercomparison Project (FishMIP) (Tittensor et al., 2018). More specifically FishMIP used the Geophysical Fluid Dynamics Laboratory Climate Model (GFDL-ESM2M, 60), the Institute Pierre Simon Laplace Climate Model (IPSL-CM5A-LR, 61) and the Max Planck Institute Mixed Resolution model (MPIMR). For the benthic-pelagic size-spectrum model, climate change projections were run by linking the lower end of the pelagic consumer size spectrum to small and large phytoplankton biomass time-series from the IPSL-CM5A-LR model only. The benthic consumer size spectrum was linked to time series estimates of near seafloor detritus obtained through sinking rates of primary producers and depth in each grid cell of the ocean. The size-dependent feeding rates in the pelagic and benthic size spectra were forced by average water column and near seafloor temperature, respectively. For the dynamic bioclimate envelope model, growth, body size, mortality, larval dispersal, adult movement and carrying capacity of the habitat of each studied species are functions of annual average ocean conditions including temperature, oxygen level, salinity, ocean advection and net primary production over the simulation timeframe (Cheung et al., 2016a).

Regional Forcing Files

Depending on the type of ecosystem model, daily to monthly climate forcing files were created by extracting and interpolating the climate variables (described above) to the geometry of the ecosystem model. Atlantis models were forced with an interpolated times series of forcing data of daily temperature, salinity and currents (oceanographic exchanges). To do this, the original monthly climate data was overlaid onto the geometry of the Atlantis models to extract mean monthly climate values for each spatial box and horizontal layer in the model domain. Where there were no climate data, the average of the adjacent box values in the appropriate layer was used. The monthly value per box and layer was then interpolated to create daily forcing data. The species and functional groups within Atlantis respond to these conditions – both through physiological rates (e.g. growth) that are conditioned on ambient temperatures, salinity, oxygen and pH levels and via modifying spatial distributions if conditions were beyond their tolerance.

The other regional ecosystem models (EwE and MICE) had coarser temporal and (vertical and horizontal) spatial resolution. For these models, mean monthly surface (0−5 m) values of climate data were extracted from the gridded data for the specific area of the regional model. Forcing time series were calculated as appropriate for the specific model. In EwE models, primary producers were forced using the time series of OFAM primary productivity anomalies, which then fed up through the food web. MICE models can be forced with a range of physical drivers (e.g. Tulloch et al., 2019), but the MICE subcomponent used here was forced with monthly temperature only because it was considered the key driver of growth and mortality for lobsters in the relatively shallow well-mixed Torres Strait region.

Projecting Biomass Changes to Climate Change and Fishing

Control and climate forcing files were applied for a projection period of 40 years, from 2010 to 2050. The two Atlantis models were run for at least 10−20 years prior to the projection period of each simulation which is standard protocol for Atlantis as it allows for consistent model 'burn-in' so that transient effects of the initial conditions in the system do not unduly influence the projections (Pethybridge et al., 2019) and so that historically realistic biomasses are present at the start of the projection period. For the MICE and EwE models, observation data was used for at least 10 years before the projection period so that the short-term historical trajectories were reproduced ensuring the ecosystems were conditioned to the correct biomasses rather than assuming an equilibrium state.

To evaluate the short and medium-term impacts of climate change, the series of 5-year averages of model-derived biomass and fisheries catches were calculated and normalized relative to the values in 2010. These averages were used rather than snapshot values so that there was not undue influence of inter-annual variation (i.e., the results were not skewed by the coincidence of a "poor" year within a reporting window).

To look at the impact of climate change alone (and not the combined effects of fishing and climate), the output for the RCP8.5 emission scenario was calculated relative to the values from the control scenario (present-day fishing and climate state). For the global benthic-pelagic size spectrum and dynamic bioclimate envelope models, biomass changes under RCP8.5 were analyzed relative to historical average biomass across 1990–1999 (reference period) without the requirement of a control run simulation. Both global models were initialized until the simulation outputs stabilized before making forward projections.

Three different anomalies were calculated to examine relative changes in biomass at a given time period (X_t):

(i) Combined impacts of climate change and fisheries projection = RCP8.5 scenario = $\left(\frac{(X_{t,r}-X_{2010})}{X_{2010}}\right)\cdot 100$

where $X_{t,r}$ is the value for that group at time t in the RCP8.5 scenario:

(ii) Fisheries impacts only projection (for regional ecosystem models only) = Control scenario = $\left(\frac{(X_{t,c}-X_{2010})}{X_{2010}}\right)\cdot 100$
where $X_{t,c}$ is the value for that group at time t in the control scenario:

(iii) Climate change impacts only projection = $\left(\frac{\text{RCP8.5}-\text{Control}}{\text{Control}}\cdot 100\right)_t - \left(\frac{\text{RCP8.5}-\text{Control}}{\text{Control}}\cdot 100\right)_{2010}$

For each regional model, we assessed the likely state of concern of all functional groups and species (*negligible – low – moderate – high*) based on: (1) sensitivity – the magnitude and direction of their projected rates of biomass change to the climate change impacts only scenario, and (2) response type – differences in the direction and sensitivity between projections of the RCP8.5 and control scenarios (**Figure 2**). For the sensitivity assessment of climate impacts only, we used 7 incremental changes of 10% as smaller changes may constitute normal inter-annual or regional variation. For the response type, functional groups were assigned to one of 7 groups based on the magnitude and direction of biomass trends (using incremental changes of 20%) for the combined impacts of climate change and fisheries projection relative to the fisheries impact only projection (**Figure 2**). This included divergent responses in which climate change and fisheries projections are in an opposite direction to that of fisheries impacts only; stable projections where biomass trends of both the combined impacts and fisheries impacts only projections are similar (with differences <20%); enhanced response in which biomass changes are in the same direction but are heightened in magnitude under climate change; and dampened responses where biomass changes are in the same direction but where the magnitude is lower under climate change. For the global benthic-pelagic size spectrum and dynamic bioclimate envelope models, a stable response type was assumed.

Ecosystem Model Comparisons and Uncertainty

Inter-regional and global model projections of relative biomass trajectories were compared where there were taxonomic agreement and fisheries or spatial overlap. Such comparisons were relatively simple between the regional models but more challenging between the regional and global models due to differing taxonomic resolutions. Outputs of the dynamic bioclimate envelope model were compared where species could be matched specifically or to the group level (where the species was the strongest representative of the regional model group). Outputs from the global benthic-pelagic size spectrum model were compared with relative trends of aggregated biomass of different species and functional groups in regional models, to determine whether the regional directions of change were consistent with larger-scale relative changes in unexploited biomass under climate forcing alone.

Uncertainty was quantified in three ecosystem models – the two regional Atlantis SEAust models and the ensemble of dynamic bioclimate envelope models (DBEM). For the DBEM, the uncertainty was reduced by using the mean outputs driven by three Earth system models (Cheung et al., 2016b). The results per species were averaged across the three models to give the final ensemble estimate of the impacts of climate change in terms of shifts in abundance. For the regional Atlantis model, uncertainty within model projections was explicitly accounted for by making subtle changes to multiple productivity and food web parameterizations. The parameter sets used were bounded so that they were constrained only to sets that produced plausible modeled systems given the available data and alternative possible system structures (based on a pattern-oriented modeling approach given in Kramer-Schadt et al., 2007). As outlined in Fulton and Gorton (2014), the alternative diet structure was expanded to allow for diets with the potential for the level of variability observed in the North Sea and on Georges Bank over the last century. All alternative parameterizations were then all carried forward in the simulations for both the dynamic and fixed (constant) fishing versions of Atlantis-SEAust. The differences in the results between the model variants were used to examine the robustness of model results.

Uncertainty within and among the ecosystem models was translated into a qualitative evaluation of model confidence (*low – medium – high*; **Figure 3**). This confidence had two components – uncertainty due to the data amount and quality used in creating the model and uncertainty around model structure. For data uncertainty, where possible this was judged based on how well the "now" state (abundance and distributions) or historical trajectories matched available data. If this was not possible then model developers used expert judgment to rank the level of confidence in the projected species responses. In doing this the modelers considered the amount and quality of data used for model parameterization and calibration of each functional group or species. This included data directly relevant to the species (such as biological rates, diets and mortality levels), but in some models also included processes (such as environmental or habitat-mediated response functions) that influence species abundance or distribution. Process uncertainty was also assessed based on the fit to data and was treated as distinct from model structural uncertainty (explained below).

For the regional ecosystem models, the data uncertainty comparisons were primarily based on how well modeled biomass and catch trajectories matched the available data. Where there were no or limited data, and particularly where there were insufficient time-series of biomass or catch data with which to constrain the model and improve its performance, functional group responses were classified as having *high* data uncertainty. Species for which modelers used a large amount of relevant data, including fitting outputs to historical time-series data, were judged as having *low* data uncertainty. For the dynamic bioclimate envelope model, simulated distribution maps for a particular species were visually assessed by comparing the "now state" of their distributions with distributional maps from the Codes for Australian Aquatic Biota[1]. Modeled species maps that corresponded well with the known distribution were ranked *low* to *low-medium* data uncertainty (this was roughly half of the modeled species). A *medium* rank was assigned

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[1] https://www.cmar.csiro.au/caab/

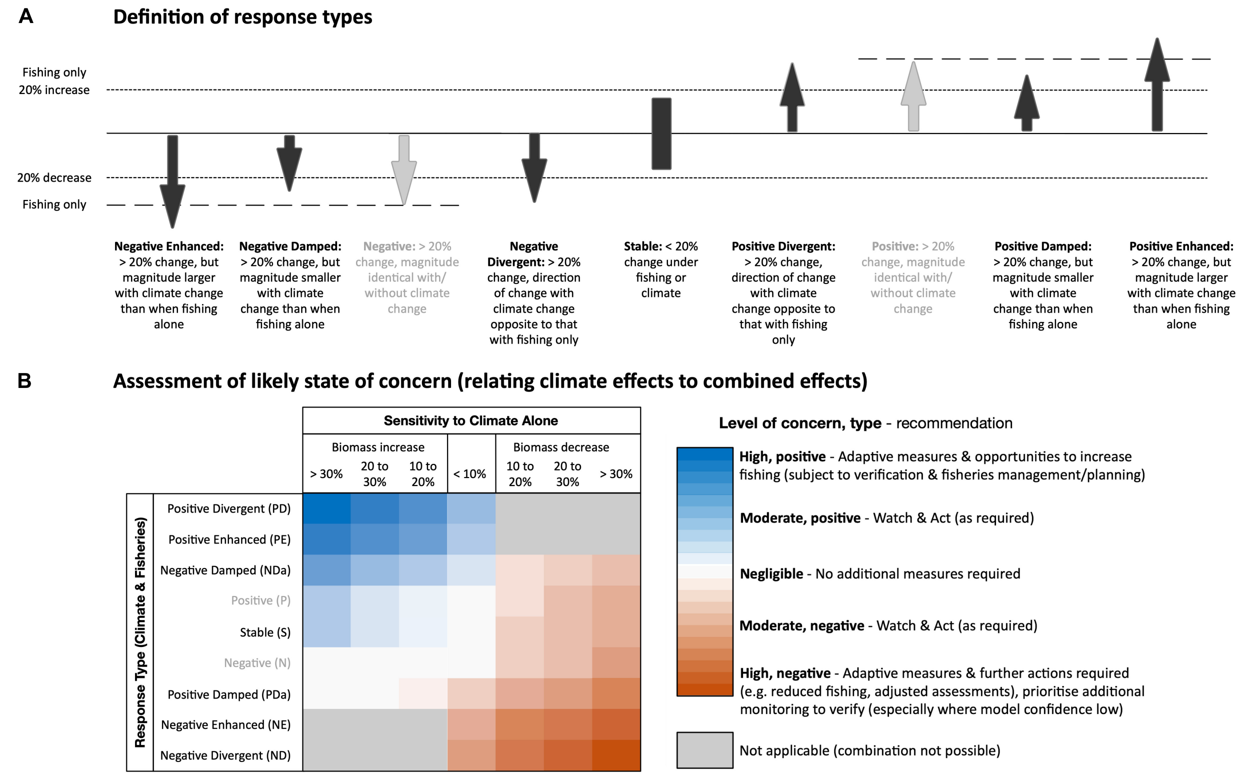

FIGURE 2 | (A) Definitions of different responses types based on differences between biomass trends under the fisheries impacts only (control scenario) and the combined impacts of climate change and fisheries (RCP8.5 scenario) between 2045 and 2050. Response types in gray were classified as stable responses as they too represent a <20% difference in biomass. **(B)** Assessment of the level and type of likely state of concern for functional groups were based on classification of (1) sensitivity or scale and direction of relative biomass changes to the climate change only scenario, and (2) the response type. Dampened response may appear to sit out of order, but this is because of their response to climate alone is in the opposite direction to their combined response.

where some part of the observed geographic distribution was missing or incorrect (this was the case for 40% of the modeled species). Species where there was significant disagreement with observed distributions were initially ranked as *high* data uncertainty, but ultimately these nine species were removed from further analysis as they had grossly incorrect spatial distributions or because the species did not actually occur in Australia.

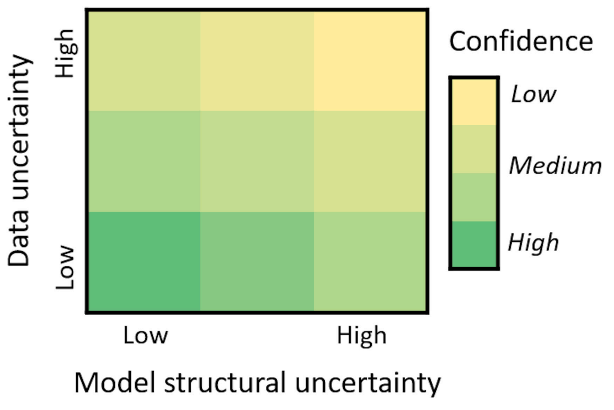

FIGURE 3 | Evaluation of confidence in ecosystem model climate projections based on expert judgment of (1) data uncertainty considering data availability, quality and fitting, and (2) model structural uncertainty reflecting the climate drivers and spatial and processes resolution of different model frameworks.

Model structural uncertainty of the different modeling frameworks used was also ranked (*low – medium – high*) according to the degree of taxonomic and spatial-temporal resolution and representation of ecological processes (trophic interactions, dispersal, phenology, habitat associations and socioeconomics) considered most important to inferring climate-mediated changes in productivity. Higher model uncertainty rankings were given to Ecosim model implementations that have low spatial and temporal resolution and are largely determined by trophic interactions. Medium ranking was given to the dynamic bioclimate envelope models that have high spatial and temporal resolution and are driven by temperature, but lack the inclusion of trophic mechanisms. Finally, lower rankings were given to the MICE model application focused on key drivers of the population dynamics and environmental tolerances of a targeted species of interest and to Atlantis model applications that represent a greater number of ecological processes and have high spatial and temporal resolution.

Our model comparisons approach, along with a qualitative assessment of model confidence, provides a more informative reflection on the associated uncertainty around potential outcomes, cognizant of underlying model assumptions that may influence the results and conclusions.

RESULTS

Temperature and Productivity Projections in Different Regional Model Domains

There was a high degree of temporal variability in sea surface temperatures (SST) and primary production projections of the Australian OFAM-v3 model for both the control and RCP8.5 scenarios. Under the RCP8.5 scenario, the mean change across all the model domains between 2010−2015 and 2045−2050 was +0.8°C for SST, while integrated primary productivity declined by 5.8%. However, there were notable regional patterns for both variables and high interannual variability for primary production projections for most regions (**Table 3**). Slightly larger increases in SST by 2050 were observed in the South East Australia region (+1.0°C) than in the Western Australia region (+0.8°C). Mean differences in primary productivity between the control and RCP8.5 scenarios were projected to be largest for the Great Australian Bight (GAB) EwE model domain and the smallest for the Eastern Bass Strait (EBS) EwE model domain, with an average decline of 34% and 2% respectively (**Table 3**). Inter-annual variability was also largest for the EwE-GAB model domain and was lowest for the North West Shelf (NWS) EwE model domain.

Regional Model Outputs

The climate change impacts scenario resulted in a range of responses for total consumer biomass, and biomass of ecological groups in the different modeled regions and fisheries (**Table 3**). By 2050, climate change was predicted to negatively impact, to varying degrees, all functional groups in the EwE-ETBF model (NE Australia region). In contrast, most groups in the EwE-Ningaloo (Western Australia) models responded positively. The least sensitive model (i.e., with the smallest deviation from zero change in average biomass) was the EwE-EBS model while the most sensitive model was the EwE-NPF model. The threatened, endangered or protected (TEP) species, including mostly marine mammals and seabirds but also turtles, were projected to be the most impacted ecological group from climate change in most regions. Pooled invertebrate and demersal fish and shark groups typically saw greater declines than pooled pelagic fish and shark groups, particularly in Western Australia.

Across all the regional models, more than half the examined functional groups (328 of the total 678) were predicted to be relatively stable and unaffected by the RCP8.5 (combined climate change and fisheries impacts) scenario, with changes between −20 and 20% from initial biomasses (**Figure 4**). There were 186 groups that showed biomass increases, and 51 groups that showed biomass declines, of between 20 and 40%. A further 15 and 46 groups showed positive and negative changes of between 40 and 60%. The groups projected to decline in biomass >60% in response to both climate change and fishing in 2045−2050 included demersal fish, dogfish sharks, rock lobster (SE Australia), reef-associated zoobenthic fish, corals and sponges, seagrass associated carnivores, and squid (W Australia), prawns, crabs, and small sharks (GoC) and turtles, seabirds, swordfish and tuna (NE Australia) (**Supplementary Table 1**). Under the climate change impacts scenario, only 3 groups declined > 60% including turtles and shelf Lutjanids and 13 groups decline between 40 and 60% including seabirds, whales, dugongs, small pelagic and shelf fish, and Carangids (**Supplementary Table 1**). Groups projected to show the largest increases in relative biomass under the climate impact scenario included jack mackerel, anchovy and demersal shelf fish (SE Australia), crabs and bugs, squid, and spantangoids (W Australia), small tunas and shelf Serranids (NW Australia), prawns and crabs (GoC) and lobsters and squid (NE Australia) (**Supplementary Table 2**).

There were 55 and 20 groups that showed enhanced negative and enhanced positive responses respectively (same direction but larger rates of change under climate change than fisheries) while a further 28 and 88 groups showed negative and positive divergent response patterns (**Figure 4A**). The assessment of the likely state of concern indicated that there were 13 groups of high negative concern (with > 40% sensitivity and divergent or enhanced negative responses) and 3 groups of high positive concern (**Supplementary Table 3**). Listed among the groups of most likely concern with respects to negative climate change impacts included small pelagic fish (*medium confidence*), pelagic and deep demersal sharks (*medium confidence*), piscivorous fish (*medium confidence*), and bight redfish (*low to medium confidence*) in SE Australia; dhufish and pink snapper (*medium to high confidence*) in SW-W Australia; and large sharks and marlin (*medium confidence*) in NE Australia. TEP species of highest negative concern (with *medium to high confidence*) included albatrosses, bottlenose dolphins, and penguins (SE Australia), dolphins and dugongs (W Australia), dugongs (N Australia), and seabirds, leatherback and green turtles (NE Australia). In the medium term (2030−2035), groups of higher negative concern included lobster (*high confidence*), morwong and gummy shark (*medium to high confidence*) (SE Australia), reef associated zooplankton feeders (*low confidence)* and lutjanids (*medium confidence*) (W Australia), all the prawn species (*medium confidence*) (GoC), and swordfish and sailfish (*low to medium confidence*) (NE Australia). Groups or species of highest positive concern from climate change impacts (with positive enhanced or divergent responses and large increases in relative biomass) included small and large pelagic fishes (anchovy, sardine and tuna) in the SE Australia (*medium to high confidence*), shallow demersal fish and trevallies in Western Australia (*medium confidence*), tunas, rays, sweetlip and red emperors in NW Australia (*low to medium confidence*), and bigeye tuna and squid in NE Australia (*medium confidence*). Time-series plots for each functional group are provided for each model in a technical report (Fulton et al., 2018a[2]).

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[2] http://www.frdc.com.au/Archived-Reports/FRDC%20Projects/2016-139-DLD.pdf

TABLE 3 | Relative percentage changes (mean standard deviation with minimum and maximum values provided in parentheses) in regional climate and ecosystem model projections averaged over model domains between 2010 and 2050. Climate model projections of temperature or primary productivity (highlighted in gray) represent mean differences between control and RPC8.5 scenarios. Biomass changes of ecological groups represent anomalies for the climate change impact only scenario. Colored values match the color used to represent different ecosystem models in the same column.

Regions	South East Australia	Western Australia	Noth West Australia	Gulf of Carpentaria	North East Australia
Ecosystem models	Atlantis-SEAust, EwE-EBS	EwE-GAB, EwE-Ningaloo, EwE-JB	EwE-NWS	EwE-NPF MICE-Lobster	Atlantis-NEMO EwE-ETBF
Temperature	2.3 ± 1.8 (−0.6 to 5.9)			3.5 ± 1.4 (0.4 to 56)	3.1 ± 1.3 (0.7 to 5.4)
Primary productivity	−1.7 ± 6 (−15 to 10)	−34 ± 17 (−84 to−12) 26 ± 6 (13 to 38) 7 ± 11 (−20 to 27)	18.9 ± 4.3 (10 to 27)	27.6 ± 2.4 (22 to 33)	−22.7 ± 11 (−49 to −0.8)
Total consumers	−2 ± 12 (−45 to 32) 2 ± 2 (−1 to 8)	−8 ± 31 (−41 to 135) 39 ± 17 (−2 to 67) −2 ± 2 (−34 to 184)	152 ± 245 (−61 to 918)	92 ± 187 (−53 to > 500)	8 ± 42 (−6 to 268) −33 ± 15 (−80 to −2)
Pelagic fish/sharks	1 ± 11 (−23 to 32) 3 ± 2 (0.8 to 8)	15 ± 35 (−12 to 135) 50 ± 17 (−2 to 67) −5 ± 24 (−23 to 93)	238 ± 346 (9 to 918)	62 ± 72 (−0.5 to 198)	0.6 ± 2 (−4 to 4) −31 ± 14 (−54 to −2)
Demersal fish/sharks	1 ± 11 (−23 to 15) 2 ± 2 (−1 to 7)	10 ± 13 (−33 to 10) 44 ± 6 (38 to 50) −4 ± 20 (−26 to 9)	88 ± 177 (61 to 509)	94 ± 74 (−34 to 198)	1 ± 2 (−2 to 4) Not assessed
Invertebrates	−3 ± 4 (−9 to 2) 2 ± 2 (−1 to 3)	10 ± 40 (−39 to 100) 39 ± 13 (8 to 56) −15 ± 53 (−23 to 184)	14 ± 7 (5 to 20)	184 ± 356 (7 to > 500) −37 (lobster)	10 ± 85 (−6 to 269)
TEP species	−10 ± 18 (−45 to 10) 3 ± 2 (0.5 to 5)	−3 ± 25 (−41 to 57) 21 ± 20 (−2 to 48) −3 ± 12(−23 to 5)	Not assessed	39 ± 94(−53 to 170)	−0.4 ± 1 (−2 to 2) −50 ± 26 (−80 to −17)

Global Model Outputs

The benthic-pelagic size spectrum model projected temporal (5-year) changes in the relative biomass of 6 size-based ecological groups to the RCP8.5 scenario for each of the assessment regions (**Figure 5**). The ecological group with the most consistent decrease, typically <10%, across all regions was pelagic predators >10 cm (all age groups combined) with biomass declining in all regions except the Gulf of Carpentaria. In contrast, benthic detritivores >30 cm were projected to increase in all regions, though again only by modest amounts (typically < 10%). Total system biomass was projected to decrease in all regions, although there was variability in this general trend across spatial regions (e.g. the Torres Strait and oceanic areas across much of southern Australia increased).

Across all regions, the ensemble of dynamic bioclimate envelope model simulations projected declines in relative abundance for most species, with only 31 species projected to increase (**Figure 4C**). The species with high model confidence, that were projected to be among the most negatively impacted from climate change included: blue endeavor prawn (regions 1, 3, and 4), bartail flathead (regions 1, 2, 3, and 5), big eye tuna (region 3 and 5), dusty whaler (regions 3 and 4), golden snapper (region 2), giant trevally (region 4), and queenfish (region 5). Key Commonwealth fishery species that were predicted to see large positive increases in relative abundance due to climate change only, with moderate to high model confidence, included Australian sardine (regions 1 and 5), gemfish (region 1), and blue mackerel (region 5). Relative changes in abundance for Commercial species are provided in **Table 4** while model projections and maps for all species are included in a technical report (Fulton et al., 2018a).

Inter-Model Comparisons and Confidence

Amongst the species that are the focus of Commonwealth fisheries there was moderate to strong agreement between models with geographic overlap (**Table 4**). There was particularly high model-model agreement for species or functional groups that scored high in the confidence assessment (had low data uncertainty) and where the models contained both trophic, life-history and distribution mechanisms. In South East Australia, all 3 ecosystem models suggested that piscivorous shelf fishes (including flathead, gemfish, and demersal sharks) were among the most negatively impacted by climate change. There was also model agreement that small pelagic fishes such as jack mackerel, blue mackerel, anchovy, and sardine were among those projected to increase in biomass under climate change. In Western Australia, the EwE models projected that pink snapper, rays and dhufish would be negatively impacted, while reef associated zoobenthos, breaksea cod, tuna and billfish, as well as mackerels would likely increase in biomass. In North West Australia, the EwE-NWS projected negative impacts of climate on bream, snappers (Lutjanids), carangids and lizard fish, and positive relative biomass shifts on tunas, seabass and groupers (Serranids), as well as red emperor. In the Gulf of Carpentaria, the EwE-NPF model indicated the relative biomass of most groups, including prawns and crabs, would likely increase with negative impacts only projected for reef-associated carnivorous fish. For

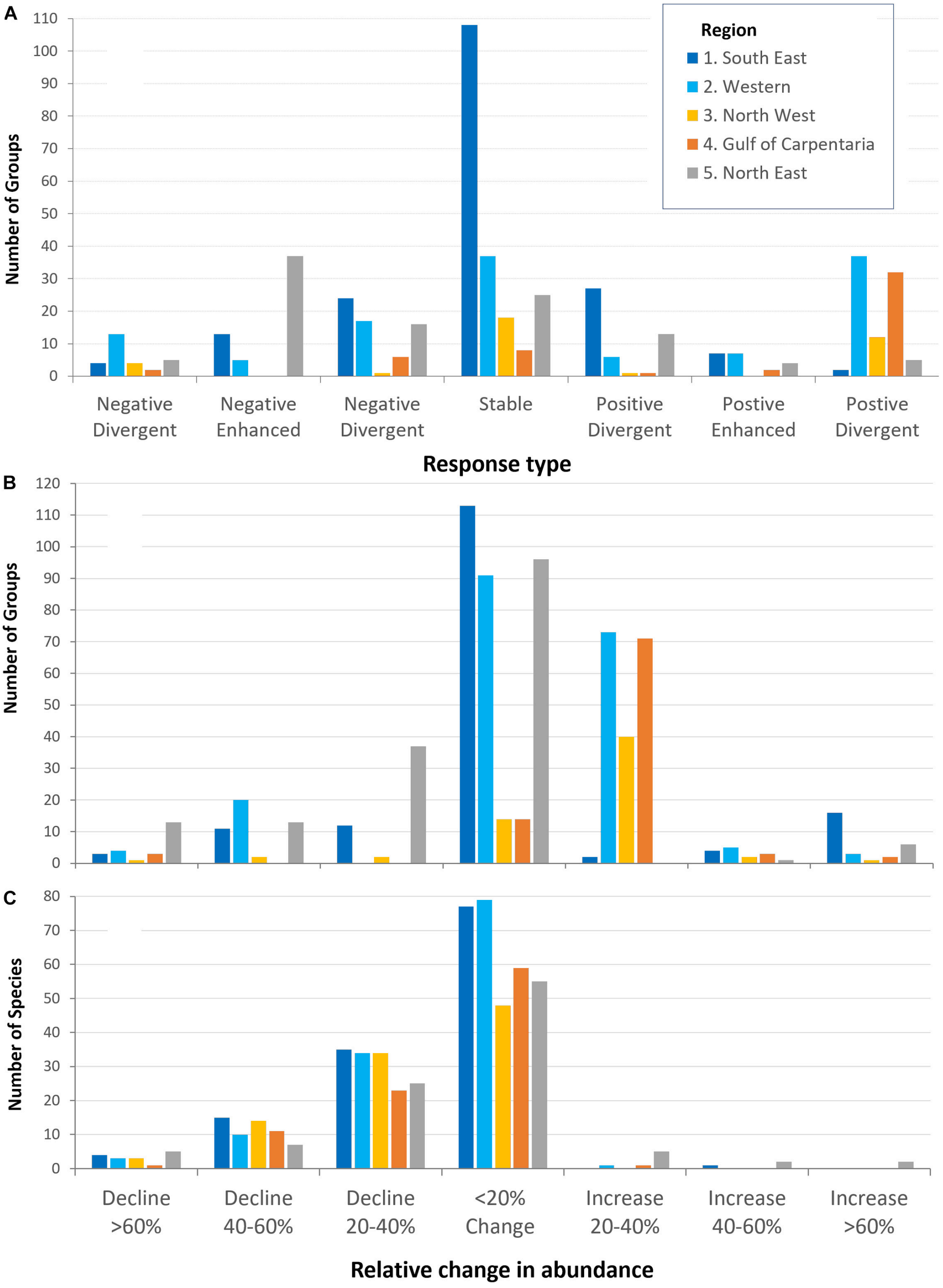


FIGURE 4 | Projected response types or abundance changes (sensitivities) to RCP8.5 greenhouse gas emission scenario (combined response to fisheries and climate change) for different assessment regions around Australia based on **(A,B)** regional ecosystem models with trophic linkages (on functional groups), and **(C)** species distribution models without trophic linkages (on individual species).

the North East Australia, the Atlantis-NEMO model projected negative impacts on large pelagic sharks, and small planktivorous fishes and positive impacts on macrobenthos and squid. The EwE-EBTF projected enhanced negative responses from large pelagic fishes including spearfish and swordfish. For yellowfin and bigeye tuna they predicted opposite trends, most probably due to assumptions with regard to diet switching. Very different biomass trends of tropical rock lobster were projected between

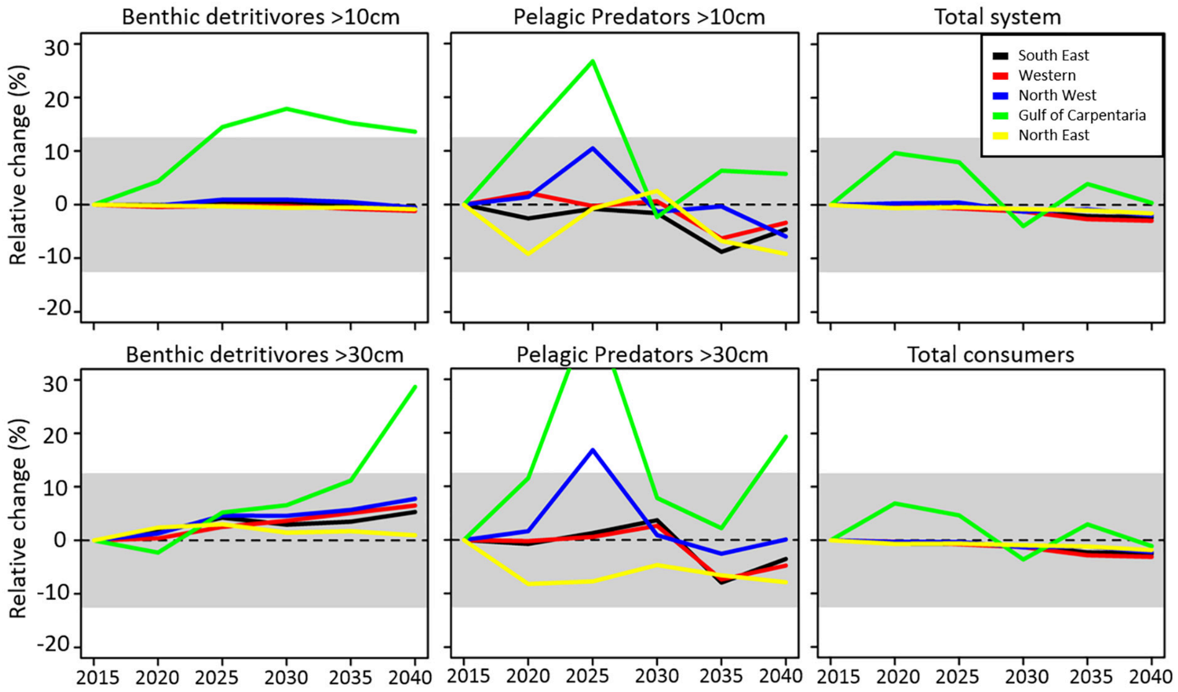


FIGURE 5 | Global benthic-pelagic size spectrum model projections of relative changes in biomass density of different model groups at 5-year intervals for each Australian region under the RCP8.5 scenario without fishing. These model outputs therefore represent relative changes in the unexploited baseline of biomass due to climate forcing alone.

the Atlantis-NEMO model (large increase) and the more targeted lobster MICE (large decline).

There was often a divergence between model projections of the regional models and the ensemble of global dynamic bioclimate envelope models (DBEM) (which do not include any trophic interactions), even where there was a high confidence and good match to current observations. This was particularly true for several small pelagic and demersal fish species, such as Australian sardine and Eastern redfish. Moreover, the DBEM generally tended to suggest higher sensitivity and more negative responses than the regional models (**Figure 4B**). Poor or mixed agreement between the model outputs were typically seen for shallow shelf demersal stocks and many of the invertebrates, which are often poorly constrained and only generally parameterized in the trophic models (i.e., have *low confidence* scores). Projections of habitat-dependent species (such as emperors and snappers) also varied between models that did and didn't explicitly represent habitat connections.

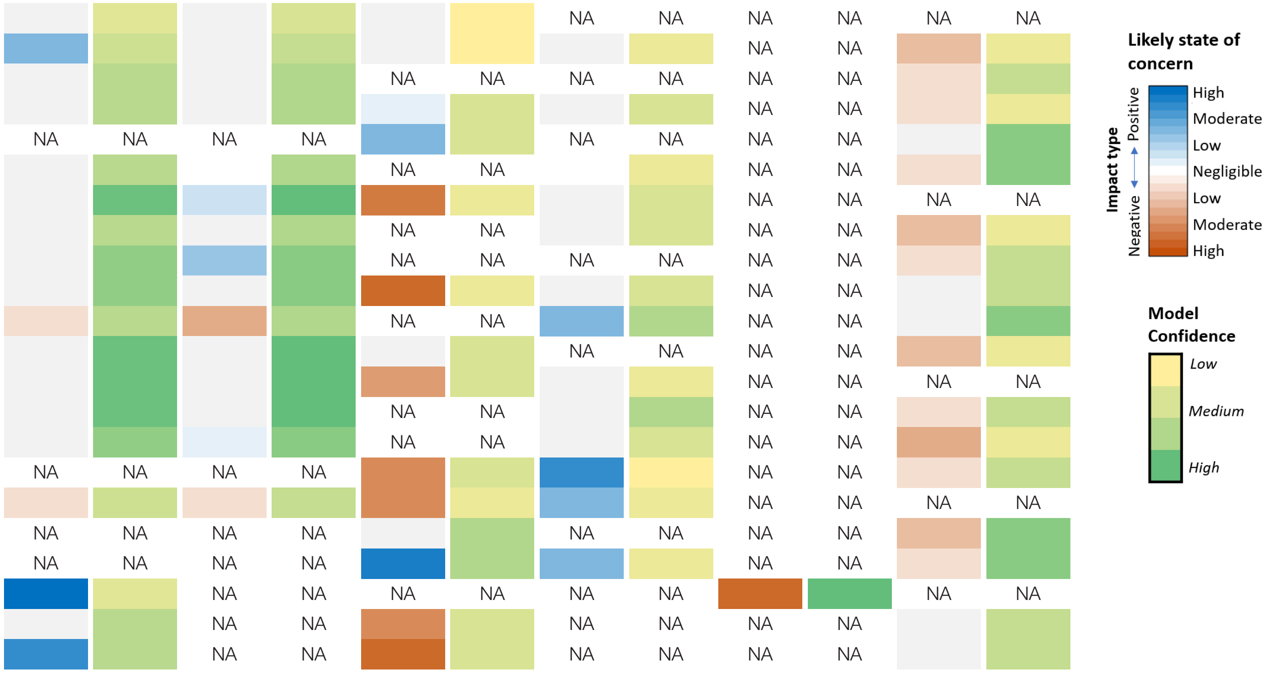
Outputs from the global benthic-pelagic size spectrum model (DBPM) can only be compared with other model outputs in terms of relative trends of aggregated biomass of different species. Whilst there was a large range of responses observed spatially and across species and functional groups for each of the regional models, there was agreement of the direction in total system biomass with the DBPM regional outputs (**Figure 5** and **Table 3**). An opposite general trend seems evident for predictions of benthic detritivores where regional ecosystem models projected some declines in group biomasses.

Atlantis SE Australian simulations under dynamic fishing management saw fewer harvested species negatively impacted by climate change over both the short and long terms compared to constant fishing effort that was applied to all other regional models (**Supplementary Table 1**). For example, grenadier, warehou, jack mackerel and school shark fared better in the Atlantis SEAust dynamic fisheries and management model (**Table 4**). In contrast, the results for invertebrates and TEP species were more variable and uncertain. This reflects the capacity of the simulated fishers and management bodies within the model to adapt to the changing conditions and mitigate negative outcomes.

DISCUSSION

Over the next century, the marine ecosystems of Australia are expected to exhibit some of the largest climate-driven changes in the Southern Hemisphere (Creighton et al., 2016; Hobday et al., 2018; Fordyce et al., 2019). Our multi-model projections provide the most comprehensive outlook on potential climate-driven ecological changes on Australia's large-scale Commonwealth fisheries stocks to date. Using multiple ecosystem models, that encompassed different assumptions and covered the entire Australian coastline, allowed for a broader view of the potential futures for Australia's fisheries – identifying the level and type of concern for commercial stocks to climate change with an accompanying measure of confidence. This information helps

TABLE 4 | Inter-model comparisons of the projected likely states of concern to climate change in key commercial species at the end of 2050 and the associated level of confidence.



Fishery^	Region*	Species	Atlantis_F (SEAust, NEMO)		Atlantis_D (SEAust)		EwE (GAB, NPF, ETBF)		EwE (JB, Ningaloo, EBS)		MICE		Global DBEM	
BSCZSF	1	Commercial Scallop	⬜	🟨	⬜	🟨	⬜	🟨	NA	NA	NA	NA	NA	NA
SPF	1, 2	Redbait	🟦	🟩	⬜	🟩	⬜	🟨	⬜	🟨	NA	NA	🟧	🟨
		Blue Mackerel	⬜	🟩	⬜	🟩	NA	NA	NA	NA	NA	NA	🟧	🟩
		Jack Mackerel	⬜	🟩	⬜	🟩	🟦	🟨	⬜	🟨	NA	NA	🟧	🟨
		Australian Sardine	NA	NA	NA	NA	🟦	🟨	NA	NA	NA	NA	⬜	🟩
SESSF	1, 2	Blue Grenadier	⬜	🟩		🟩	NA	NA		🟨	NA	NA	🟧	🟩
		Tiger Flathead	⬜	🟩	🟦	🟩	🟧	🟨	⬜	🟨	NA	NA	NA	NA
		Pink Ling	⬜	🟩	⬜	🟩	NA	NA	⬜	🟨	NA	NA	🟧	🟨
		Silver/blue Warehou	⬜	🟩	🟦	🟩	NA	NA	NA	NA	NA	NA	🟧	🟩
		Eastern Redfish	⬜	🟩	⬜	🟩	🟧	🟨	⬜	🟨	NA	NA	⬜	🟩
		Eastern Gemfish	🟧	🟩	🟧	🟩	NA	NA	🟦	🟩	NA	NA	⬜	🟩
		School Shark	⬜	🟩	⬜	🟩	⬜	🟨	NA	NA	NA	NA	🟧	🟨
		Gulper Shark	⬜	🟩	⬜	🟩	🟧	🟨	⬜	🟨	NA	NA	NA	NA
		Jackass Morwong	⬜	🟩	⬜	🟩	NA	NA	⬜	🟩	NA	NA	🟧	🟩
		Orange Roughy	⬜	🟩	🟦	🟩	NA	NA	⬜	🟨	NA	NA	🟧	🟨
SBTF	2	Southern Bluefin Tuna	NA	NA	NA	NA	🟧	🟨	🟦	🟨	NA	NA	🟧	🟩
WTBF	3	Tuna (all species)	🟧	🟨	🟧	🟩	🟧	🟨	🟦	🟨	NA	NA	NA	NA
NPF	4	Banana Prawn	NA	NA	NA	NA	⬜	🟩	NA	NA	NA	NA	🟧	🟩
		Brown Tiger Prawn	NA	NA	NA	NA	🟦	🟩	🟦	🟨	NA	NA	🟧	🟩
TSRLF	4, 5	Lobster	🟦	🟨	NA	NA	NA	NA	NA	NA	🟧	🟩	NA	NA
ETBF	1, 5	Yellowfin Tuna	⬜	🟩	NA	NA	🟧	🟨	NA	NA	NA	NA	⬜	🟩
		Bigeye Tuna	🟦	🟩	NA	NA	🟧	🟨	NA	NA	NA	NA	⬜	🟩

*Atlantis_F, models run under constant fisheries; Atlantis_D, SEAust model run under dynamic representation of fisheries. NA indicates that the species in that operating fisheries and region was not considered in that model or assessment. For the DBEM model outputs, a stable response type was assumed in the assessment of likely state of concern. ˆCommonwealth fisheries include: Small Pelagic Fishery (SPF), Northern Prawn Fishery (NPF), Eastern and Western Tuna and Billfish Fishery (ETBF and WTBF), Southern Bluefin Tuna Fishery (SBTF), Torres Strait Rock Lobster Fisheries (TSRLF), and Bass Strait Central Zone Scallop Fishery (BSCZSF). *Assessment regions: 1, South East Australia, 2, Western Australia, 3, North West Australia, 4, Gulf of Carpentaria, 5, North East Australia.*

managers and the fishing industry to be better prepared over the next 30 years by highlighting those species that may be at risk and those that might benefit from climate change. Results presented here also provide recommendations that can help shape future management and prioritize research directions – both to guide alterations in management to allow for greater adaptation to changes in the fisheries and to identify actions that can help clarify what is occurring and reduce uncertainty.

Consistent with previous ecosystem modeling work, the direction of response to climate drivers seems to be species- and system-dependent. We found that both temperate and demersal systems are likely to be more strongly affected by climate change than tropical and pelagic systems which is in line with previous vulnerability analyses (Pecl et al., 2014, and updated in Fulton et al. (2018a)) and climate-ecosystem model assessments (Brown et al., 2010; Fulton, 2011) of Australian ecosystems. In addition, nearly all models in our study predicted that coastal or shallow water species, and particularly benthic invertebrate species, such as lobster, were among the first to respond and to the largest extent. This probably reflects the more responsive life-history traits of invertebrates, compared to sharks and most fish, which make them more sensitive to sequences of stochastic events such as marine heatwaves (Hobday et al., 2018) projected in the immediate and near future. Some of the models were also able to reflect that many benthic invertebrates live in shallower waters, which may provide less buffering from temperature-driven changes and/or are dependent on particularly vulnerable habitats (such as reef structures or seagrass), which are more sensitive to changes in temperature (Babcock et al., 2019), whereas many large pelagic species are cosmopolitan and roam over ocean basins.

Some of our single and multiple model results suggest that the coming decades may prove to be challenging for Australian fisheries operators and managers, particularly as there is a strong reliance on seafood sourced from demersal food webs. All regional models in this study showed that the combined effects of fishing and climate change are often non-additive (synergistic or antagonistic), as has been shown previously for south eastern Australia (Griffith et al., 2012; Fulton and Gorton, 2014) and in other areas of the world (Mackinson et al., 2009; Travers-Trolet et al., 2014; Fu et al., 2018). Our categorization of the responses of species groups to climate drivers, and the interplay with fisheries on the ecosystem, can be used to prioritize management decisions at a species and regional level. For fishing stocks ranked as high negative concern, the utilization of combined ecosystem-based, adaptive and co-management approaches are likely to be the best ways of enabling climate change adaption, as they have already been shown to be particularly promising in Australian fisheries (Ogier et al., 2016).

From our study, biomass changes most likely to worry management and fishing industry are those to do with climate mediated declines where a species decline only occurs, or is greater, under scenarios of climate change rather than just fisheries alone (response types ND and NE). While including recognition of climate effects in assessments (e.g. Wayte, 2013; Ianelli et al., 2016) and on reference points (Holsman et al., 2016) is a direct means of folding in climate considerations, responses may need to go further. Moreover, it is recognized that it is challenging to explicitly incorporate climate drivers in stock assessment models that can reliably be used in forward projections. A preferred approach is to use Management Strategy Evaluation (MSE) to test the robustness of Harvest Control Rules (HCRs) to climate variability (Plagányi et al., 2019), as applied using MICE in the Northern Prawn Fishery (Plagányi et al., 2013).

Across our models, nine species were categorized as being of high negative concern due to climate change, including mostly demersal fish species and sharks. Future management plans for stocks affected to this degree will likely need to incorporate climate adaptation approaches that rapidly increase their adaptive or absorptive capacity. While adaptive management approaches used for these species are likely to facilitate some adaptation (Melnychuk et al., 2014), further action may be needed to provide the species greater capacity to cope with the combined pressure of climate and other anthropogenic pressures, such as reducing what is considered acceptable levels of fishing pressure and/or increasing protection measures to ensure future sustainability.

Different management approaches are recommended for stocks that are likely to benefit from climate change and to have highly positive responses under combined impacts of fishing and climate change (response types PD and PE). In our study, this categorization was given to three pelagic fish groups (anchovy, sardine, and tuna) in the SE Australia region which managers could seek to increase fishing effort or promote new commercial opportunities in the future. However, before implementing any changes to existing management, more targeted consideration of species responses is needed, including scrutiny of spatial variability, which although represented by some ecosystem models (Atlantis and DBEM) are likely to need further refinement given the level of data available to condition these models. Our results also noted that many fishing stocks transition through different likely states of concern over time and are currently observed to have only undergone negligible or low to moderate levels of change, which demonstrates the need for fisheries management to be as flexible as possible. The complexity of possible stock responses shown among the ecosystem models also highlights the strong need to incorporate uncertainty information.

Identifying, quantifying, and reporting multiple sources of uncertainty is a key step for multiple and ensemble ecosystem model predictions to be taken up and used effectively by fisheries managers and policy makers (Payne et al., 2016). This includes the inclusion of regional and global ecosystem model results in future IPCC assessments that currently only report results from the global ensemble of dynamic bioclimate envelope models (DBEM) (IPCC, 2018). While such species distribution models have been shown to provide reliable predictions of both abundance and distribution for targeted and data-rich species (Cheung et al., 2011), our study demonstrated large discrepancies between these model results and those that incorporate trophic interactions for Australia. For example, jack mackerel increases in Atlantis-SEAust but decreases in the DBEM. Both are spatial models, allowing for range shifts, but trophic interactions (starting from interannually variable seasonal plankton blooms in Atlantis) enable the pelagic food web, including jack mackerel, to be supported and this compensates for any loss in individual response rates due to thermal conditions moving into sub-optimal conditions. In contrast, the DBEM is heavily influenced by the environmental conditions alone. Only by stepping through and acknowledging the various major sources of uncertainty, such as the structural uncertainty introduced by the processes that are or are not represented, will we be able to obtain more robust and meaningful ecosystem and species projections.

The first source of uncertainty to consider is that related to climate projections of the ocean forecasting or global climate model(s). All climate models typically predict temperature with much more confidence than primary production (Laufkötter et al., 2015) which has notable flow-on effects to the different ecosystem models. For example, drops in production were projected by the coupled OFAM-production model for many of the EwE model domains. However, while Atlantis did see declines and changes in plankton composition, that were in rough alignment with what was seen in the OFAM-production model it was not an exact match – partly due to a different spatial resolution, but also due to additional variability induced by top-down, predator mediated processes not represented in the OFAM-production model. This is not to say Atlantis is more accurate than the OFAM-production model, just that it highlighted another potential source of uncertainty. In addition, the spatio-temporal scale at which climate projections are provided have flow-on implications with higher confidence likely provided for downscaled regional than global climate models and for those ecosystem models that reflect finer (daily to weekly rather than monthly or seasonal) temporal dynamics. In this study, the degree of change in the climate forcing variable largely determined the direction and magnitude of broad system outputs of the regional ecosystem models which has been noted in other ensemble ecosystem modeling studies (Thuiller et al., 2019). In some regions, such as the Great Australian Bight, larger variability in annual mean primary productivity anomalies meant that predicted responses of fishing stocks and other ecosystem components were also highly variable. In contrast there were only small changes in primary productivity and thus biomass projected in eastern Bass Strait, Torres Strait, and Ningaloo Reef EwE model domains. In regions where primary production is predicted to increase, typically we saw an increase in commercially harvested and TEP species under the climate change scenario, as observed by Brown et al. (2010). In the future, uncertainty of climate model projections should be incorporated by undertaking multiple ecosystem modeling runs that span upper and lower confidence intervals of the climate model outputs.

Uncertainty related to the availability and quality of data or knowledge used to parameterize ecosystem models needs to be carefully considered, even where there is good model-model agreement. Acknowledgment of such uncertainty is important because previous work has shown that ecosystem models can be quite skillful, but in the absence of data for a specific group they may only be producing a plausible system not one reflective of reality (Olsen et al., 2016). In this study, higher incidences of model-model discrepancy were noted for data-poor lower-trophic and invertebrate functional groups with less taxonomic resolution. For such data-poor species assessment tools such as qualitative models (e.g. Dambacher et al., 2009) or trait-based sensitivity or vulnerability assessments (e.g. Sunday et al., 2015) are likely to provide additional or higher levels of confidence than more complicated ecosystem model outputs alone. Another important factor to consider is that biological data (e.g. size at maturity, growth rates, diets) used in the ecosystem models typically come from disparate data sources and may be out-of-date in fast-changing areas. This also highlights the need for all ecosystem models to be periodically updated, assessed and refined (every 5–10 years) if they are to continue being effective strategic tools for management and policy decision making. Whilst not every component of the ecosystem can be studied, rankings of data uncertainty and model confidence should be used to determine which species or functional groups to prioritize monitoring or data collection programs, particularly if it is deemed to be of high level of concern. Whereas the qualitative confidence assessments used here provided a reasonable and rapid check when comparing model-model outputs, in the future more rigorous pedigree routines undertaken during model development could be used such as those presented for EwE (Christensen et al., 2005) and Atlantis (Pethybridge et al., 2019), in addition to the reporting of model skills statistics (e.g. Olsen et al., 2016).

A particularly challenging source of uncertainty to account for when comparing model outputs is related to the core assumptions and structure of the modeling framework which includes differences in model processes considered and taxonomic, temporal and spatial resolution (**Table 1**). In this study, the greatest model discrepancies were found between the regional ecosystem models that represent trophic interactions and the ensemble of dynamic bioclimate envelope models (DBEM). Around a third of the species represented by the DBEM simulated negative responses to climate change, while regional ecosystem models predicted a broader range of both potential winners and losers (**Figure 4**). These results suggest that indirect climate effects through changing trophic interactions, such as changing predation pressures, play an important role in mediating the sensitivity and impacts on many marine species and thus are crucial to consider in future climate projections. This has broader management implications because of the complex interactions between species and highlights the importance of using multiple modeling approaches to explore ecosystem responses to future climate and fisheries scenarios.

Another source of model-model discrepancy was between some of the EwE and Atlantis regional models, particularly for the NE Australia region. While both models were set up with the primary purpose to assess tuna population dynamics, the Atlantis-NEMO model domain is larger covering more oceanic habitats. NEMO projected an increase in many of the tunas, as they shift with the conditions and congregate on prey fields along oceanic fronts, whereas the EwE-EBTF model (which was forced by a primary production anomaly estimated for a static geographic location) saw the same tuna species decline. Such a result demonstrates the value in acknowledging that inconsistency in the degree of spatial overlap and resolution, or vastly different representation pf physical forcing and ecological processes (trophic interactions, dispersal, phenology, habitat associations and socioeconomics), will create very different responses for particular species for which these processes are important and should be reflected in confidence ratings provided alongside projected outcomes. Extending the EwE models by implementing their spatial modules (Ecospace) may address the spatially mediated results where prey availability influences abundance and lead to less divergence in outcomes (Steenbeek et al., 2013; Christensen et al., 2014). However, that is not guaranteed for species such as squids and mesopelagics, where depth mediated processes are involved (which Ecospace does not resolve) or if the responses are due to bottom-up primary production processes. Another discrepancy was the opposing direction of change in the biomass of tropical rock lobster projected by the MICE (decline) and the Atlantis-NEMO (increase) model, demonstrating that managers should acknowledge model confidence rankings. High rankings were given to projections of the MICE as it is focused on representing the main species relevant processes and environmental drivers and is closely fit to data, whereas very limited empirical data was used to represent lobster (as 1 of 58 groups) in the NEMO model, with mortality due to heat stress also not modeled.

A final source of uncertainty stems from being able to reflect in ecosystem models the adaptive capacity of human users and the role of management in mitigation or even interventionist actions. Representing adaptive HCRs is a useful elaboration many models could include, even if the HCRs are applied using simple measures of fishing mortality F such as dynamic location choice method (Plagányi et al., 2013), rather than explicitly modeling the full fishing effort dynamics which can include different fleets and gear types (as can occur in Atlantis, Fulton et al., 2014). A lot of attention in fisheries science and ecosystem modeling has gone into capturing dynamic ecological responses, less so into human dynamic responses. Over the past couple of decades the number of bioeconomic and effort dynamics models have grown considerably (e.g. Nielsen et al., 2018), but currently few ecosystem models are capable of representing socio-economics and human behavior, with the Atlantis-SEAust model being one of the first. This is a rapidly advancing space, with many more models likely to have some capacity in this area in the near future, benefiting from increased attention being placed on understanding fisher behavior and the feedback between human users and ecosystem dynamics (e.g. Van Putten et al., 2018; Bourdaud et al., 2019).

The move to more consideration of human components is important as comparison between the Atlantis-SEAust model run with a fixed fishing mortality and with dynamically responding fisheries illustrated that there is the capacity to avoid fisheries activities amplifying climate effects through adaptive management and autonomous fisher responses. Some of the model responses included shifting fishing patterns (spatially or in terms of species fished) and management restructuring to support ongoing recovery from past overfishing and relieving pressure on species declining due to climate change. The Atlantis-SEAust model also illustrated that with human adaptation, and sustainable, economically viable fisheries can be maintained over the next few decades with little radical change for many species. However, to have "ensemble level" confidence in these results more models will need to include dynamic representations of fishing and management activities.

While we recognize that greater uncertainty quantification is needed, our model projections and assessments of the likely state of concern and model confidence do provide new insight into how Australia's fishing stocks may respond to projected climate change in the future. These findings are much more relevant to regional fisheries management around Australia than those previously provided by the FISH-MIP global studies. The high occurrences of low confidence projections in this study, typically associated with data-poor species, clearly point to the need for greater data collection and research on lower trophic and invertebrate species around much of Australia. Low confidence rankings for species or groups classified to be of high concern, such as commercial scallops, should be prioritized by managers for monitoring and data collection programs. For data-rich and often more taxonomically resolved species, we recommend using a similar assessment framework to that developed here. This includes classifying the species state of concern based on both changes in sensitivity but also the type of response of the climate impacts compared to combined effects of climate and fisheries. Rankings of high concern can be used to directly prioritize which stocks to apply climate adaptation measures to potentially review levels of fishing pressure. This study has highlighted the importance of representing key trophic and human interactions in addition to physiological processes (such as species tolerance limits) and responses to environmental variability in models used to project species biomass changes under climate change. Certainly, the complexity of possible species responses shown among our different models and the increasing importance of environmental drivers means that current approaches for advising on acceptable catch levels may be insufficient for understanding stock patterns under climate change and would benefit from strategic consideration of projections from ecosystem models. Considering outputs from a multiple or ensemble ecosystem modeling approaches should assist managers in understanding the most important climate feedbacks and the range of model sensitivity estimates. In future studies, we suggest greater effort should be put into obtaining quantified estimates of uncertainty by running all models under a range of plausible parametrizations for key ecological processes (e.g. different diet compositions) and various scenarios (including a greater suite of climate drivers, potential human impact effects, and socioeconomic characteristics). For example, development of multispecies and trait-based size spectrum models for use in climate projections (Woodworth-Jefcoats et al., 2019) has focused on testing the effects of alternative climate processes and mechanisms as well as the use of statistical models to quantify their contribution toward uncertainty (Reum et al., 2020). Such advances, in addition to those discussed above, will provide more confidence in the robustness of individual, multiple and ensemble ecosystem model projections of the future.

DATA AVAILABILITY STATEMENT

Modelled biomass and catch time series used in this article is available from the authors on request.

AUTHOR CONTRIBUTIONS

HRP carried out the resources, data curation, and formal analysis, investigated and visualized the data, performed the methodology, wrote the original draft of the manuscript, and reviewed and edited the manuscript. EAF did the conceptualization, carried out the funding acquisition, resources, and project administration, performed the methodology, wrote the original draft of the manuscript, and reviewed and edited the manuscript. AJH did the conceptualization, carried out the funding acquisition, resources, and project administration, performed the methodology, and wrote, reviewed, and edited the manuscript. IRB directed and supervised the project, did the conceptualization and wrote, reviewed, and edited the manuscript.

JB, CMB, WWLC, LXCD, RG, TH, RM, HL-M, EEP, CV, and XZ carried out the resources, performed the methodology of the model development, and wrote, reviewed, and edited the manuscript.

FUNDING

This is a synthesis of work undertaken for the Australian Fisheries Research and Development Corporation project 2016-2018/138.

ACKNOWLEDGMENTS

We thank Prof. Greta Pecl for providing input into earlier versions of this manuscript and for constructive suggestions from our reviewers.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.577964/full#supplementary-material

REFERENCES

Allison, E. H., and Bassett, H. R. (2015). Climate change in the oceans: human impacts and responses. *Science* 350, 778–782. doi: 10.1126/science.aac8721

Audzijonyte, A., Pethybridge, H., Porobic, J., Gorton, R., Kaplan, I., and Fulton, E. A. (2019). Atlantis: a spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules. *Methods Ecol. Evol.* 10, 1814–1819. doi: 10.1111/2041-210x.13272

Babcock, R. C., Bustamante, R. H., Fulton, E. A., Fulton, D. J., Haywood, M. D. E., Hobday, A. J., et al. (2019). Severe and extensive climate change impacts are happening now: recent dieback of marine habitat forming communities along 40% of the Australian coast. *Front. Mar. Sci.* 6:411. doi: 10.3389/fmars.2019.00411

Barange, M., Bahri, T., Beveridge, M. C. M., Cochrane, K. L., Funge-Smith, S., and Poulain, F. (eds). (2018). *Impacts of Climate Change on Fisheries and Aquaculture: Synthesis of Current Knowledge, Adaptation and Mitigation Options*. FAO Fisheries and Aquaculture Technical Paper No. 627. Rome: FAO, 628.

Blanchard, J. L., Jennings, S., Law, R., Castle, M. D., McCloghrie, P., Rochet, M. J., et al. (2009). How does abundance scale with body size in coupled size-structured food webs? *J. Anim. Ecol.* 78, 270–280. doi: 10.1111/j.1365-2656.2008.01466.x

Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., et al. (2012). Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 2979–2989. doi: 10.1098/rstb.2012.0231

Bourdaud, P., Travers-Trolet, M., Vermard, Y., and Marchal, P. (2019). Improving the interpretation of fishing effort and pressures in mixed fisheries using spatial overlap metrics. *Can. J. Fisher. Aquat. Sci.* 76, 586–596. doi: 10.1139/cjfas-2017-0529

Brown, C. J., Fulton, E. A., Hobday, A. J., Matear, R. J., Possingham, H. P., Bulman, C., et al. (2010). Effects of climate-driven primary production change on marine food webs: implications for fisheries and conservation. *Glob. Change Biol.* 16, 1194–1212. doi: 10.1111/j.1365-2486.2009.02046.x

Bryndum-Buchholz, A., Tittensor, D. P., Blanchard, J. L., Cheung, W. W., Coll, M., Galbraith, E. D., et al. (2019). Twenty-first-century climate change impacts on marine animal biomass and ecosystem structure across ocean basins. *Glob. Change Biol.* 25, 459–472. doi: 10.1111/gcb.14512

Bulman, C., Condie, S., Furlani, D., Cahill, M., Klaer, N., Goldsworthy, S., et al. (2002). *Trophic Dynamics of the Eastern Shelf and Slope of the South East Fishery: Impacts of and on the Fishery*. Final Report for the Fisheries Research and Development Corporation, Project, 2002/028. Canberra: Fisheries Research and Development Corporation.

Bulman, C. M. (2006). *Trophic Webs and Modelling of Australia's North West Shelf*. Northwest Shelf Joint Environmental Management Study Technical Report CSIRO Report No. 9. Canberra: CSIRO.

Bulman, C. M. (2008). Preliminary trophic models of the South east fishery and North West shelf. *Fish. Centre Res. Rep.* 14:32.

Busch, D. S., Griffis, R., Link, J., Abrams, K., Baker, J., Brainard, R. E., et al. (2016). Climate science strategy of the US national marine fisheries service. *Mar. Policy* 74, 58–67. doi: 10.1016/j.marpol.2016.09.001

Bustamante, R. H., Dichmont, C. M., Ellis, N., Griffiths, S., Rochester, W. A., Burford, M. A., et al. (2011). *Morello Effects of Trawling on the Benthos and Biodiversity: Development and Delivery of a Spatially-Explicit Management Framework for the Northern Prawn Fishery*. Final Report, FRDC No. 2005/050. Hobart: CSIRO Marine and Atmospheric Research.

Cheung, W. W., Dunne, J., Sarmiento, J. L., and Pauly, D. (2011). Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. *ICES J. Mar. Sci.* 68, 1008–1018. doi: 10.1093/icesjms/fsr012

Cheung, W. W., Lam, V. W., Sarmiento, J. L., Kearney, K., Watson, R., and Pauly, D. (2009). Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish.* 10, 235–251. doi: 10.1111/j.1467-2979.2008.00315.x

Cheung, W. W., Lam, V. W., Sarmiento, J. L., Kearney, K., Watson, R. E. G., Zeller, D., et al. (2010). Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Glob. Change Biol.* 16, 24–35. doi: 10.1111/j.1365-2486.2009.01995.x

Cheung, W. W. L., Frölicher, T. L., Asch, R. G., Jones, M. C., Pinsky, M. L., Reygondeau, G., et al. (2016a). Building confidence in projections of the responses of living marine resources to climate change. *ICES J. Mar. Sci.* 73, 1283–1296. doi: 10.1093/icesjms/fsv250

Cheung, W. W. L., Jones, M. C., Reygondeau, G., Stock, C. A., Lam, V. W. Y., and Frölicher, T. L. (2016b). Structural uncertainty in projecting global fisheries catches under climate change. *Ecol. Modell.* 325, 57–66. doi: 10.1016/j.ecolmodel.2015.12.018

Cheung, W. W. L., Reygondeau, G., and Frölicher, T. L. (2016c). Large benefits to marine fisheries of meeting the 1.5C global warming target. *Science* 354, 1591–1594. doi: 10.1126/science.aag2331

Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., and Walters, C. J. (2014). Representing variable habitat quality in a spatial food web model. *Ecosystems* 17, 1397–1412. doi: 10.1007/s10021-014-9803-3

Christensen, V., and Walters, C. J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Modell.* 172, 109–139. doi: 10.1016/j.ecolmodel.2003.09.003

Christensen, V., Walters, C. J., and Pauly, D. (2005). *Ecopath with Ecosim: a User's Guide*. Vancouver: University of British Columbia, 154.

Colléter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., and Christensen, V. (2015). Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecol. Modell.* 302, 42–53. doi: 10.1016/j.ecolmodel.2015.01.025

Creighton, C., Hobday, A. J., Lockwood, M., and Pecl, G. T. (2016). Adapting management of marine environments to a changing climate: a checklist to guide reform and assess progress. *Ecosystems* 19, 187–219. doi: 10.1007/s10021-015-9925-2

Dambacher, J. M., Gaughan, D. J., Rochet, M. J., Rossignol, P. A., and Trenkel, V. M. (2009). Qualitative modelling and indicators of exploited ecosystems. *Fish Fish.* 10, 305–322. doi: 10.1111/j.1467-2979.2008.00323.x

Dichmont, C. M., Ellis, N., Bustamante, R. H., Deng, R., Tickell, S., Pascual, R., et al. (2013). Evaluating marine spatial closures with conflicting fisheries and conservation objectives. *J. Appl. Ecol.* 50, 1060–1070. doi: 10.1111/1365-2664.12110

Dutkiewicz, S., Scott, J. R., and Follows, M. J. (2013). Winners and losers: ecological and biogeochemical changes in a warming ocean. *Glob. Biogeochem. Cycles* 27, 463–477. doi: 10.1002/gbc.20042

Feng, M., Zhang, X., Sloyan, B., and Chamberlain, M. (2017). Contribution of the deep ocean to the future changes of the Indonesian Throughflow. *Geophys. Res. Lett.* 44, 2859–2867. doi: 10.1002/2017gl072577

Fordyce, A. J., Ainsworth, T. D., Heron, S. F., and Leggat, W. (2019). Marine heatwave hotspots in coral reef environments: physical drivers, ecophysiological outcomes, and impact upon structural complexity. *Front. Mar. Sci.* 6:498. doi: 10.3389/fmars.2019.00498

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., and Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science* 363, 979–983. doi: 10.1126/science.aau1758

Fu, C., Travers-Trolet, M., Velez, L., Grüss, A., Bundy, A., Shannon, L. J., et al. (2018). Risky business: the combined effects of fishing and changes in primary productivity on fish communities. *Ecol. Modell.* 368, 265–276. doi: 10.1016/j.ecolmodel.2017.12.003

Fulton, E. A. (2011). Interesting times: winners, losers, and system shifts under climate change around Australia. *ICES J. Mar. Sci.* 68, 1329–1342. doi: 10.1093/icesjms/fsr032

Fulton, E. A., Bulman, C. M., Pethybridge, H., and Goldsworthy, S. D. (2018a). Modelling the great Australian bight ecosystem. *Deep Sea Res. II Top. Stud. Oceanogr.* 157, 211–235. doi: 10.1016/j.dsr2.2018.11.002

Fulton, E. A., Hobday, A. J., Pethybridge, H., Blanchard, J., Bulman, C., Butler, I., et al. (2018b). *Decadal Scale Projection of Changes in Australian Fisheries Stocks under Climate Change*. FRDC Final Report No. 2016/139. Canberra: CSIRO.

Fulton, E. A., and Gorton, R. (2014). *Adaptive Futures for SE Australian Fisheries & Aquaculture: Climate Adaptation Simulations*. Canberra: CSIRO, 309.

Fulton, E. A., Gray, R., Sporcic, M., Scott, R., Little, R., Hepburn, M., et al. (2011a). *Ningaloo Collaboration Cluster: Adaptive Futures for Ningaloo*. Ningaloo Collaboration Cluster Final Report No. 5.3. Canberra: CSIRO.

Fulton, E. A., Link, J. S., Kaplan, I. C., Savina-Rolland, M., Johnson, P., Ainsworth, C., et al. (2011b). Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish Fish.* 12, 171–188. doi: 10.1111/j.1467-2979.2011.00412.x

Fulton, E. A., Punt, A. E., Dichmont, C. M., Gorton, R., Sporcic, M., Dowling, N., et al. (2016). Developing risk equivalent data-rich and data-limited harvest strategies. *Fish. Res.* 183, 574–587. doi: 10.1016/j.fishres.2016.07.004

Fulton, E. A., Smith, A. D. M., Smith, D. C., and Johnson, P. (2014). An integrated approach is needed for ecosystem based fisheries management: insights from ecosystem-level management strategy evaluation. *PLoS One* 9:e84242. doi: 10.1371/journal.pone.0084242

Griffith, G. P., Richardson, A. J., Fulton, E. A., and Gorton, R. (2012). Evaluating the interaction effects of ocean warming, ocean acidification and fisheries. *Conserv. Biol.* 26, 1145–1152. doi: 10.1111/j.1523-1739.2012.01937.x

Griffiths, S. P., Young, J. W., Lansdell, M. J., Campbell, R. A., Hampton, J., Hoyle, S. D., et al. (2010). Ecological effects of the longline fishery and climate change on the pelagic ecosystem off eastern Australia. *Rev. Fish Biol. Fish.* 20, 239–272. doi: 10.1007/s11160-009-9157-7

Heenan, A., Pomeroy, R., Bell, J., Munday, P. L., Cheung, W., Logan, C., et al. (2015). A climate-informed, ecosystem approach to fisheries management. *Mar. Policy* 57, 182–192.

Hobday, A. J., and Pecl, G. T. (2014). Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. *Rev. Fish Biol. Fish.* 24, 415–425. doi: 10.1007/s11160-013-9326-6

Hobday, A. J., Oliver, E. C., Gupta, A. S., Benthuysen, J. A., Burrows, M. T., Donat, M. G., et al. (2018). Categorizing and naming marine heatwaves. *Oceanography* 31, 162–173. doi: 10.5670/oceanog.2018.205

Hollowed, A. B., Holsman, K. K., Haynie, A. C., Hermann, A. J., Punt, A. E., Aydin, K., et al. (2020). Integrated modeling to evaluate climate change impacts on coupled social-ecological systems in Alaska. *Front. Mar. Sci.* 6:775. doi: 10.3389/fmars.2019.00775

Holsman, K. K., Ianelli, J., Aydin, K., Punt, A. E., and Moffitt, E. A. (2016). A comparison of fisheries biological reference points estimated from temperature-specific multi-species and single-species climate-enhanced stock assessment models. *Deep Sea Res. II Top. Stud. Oceanogr.* 134, 360–378. doi: 10.1016/j.dsr2.2015.08.001

Hutton, T., Rochester, W., Fulton, E. A., Gorton, B., Campbell, R., and Smith, D. C. (2017). *A Coral Sea and Temperate East Marine Region Spatially Explicit Ecosystem Model: an Application of Atlantis*. Canberra: CSIRO.

Ianelli, J., Holsman, K. K., Punt, A. E., and Aydin, K. (2016). Multi-model inference for incorporating trophic and climate uncertainty into stock assessments. *Deep Sea Res. II Top. Stud. Oceanogr.* 134, 379–389. doi: 10.1016/j.dsr2.2015.04.002

IPCC, (2018). *Global Warming of 1.5°C. An IPCC Special Report on the Impacts of Global Warming of 1.5°C Above Pre-Industrial Levels and Related Global Greenhouse gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty*, eds V. Masson-Delmotte, P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P. R. Shukla, et al. (Geneva: IPCC).

Kaplan, I. C., Francis, T. B., Punt, A. E., Koehn, L. E., Curchitser, E., Hurtado-Ferro, F., et al. (2019). A multi-model approach to understanding the role of Pacific sardine in the California Current food web. *Mar. Ecol. Prog. Ser.* 617, 307–321.

Kramer-Schadt, S., Revilla, E., Wiegand, T., and Grimm, V. (2007). Patterns for parameters in simulation models. *Ecol. Modell.* 204, 553–556. doi: 10.1016/j.ecolmodel.2007.01.018

Laufkötter, C., Vogt, M., Gruber, N., Aita-Noguchi, M., Aumont, O., Bopp, L., et al. (2015). Drivers and uncertainties of future global marine primary production in marine ecosystem models. *Biogeosciences* 12, 6955–6984. doi: 10.5194/bg-12-6955-2015

Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W., Galbraith, E. D., et al. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc. Nat. Acad. Sci. U.S.A.* 116, 12907–12912.

Lough, J. M., and Hobday, A. J. (2011). Observed climate change in Australian marine and freshwater environments. *Mar. Freshw. Res.* 62, 984–999. doi: 10.1071/mf10272

Lozano-Montes, H., Loneragan, N., Babcock, R., and Caputi, N. (2013). Evaluating the ecosystem effects of variation in recruitment and fishing effort in the western rock lobster fishery. *Fish. Res.* 145, 128–135. doi: 10.1016/j.fishres.2013.01.009

Lozano-Montes, H., Loneragan, N. R., Babcock, R., and Jackson, K. (2011). Using trophic flows and ecosystem structure to model the effects of fishing in the Jurien Bay Marine Park, temperate Western Australia. *Mar. Freshw. Res.* 62, 421–431. doi: 10.1071/mf09154

Mackinson, S., Daskalov, G., Heymans, J. J., Neira, S., Arancibia, H., Zetina-Rejón, M., et al. (2009). Which forcing factors fit? Using ecosystem models to investigate the relative influence of fishing and changes in primary productivity on the dynamics of marine ecosystems. *Ecol. Modell.* 220, 2972–2987. doi: 10.1016/j.ecolmodel.2008.10.021

Melnychuk, M. C., Banobi, J. A., and Hilborn, R. (2014). The adaptive capacity of fishery management systems for confronting climate change impacts on marine populations. *Rev. Fish Biol. Fish.* 24, 561–575. doi: 10.1007/s11160-013-9307-9

Nielsen, J. R., Thunberg, E., Holland, D. S., Schmidt, J. O., Fulton, E. A., Bastardie, F., et al. (2018). Integrated ecological–economic fisheries models: evaluation, review and challenges for implementation. *Fish Fish.* 19, 1–29. doi: 10.1007/978-90-481-2655-2_1

Norman-López, A., Pascoe, S., and Hobday, A. J. (2011). Potential economic impacts of climate change on Australian fisheries and the need for adaptive management. *Clim. Change Econ.* 2, 209–235. doi: 10.1142/s2010007811000279

Ogier, E. M., Davidson, J., Fidelman, P., Haward, M., Hobday, A. J., Holbrook, N. J., et al. (2016). Fisheries management approaches as platforms for climate change adaptation: comparing theory and practice in Australian fisheries. *Mar. Policy* 71, 82–93. doi: 10.1016/j.marpol.2016.05.014

Olsen, E., Fay, G., Gaichas, S., Gamble, R., Lucey, S., and Link, J. S. (2016). Ecosystem model skill assessment. Yes we can! *PLoS One* 11:e0146467. doi: 10.1371/journal.pone.0146467

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES J. Mar. Sci.* 39, 175–192. doi: 10.1093/icesjms/39.2.175

Pauly, D., Zeller, D., and Palomares, M. L. D. (eds). (2020). *Sea Around Us Concepts, Design and Data*. Vancouver: University of British Columbia.

Payne, M. R., Barange, M., Cheung, W. W., MacKenzie, B. R., Batchelder, H. P., Cormon, X., et al. (2016). Uncertainties in projecting climate-change impacts in marine ecosystems. *ICES J. Mar. Sci.* 73, 1272–1282.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., et al. (2017). Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355:eaai9214.

Pecl, G. T., Ward, T., Doubleday, Z. A., Clarke, S., Day, J., Dixon, C., et al. (2014). Rapid assessment of fisheries species sensitivity to climate change. *Clim. Change* 127, 505–520. doi: 10.1007/s10584-014-1284-z

Pethybridge, H. R., Weijerman, M., Perrymann, H., Audzijonyte, A., Porobic, J., McGregor, V., et al. (2019). Calibrating process-based marine ecosystem models: an example case using Atlantis. *Ecol. Modell.* 412:108822. doi: 10.1016/j.ecolmodel.2019.108822

Plagányi, E. E., Bell, J. D., Bustamante, R. H., Dambacher, J. M., Dennis, D., Dichmont, C. M., et al. (2011). Modelling climate change effects on Australian and Pacific aquatic ecosystems: a review of analytical tools and management implications. *Mar. Freshw. Res.* 62, 1132–1147. doi: 10.1071/mf10279

Plagányi, É. E., Haywood, M. D., Gorton, R. J., Siple, M. C., and Deng, R. A. (2019). Management implications of modelling fisheries recruitment. *Fish. Res.* 217, 169–184. doi: 10.1016/j.fishres.2019.03.007

Plagányi, É. E., Punt, A. E., Hillary, R., Morello, E. B., Thébaud, O., Hutton, T., et al. (2014). Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish Fish.* 15, 1–22. doi: 10.1111/j.1467-2979.2012.00488.x

Plagányi, É. E., Skewes, T., Haddon, M., and Dowling, N. (2013). Risk management tools for sustainable fisheries management under changing climate: a sea cucumber example. *Clim. Change* 119, 181–197. doi: 10.1007/s10584-012-0596-0

Reum, J. C., Blanchard, J. L., Holsman, K. K., Aydin, K., Hollowed, A. B., Hermann, A. J., et al. (2020). Ensemble projections of future climate change impacts on the Eastern Bering Sea food web using a multispecies size spectrum model. *Front. Mar. Sci.* 7:124. doi: 10.3389/fmars.2020.00124

Sheaves, M., Sporne, I., Dichmont, C. M., Bustamante, R., Dale, P., Deng, R., et al. (2016). Principles for operationalizing climate change adaptation strategies to support the resilience of estuarine and coastal ecosystems: an Australian perspective. *Mar. Policy* 68, 229–240. doi: 10.1016/j.marpol.2016.03.014

Smith, D. C., Fulton, E. A., Apfel, P., Cresswell, I. D., Gillanders, B. M., Haward, M., et al. (2017). Implementing marine ecosystem-based management: lessons from Australia. *ICES J. Mar. Sci.* 74, 1990–2003. doi: 10.1093/icesjms/fsx113

Spence, M. A., Blanchard, J. L., Rossberg, A. G., Heath, M. R., Heymans, J. J., Mackinson, S., et al. (2018). A general framework for combining ecosystem models. *Fish Fish.* 19, 1031–1042. doi: 10.1111/faf.12310

Steenbeek, J., Coll, M., Gurney, L., Mélin, F., Hoepffner, N., Buszowski, J., et al. (2013). Bridging the gap between ecosystem modeling tools and geographic information systems: driving a food web model with external spatial-temporal data. *Ecol. Modell.* 263, 139–151. doi: 10.1016/j.ecolmodel.2013.04.027

Sumaila, U. R., Cheung, W. W., Lam, V. W., Pauly, D., and Herrick, S. (2011). Climate change impacts on the biophysics and economics of world fisheries. *Nat. Clim. Change* 1, 449–456. doi: 10.1038/nclimate1301

Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., et al. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol. Lett.* 18, 944–953. doi: 10.1111/ele.12474

Taylor, K. E., Stouffer, R. J., and Meehl, G. A. (2012). An overview of CMIP5 and the experiment design. *Bull. Am. Meteorol. Soc.* 93, 485–498. doi: 10.1175/bams-d-11-00094.1

Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., and Zimmermann, N. E. (2019). Uncertainty in ensembles of global biodiversity scenarios. *Nat. Commun.* 10:1446.

Tittensor, D. P., Eddy, T. D., Lotze, H. K., Galbraith, E. D., Cheung, W., and Barange, M. (2018). A protocol for the intercomparison of marine fishery and ecosystem models: FISH-MIP v1.0. *Geosci. Model Dev.* 11, 1421–1442.

Travers-Trolet, M., Shin, Y. J., Shannon, L. J., Moloney, C. L., and Field, J. G. (2014). Combined fishing and climate forcing in the southern Benguela upwelling ecosystem: an end-to-end modelling approach reveals dampened effects. *PLoS One* 9:e94286. doi: 10.1371/journal.pone.0094286

Tulloch, V. J. D., Plagányi, E., Brown, C., Matear, R., and Richardson, A. J. (2019). Future recovery of baleen whales is imperiled by climate change. *Glob. Change Biol.* 25, 1263–1281. doi: 10.1111/gcb.14573

Van Putten, E. I., Plagányi, E., Booth, K., Ctivanovic, C., Kelly, R., Punt, A., et al. (2018). A framework for incorporating Sense of Place into the management of marine systems. *Ecol. Soc.* 23, 1–24.

Van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., et al. (2011). The representative concentration pathways: an overview. *Clim. Change* 109:5. doi: 10.1007/s10584-011-0148-z

Wayte, S. E. (2013). Management implications of including a climate-induced recruitment shift in the stock assessment for jackass morwong (*Nemadactylus macropterus*) in south-eastern Australia. *Fish. Res.* 142, 47–55. doi: 10.1016/j.fishres.2012.07.009

Woodworth-Jefcoats, P. A., Blanchard, J. L., and Drazen, J. C. (2019). Relative impacts of simultaneous stressors on a pelagic marine ecosystem. *Front. Mar. Sci.* 6:383. doi: 10.3389/fmars.2019.00383

Zhang, X., Church, J. A., Monselesan, D., and McInnes, K. (2017). sea level projections for the Australian Region in the 21st Century. *Geophys. Res. Lett.* 44, 8481–8491. doi: 10.1002/2017gl074176

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.

frontiers
in Marine Science

ORIGINAL RESEARCH
published: 06 November 2020
doi: 10.3389/fmars.2020.568232

The Risky Decrease of Fishing Reference Points Under Climate Change

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In Europe, implementation of sustainable fisheries management has been reinforced in the latest common fisheries policy, and presently marine fish stocks are mostly managed through assessment of their exploitation and ecological status compared to reference points such as Maximum Sustainable Yield (MSY). However, MSY and its associated fishing mortality rate F_{MSY} are sensitive to both stock characteristics and environment conditions. In parallel, climate change impacts are increasingly affecting fish stocks directly and indirectly but might also change the exploitation reference points and the associated level of catch. Here we explored the variability of MSY reference points under climate change by using a multi-species model applied to the Eastern English Channel, a highly exploited semi-continental sea. The spatial individual-based OSMOSE explicitly represents the entire fish life cycle of 14 species interacting through size-based opportunistic predation. The model was first parameterized and run to fit the historical situation (2000–2009) and then used to assess the ecosystem state for the 2050–2059 period, using two contrasting climate change scenarios (RCP 4.5 and RCP 8.5). For each condition, a monospecific MSY estimation routine was performed by varying species fishing mortality independently and allowed estimation of reference points for each species. The F_{MSY} estimated with OSMOSE were mostly in accordance with available values derived from stock assessment and used for fishing advice. Evolution of reference points with climate change was compared across species and highlighted that overexploited cold-water species are likely to have both MSY and F_{MSY} declining with climate warming. Considering all species together, MSY under RCP scenarios was expected to be higher than historical MSY for half of them, with no clear link with species temperature preferences, exploitation status or trophic level, but in relation with expected change of species biomass under climate change. By contrast, for 80% of cases F_{MSY} projections showed consistent decreasing pattern as climate conditions changed from historical to RCP scenarios in the Eastern English Channel. This result constitutes a risk for fisheries management, and anticipation of climate change impacts on fish community would require targeting a smaller fishing mortality than F_{MSY} to ensure sustainable exploitation of marine stocks.

Keywords: maximum sustainable yield, climate change, biological reference points, ecosystem model, fishery management

Edited by:
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Specialty section:
*This article was submitted to
Marine Fisheries, Aquaculture
and Living Resources,
a section of the journal
Frontiers in Marine Science*

Received: *31 May 2020*
Accepted: *18 September 2020*
Published: *06 November 2020*

Citation:
*Travers-Trolet M, Bourdaud P,
Genu M, Velez L and Vermard Y
(2020) The Risky Decrease of Fishing
Reference Points Under Climate
Change. Front. Mar. Sci. 7:568232.
doi: 10.3389/fmars.2020.568232*

INTRODUCTION

Sustainable fisheries management has been advocated worldwide for decades, with several milestones reinforcing this principle. Adopted by more than 17O Members of the Food and Agriculture Organization of the United Nations (UN) in 1995, the Code of Conduct for Responsible Fisheries provides principles applicable to the conservation, management and development of all fisheries and aims at promoting sustainable development and exploitation of world fisheries (Food and Agriculture Organization [FAO], 1995). The 2002 World Summit on Sustainable Development held at Johannesburg reaffirmed the necessity of continuing efforts toward sustainable development of the oceans and ecosystem approach for fisheries management. Particularly, UN member states committed themselves to maintain or restore fish stocks to a level that can produce their maximum sustainable yield (MSY) no later than 2015 (Froese and Quaas, 2013). This decision has been implemented in Europe through the 2013 reform of the Common Fisheries Policy (CFP; European Union [EU], 2013), in which a sustainable exploitation rate corresponding to MSY should be achieved by 2015, or in 2020 at the latest depending on the socio-economic context of the stocks considered (Salomon et al., 2014). The same reference point is used as one of the primary criteria to assess the good environmental status of commercially exploited fish and shellfish under the descriptor 3 of the Marine Strategy Framework Directive (MSFD, European Commission, 2017).

The concept of optimum or maximum yield started to be presented as management objective in the middle of the 20th century (Mesnil, 2012), but MSY was not specifically used as reference point for fishery management in European Union (EU) prior the 2013 CFP reform. MSY is defined as the largest yield that can be continuously taken on average from a stock under average environmental conditions without affecting significantly the reproduction process. The fishing mortality rate F_{MSY} is the level at which average yield is equal to MSY, and corresponds to the target reference point explicitly mentioned in the CFP (European Union [EU], 2013). F_{MSY} is a manageable target reference point directly linked to fishing effort in contrast to biomass reference points that are also influenced by the ecosystem state. However, reaching F_{MSY} does not imply that fish stocks are truly exploited at levels allowing MSY as other factors than fishing pressure can affect stock dynamics and status.

In EU, operational F_{MSY} values are mainly estimated by ICES (International Council for the Exploration of the Sea) working groups using monospecific stock assessment models. Estimations of current stock status and reference points are based on analysis of catch/biomass time series, and life history characteristics such as population growth rates and stock–recruitment relationships. Furthermore, models used for stock assessment typically assume constant values of factors not explicitly considered in the models, such as trophic interactions or abiotic environment (ICES, 2019). Reviewing the effects of fisheries-induced evolution on life-history traits and resultant stock properties, Heino et al. (2013) highlighted the possible change these effects can have on reference points. They particularly noted that F_{MSY} was expected to increase through fisheries-induced evolution, while MSY change was ambiguous. As environmental conditions are expected to drift from the historical mean due to climate change, fishing reference points estimated under average conditions might be inappropriate under future climate conditions (Perry et al., 2010). Using scenarios of temperature increase on North Sea cod (*Gadus morhua*), Kell et al. (2005) showed that reference points based on fishing mortality were more robust to uncertainty about dynamic processes and future conditions than those based on biomass. Specifically F_{MSY} was found not to be affected by changes in carrying capacity, but was found to decrease when temperature increased, resulting in decreased juvenile survival. To compensate the possible evolution of reference points, ICES considers MSY reference points to be valid only in the medium term, and regularly assesses the validity of the estimations through regular reviews (ICES, 2019). During benchmarks (classically every 5 years), data sources, stock-assessment model and assumptions are updated to include possible evolution of abiotic (e.g., habitat), biotic (e.g., trophic interactions and predation mortality) and exploitation conditions (e.g., fishing selectivity). This pragmatic approach allows producing advice and reference points in a dynamic mode, however, anticipation of future evolution of reference points would make fisheries management more sustainable.

Here we aim at exploring how fishing reference points would evolve under climate change, and if general patterns emerge that could be used in anticipation for fisheries management. To do so, we applied the multi-species model OSMOSE to an exploited shallow sea ecosystem and estimate F_{MSY} for several species in different long term abiotic conditions. This model has been successfully applied to a variety of ecosystems, such as upwellings (e.g., Marzloff et al., 2009; Travers-Trolet et al., 2014a), estuaries (e.g., Brochier et al., 2013), semi-enclosed seas (Fu et al., 2012) and shelf seas (e.g., Grüss et al., 2015; Halouani et al., 2016), and has been used for addressing various objectives. Particularly OSMOSE has been used for exploring combined effects of fishing and climate on the food web (Travers-Trolet et al., 2014b; Fu et al., 2018), management strategy evaluation of total allowable catch strategies (Grüss et al., 2016) and for exploration of multi-species reference points (Briton et al., 2019; Guo et al., 2019). It was also used to investigate sensitivity of various ecosystem indicators to fishing or environmental conditions (Travers et al., 2006; Shin et al., 2018), but it has never been used to explore the evolution of management reference points under climate change projections.

MATERIALS AND METHODS

Eastern English Channel Fish Community Modeled With OSMOSE

Object-oriented Simulator of Marine Ecosystems (OSMOSE) is a spatial multispecies size-structured model based on opportunistic predation between a predator and its prey (Shin and Cury, 2001, 2004; Travers et al., 2009)[1]. This individual-based model represents the whole life cycle of several fish species from eggs

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[1] www.osmose-model.org

and larvae up to juveniles and adults. Each individual element corresponds to a "school" or super-individual of identical fish, i.e., of the same size, same age, same trophic level (TL), same location and belonging to the same species. At each time step of 2-weeks schools undergo different processes: foraging movement, interactions with the environment and other schools (resulting in explicit predation and several sources of mortality: predation, starvation and fishing mortalities, and residual mortality due to causes not explicitly modeled), growth and reproduction. Opportunistic predation relies on spatio-temporal co-occurrence and size adequacy between a predator and its prey, which allows food web structure not to be fixed but to emerge from local trophic interactions between schools (Travers-Trolet et al., 2019). Fishing pressure is modeled through a species-specific fishing mortality rate F that can vary temporally and/or spatially according to available knowledge and which affects only recruited fish (here a knife-edge selectivity was used, i.e., only fish older than the species age at recruitment were caught). An extended description of the OSMOSE model and its parameterization is available as **Supplementary Material S1** and **Supplementary Table S1**.

OSMOSE has been applied to the Eastern English Channel (EEC) to better understand the trophic functioning of this shallow-water sea ecosystem, by explicitly representing 14 species which constitute 80% of the international landings from this area (ICES area 7d, excluding invertebrates), more than two-thirds of the fish biomass sampled during the scientific bottom trawl Channel Ground Fish Survey (CGFS, Coppin et al., 1988) and represent important trophic groups. This set of species is composed of mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*), sardine (*Sardina pilchardus*), herring (*Clupea harengus*), poor cod (*Trisopterus minutus*), North Sea cod, whiting (*Merlangius merlangus*), pouting (*Trisopterus luscus*), striped red mullet (*Mullus surmuletus*), dragonet (mostly *Callionymus lyra*), lesser spotted dogfish (*Scyliorhinus canicula*), sole (*Solea solea*), plaice (*Pleuronectes platessa*), and squids (*Loligo forbesii* and *Loligo vulgaris*). This high TL community can additionally feed on spatially and temporally variable biomass prey fields of both pelagic and benthic resource groups coming from the forcing ECO-MARS3D biogeochemical model (Vanhoutte-Brunier et al., 2008; Le Goff et al., 2017). OSMOSE has been parameterized to represent the average state of the EEC ecosystem over the period 2000–2009 using biological parameters from the literature and information derived from surveys (Travers-Trolet et al., 2019; **Supplementary Table S1**). The model was then calibrated with an automatic evolutionary algorithm (Oliveros-Ramos et al., 2017) during which the remaining unknown parameters were tuned in order for the simulated biomass and catch to approach the values observed over 2000–2009. Plankton accessibilities, larval mortalities (applied at the first time step only, i.e., when organisms are 2 weeks old) and fishing mortalities (applied to all fish older than recruitment age) have been adjusted during this phase. Observed catches have been extracted from the ICES Fisheries Statistics official database (ICES, 2011a) for the ICES area 7d (corresponding to the EEC) over the period 2000–2009. Total stock biomass estimates were not available for all species. They came directly from stock assessment reports for sole and plaice (ICES, 2011b), while for whiting, North Sea cod, mackerel and herring, total stock biomass estimates were derived from stock assessments covering a wider area (ICES, 2011b, 2012) and were therefore scaled to the EEC proportionally to the relative landings in this area. Finally, the EEC OSMOSE application was validated using independent data, i.e., neither used during parameterization nor calibration. Simulated mean TL per species and pattern of TL evolution with size were similar to trophic observations available in the EEC during the same period (Travers-Trolet et al., 2019).

Climate Change Scenarios

Projections of the fish community under climate change were performed using two contrasting greenhouse gas concentration scenarios for which downscaled biogeochemical runs were available regionally (CERES, 2018). The scenarios are the Representative Concentration Pathway (RCP) 4.5 and RCP 8.5 used by the Intergovernmental Panel on Climate Change (IPCC, 2014), which correspond at the EEC scale to an averaged increase of sea temperature of respectively +0.24 and +0.83°C at the 2050–2059 horizon compared to the historical state (13.11°C in average over 2000–2009). The 2050–2059 time frame corresponds to mid-term projections, i.e., a compromise far enough in the future to perceive the impacts of climate change on the ecosystem, but close enough for fisheries management tools (reference points) to stay relevant. As temperature is not explicitly integrated in the formulation of OSMOSE processes, effects of global warming were simulated through the modification of parameters of several processes classically impacted by climate change (Scheffers et al., 2016). Primary and secondary productions were slightly decreased, following the projections of the downscaled POLCOMS-ERSEM biogeochemical model (Butenschön et al., 2016) available for the North East Atlantic. Growth parameters were modified following Kielbassa et al. (2010) approach, either through an increase or decrease of the parameters depending on the optimal temperature computed for each species, the historical temperature and the projected temperature of the RCP scenarios. Reproduction phenology was advanced depending on the cumulated degree × day duration in each scenario (resulting in earlier reproduction season, up 14 days in advance depending on the scenario and the species considered). Spatial distribution was only impacted for species in their southern boundaries of distribution (North Sea cod, whiting, herring, and plaice), by cutting their spatial distribution according to thermal clines for both scenarios. Details on the references used and computations realized to change parameters values and on the resulting ecosystem response to climate change simulated with OSMOSE can be found in Genu (2017) and **Supplementary Material S2**.

To assess the importance of species sensitivity to temperature in the possible evolution of reference points under climate change, a temperature status was computed for each species relative to their optimal temperature T_{opt} (Eq. 1).

$$T^{\circ}status = \frac{T_{opt} - T_{hist}}{T_{hist}} \qquad (1)$$

where T_{hist} is the reference state of the historical EEC temperature equal to 13.11°C.

According to this metric, species with a temperature optimum smaller than the current temperature, i.e., susceptible to negative impact from warming, were North Sea cod, herring, whiting, and to a lesser extent plaice, mackerel, lesser spotted dogfish, striped red mullet and poor cod. Species with a relatively high optimal temperature were squids, sardine, sole, pouting, dragonet and horse mackerel (**Table 1** and **Supplementary Table S2**).

Estimation of MSY Reference Points

Maximum Sustainable Yield reference points were estimated for each species by analyzing the simulated catch obtained for a wide range of fishing mortality rates F. The F space is explored regularly from 0 to 0.5 $year^{-1}$ or up to 5 $year^{-1}$ depending on species (resulting in about 100 *F* values for each species, see **Supplementary Material S4**). This exploration was performed for each species independently, i.e., while the *F* values of the species of interest were modified the *F* values of other species were kept constant at their historical levels. For each value of fishing mortality, 30 replicates were run as OSMOSE is a stochastic model and the corresponding simulated catches were saved. To determine the maximal catch corresponding to MSY and the associated annual fishing mortality rate (F_{MSY}), local polynomial regressions were adjusted to catch data points using the loess function in R (Briton et al., 2019).

To investigate the possible importance of the current exploitation status compared to MSY in the evolution of reference points under climate change, a fishing status was computed for each species (Eq. 2) based on the relative difference between the historical F_{hist} value (corresponding to the calibrated values over the 2000–2009 period) and F_{MSY} determined as previously described.

$$Fstatus = \frac{F_{hist} - F_{MSY}}{F_{MSY}} \tag{2}$$

For some species the yield versus F curve can display a plateau rather than the classic dome-shape curve. To deal with this pattern, Briton et al. (2019) computed the yield at 98% of the MSY as it usually corresponds to the beginning of the plateau in their study. Here we used a similar approach: the yield at 95% of MSY was computed and used to derive the corresponding fishing mortality (F_{95MSY}). This percentage corresponds to the precautionary approach followed by ICES when providing advice on F ranges from stock assessment (ICES, 2016).

First, the MSY computation procedure was applied under historical (2000–2009) conditions, to determine current MSY, F_{MSY} and F_{95MSY} as well as fishing status for all species. The same procedure was then applied under climate change (2050–2059) conditions, using RCP scenarios as described above, to estimate the reference points for all species under two scenarios of climate change.

RESULTS

MSY Estimation Under Historical Period

A total of 40050 simulations (including replicates) were run on a super-computer to compute MSY reference points for all species under historical conditions (**Table 1**). For most species, the relationship between catch and F followed a dome shape curve of variable width (**Figure 1**). However, for few species (pouting, poor cod, sole and squids) a plateau was observed as F increased.

TABLE 1 | Species characteristics and reference points estimated under different conditions.

Species name	Species characteristics					F_{MSY}*			MSY		
	TL	T_{opt}	T° status	F_{hist}	F status	historical	RCP 4.5	RCP 8.5	historical	RCP 4.5	RCP 8.5
Lesser spotted dogfish (SYC)	4.59	12.97	−0.010	0.09	−0.615	0.234	0.379	0.39	2692	6347	5935
Striped red mullet (MUR)	3.86	12.7	−0.031	0.194	−0.517	0.402	0.373	0.334	1228	1911	1906
Pouting (BIB)	3.94	15.74	0.201	0.106	−0.962	2.792	1.288	0.798	6765	5460	5294
Whiting (WHG)	4.64	8.21	−0.374	0.122	−0.252	0.163	0.072	0	4931	1714	<1
Poor cod (POD)	3.94	12.01	−0.084	0	−1.000	1.953	1.527	1.263	3573	3107	1920
North Sea Cod (COD)	4.70	6.63	−0.494	0.219	1.009	0.109	0.062	0.009	4196	1359	<1
Dragonet (LYY)	3.94	14.86	0.134	0	−1.000	0.968	0.912	0.83	4541	5122	5884
Sole (SOL)	3.90	16.34	0.247	0.187	−0.861	1.35	0.748	0.704	5701	7844	10447
Plaice (PLE)	4.08	12.14	−0.074	0.44	0.673	0.263	0.276	0.222	3054	3074	1727
Horse mackerel (HOM)	3.87	13.31	0.016	0.052	−0.787	0.244	0.224	0.242	16332	16461	17695
Mackerel (MAC)	4.18	12.41	−0.053	0.142	−0.503	0.286	0.203	0.308	7461	10289	13562
Herring (HER)	2.75	7.13	−0.456	0.156	−0.795	0.762	0.717	0.223	28809	13784	71
Sardine (PIL)	2.90	18.79	0.434	0.03	−0.932	0.614	0.583	0.683	85979	97112	107534
Squids (SQZ)	4.61	20.11	0.534	0.036	−0.914	0.419	0.66	0.396	12375	8399	11902

Mean trophic level (TL), optimal temperature (T_{opt} in Celsius degree), temperature status (T° status), historical fishing mortality (F_{hist} in $year^{-1}$) and fishing status (F status) correspond to historical conditions (2000–2009). Reference points corresponding to the maximum sustainable yield (MSY in tons) and the fishing mortality (F_{MSY} in $year^{-1}$) corresponding to MSY are estimated for historical conditions, and under climate change scenarios RCP 4.5 and RCP 8.5 (2050–2059). Gray cells indicate situations where the fishing mortality corresponding to 95% of MSY (F_{95MSY}) is used instead of F_{MSY} due to the presence of a plateau in the catch versus F curve (see text). Species codes indicated in brackets are used in the figures.*

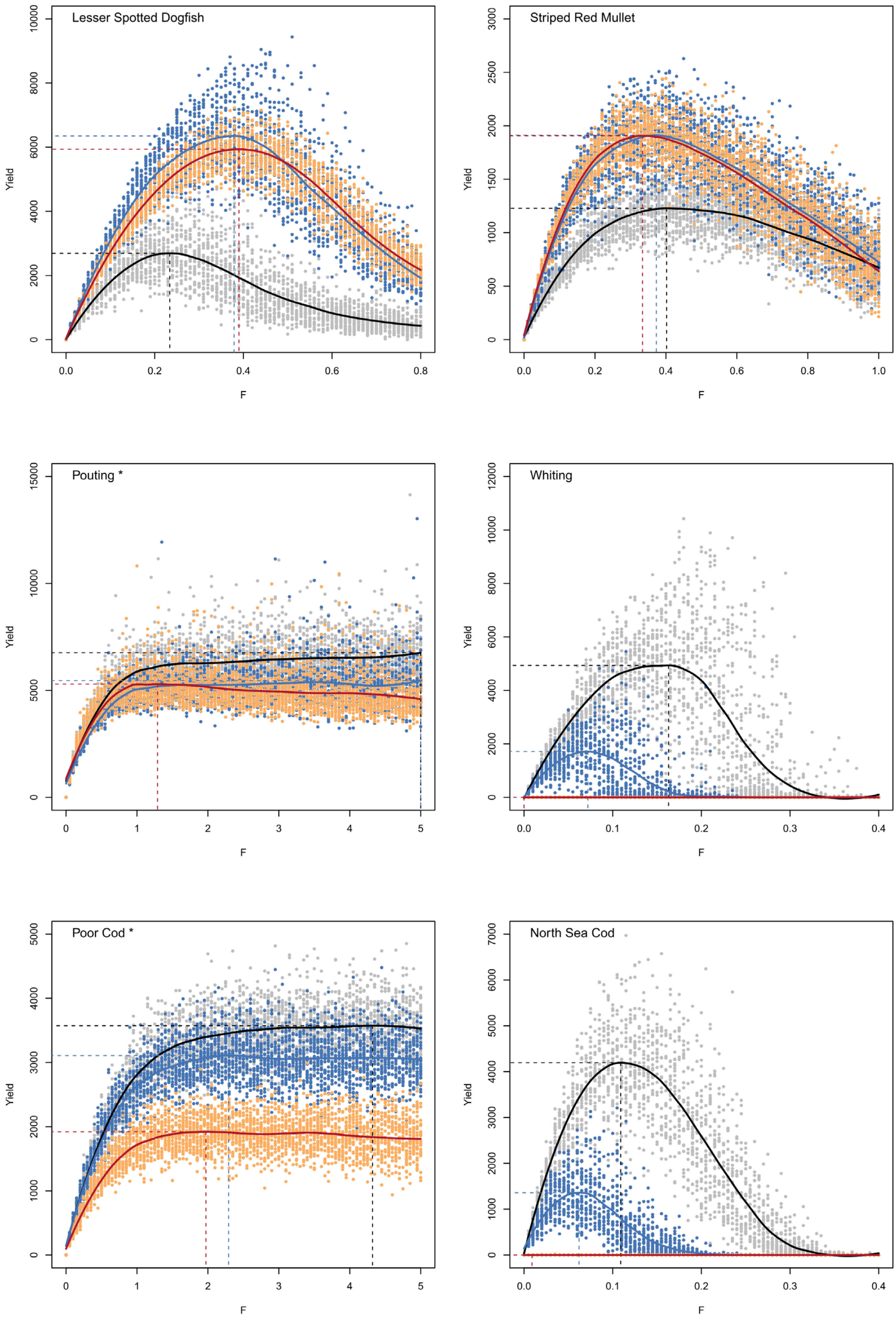

FIGURE 1 | Continued

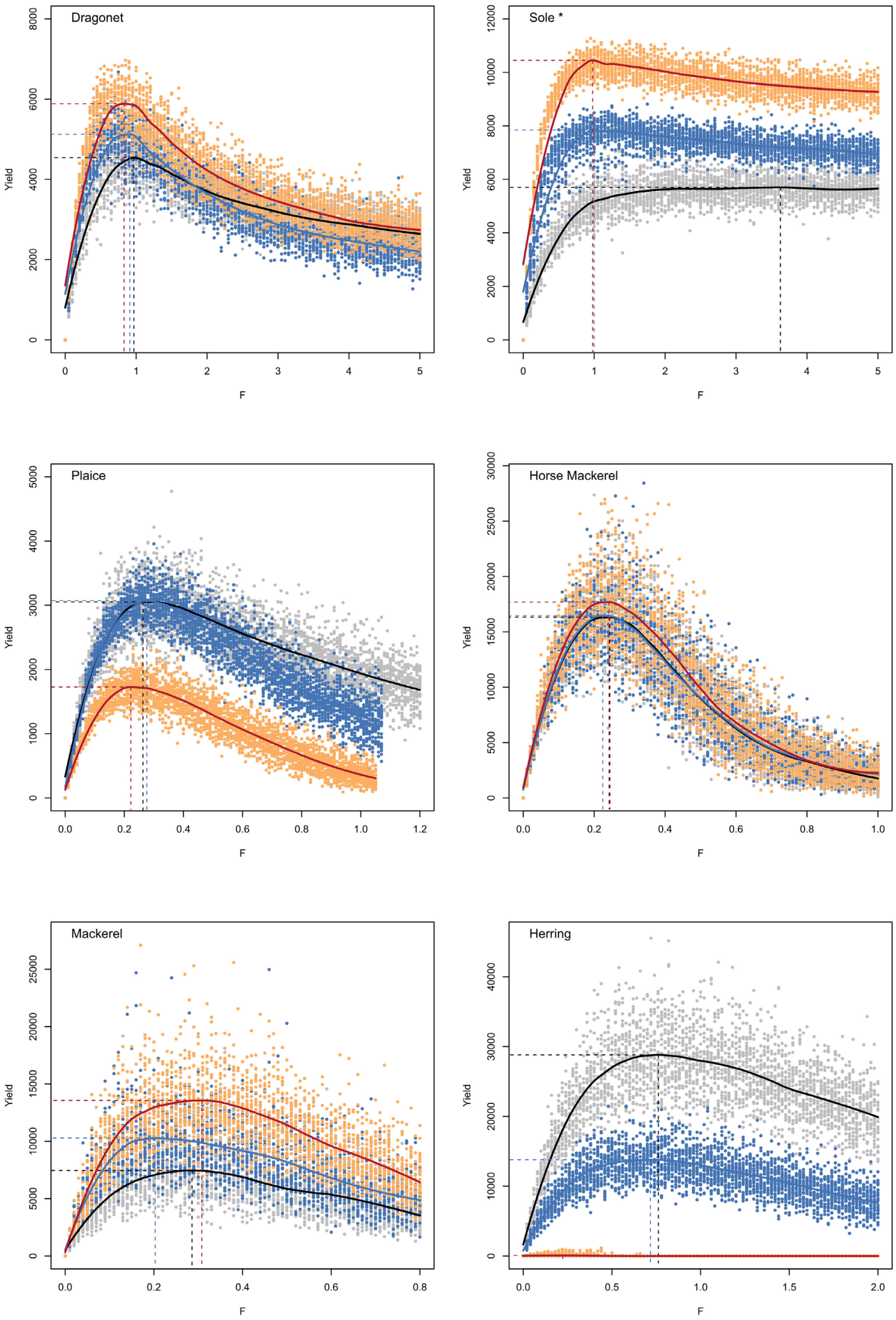

FIGURE 1 | Continued

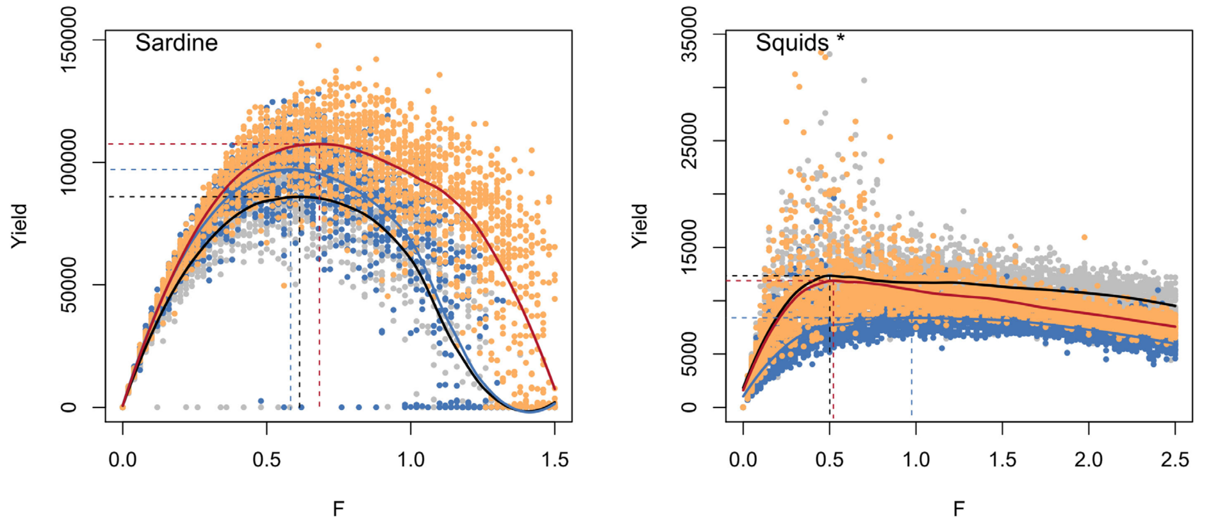

FIGURE 1 | Evolution of yield with fishing mortality rate (F) for each species, under historical conditions (gray and black), and under climate change scenarios RCP 4.5 (blue) and RCP 8.5 (orange and red). Dots correspond to the simulated yield (using 30 replicates) and the line corresponds to the adjusted loess function. Horizontal dashed lines indicate MSY, and vertical dashed lines indicate F_{MSY} for most species and F_{95MSY} for species for which the curve shows a plateau (indicated by * next to species name).

While the estimate of MSY remains valid in case of a plateau, the value obtained for F_{MSY} is highly variable and depends on the regression function used. Therefore, F_{95MSY} is more reliable and was used as reference point and for the computation of F-status for these four species (**Table 1**).

According to the F_{MSY} estimates determined using OSMOSE, most species were under-exploited (negative F status) during the 2000–2009 period. The two over-exploited species, i.e., having a fishing mortality rate over 2000–2009 higher than the reference point F_{MSY}, were North Sea cod and plaice. Absolute values of reference points derived from single stock assessments cannot be compared directly to estimates determined in this study because the models used largely differ, but relative values can be helpful. Only few species inhabiting the EEC are assessed by ICES stock assessment groups at a level allowing MSY estimation. Analysis of plaice stock assessment for the same area (ICES 7d) indicated that the fishing mortality averaged over 2000–2009 corresponded to 1.3 times the F_{MSY} estimate (ICES, 2017, values reported in **Supplementary Table S5**). Using OSMOSE, historical fishing mortality of plaice were found to be 1.7 times the level of the reference F_{MSY}. Sole was also found to be overfished in the ICES area 7d from stock assessment, with average fishing

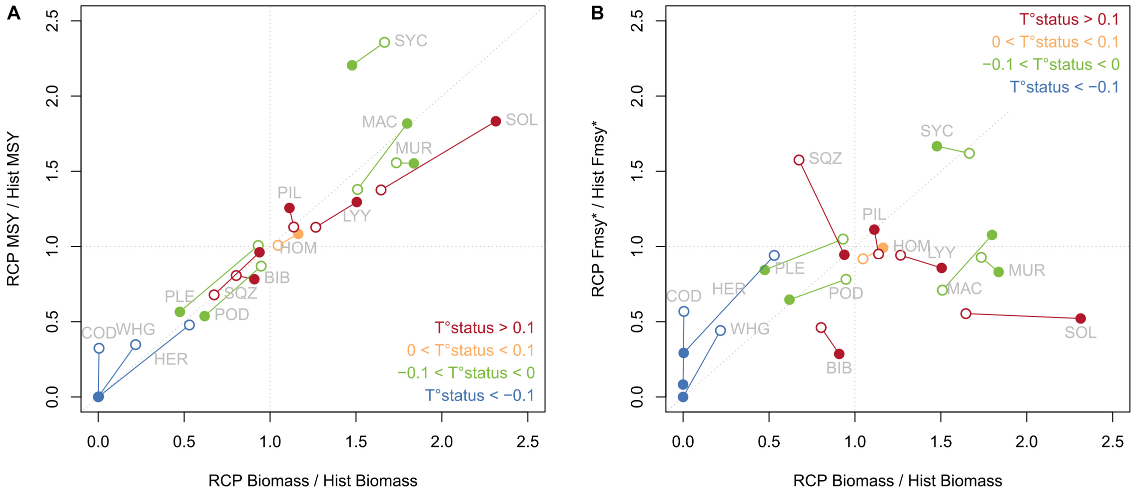

FIGURE 2 | Evolution of MSY **(A)** and F_{MSY}* **(B)** (corresponding to F_{MSY} for most species, and to F_{95MSY} for species displaying a plateau in their catch-F curve) under RCP 4.5 (open dots) and RCP 8.5 (filled dots) compared to historical values. Color of the dots indicates the T° status of the species. Species code name are explicit in **Table 1**.

mortality rates being 1.43 times higher than F_{MSY} (ICES, 2017). Conversely, in OSMOSE this species appeared to be exploited at a smaller level than MSY (F_{hist} corresponds to only 0.14 times F_{95MSY}, the reference point preferably used as the catch versus F curve displayed a plateau). Stock assessment of North Sea cod performed over a broader area (ICES areas 4 and 7d), indicated that this stock was over-exploited with 2000s averaged fishing mortality rates being 2.7 times higher than F_{MSY} determined via stock assessment (ICES, 2017). In OSMOSE, North Sea cod was also found to be overexploited, with a fishing mortality averaged over 2000–2009 corresponding to twice the F_{MSY}. Finally, whiting was also assessed over the wider area ICES 4 and 7d and was estimated to be exploited during the 2000s at half the level of F_{MSY} (ICES, 2017). Similarly in OSMOSE the exploitation level was found to be smaller than F_{MSY} (0.75 times the reference value F_{MSY}).

Evolution of MSY and F_{MSY} Under Climate Change

Under RCP scenarios, the evolution of fish community structure was characterized by a strong decrease of cold-water species (North Sea cod, whiting, herring), especially under RCP 8.5 with North Sea cod and whiting collapsing in the EEC. Conversely, other species increased in biomass, notably lesser spotted dogfish, mackerel, striped red mullet and sole (**Supplementary Table S3**). Associated to these changes in species biomass, similar changes were simulated for species catch under climate change because fishing mortality rates were not modified compared to historical values. In the same vein, evolution of MSY reference points tends to scale with evolution of biomass (**Figure 2A**), except for lesser spotted dogfish for which the biomass increased by 1.5 under climate change was associated with an increase of MSY by more than 2. While species with a T° status smaller than −0.1 displayed a strong decrease in biomass under RCP scenarios, species with intermediate (between −0.1 and 0.1) and high T° status (higher than 0.1) showed either a decrease or increase in biomass, with no consistent pattern. Biomass changes under climate change were not directly linked to species T° status as the flexible trophic links of OSMOSE allowed multiple indirect effects of climate change. In contrast to MSY, F_{MSY} evolution under climate change was not linked to changes in biomass of the associated species (**Figure 2B**). Again, except for species with low T° status which showed a decrease of F_{MSY} under climate change, no link was evidenced between T° status and F_{MSY} evolution. Under RCP scenarios, the species catch versus F curves displayed similar shape than under historical conditions, i.e., a plateau was observed for the same four species (**Figure 1**).

The co-evolution of both MSY and F_{MSY} reference points displayed different patterns for different species (**Table 1**). For instance, both MSY and F_{MSY} decreased under climate change for North Sea cod and whiting, with an intensity proportional to warming. Conversely, both reference points increased for lesser spotted dogfish under climate change, but with little difference between the two RCP scenarios. For plaice, reference points were similar between historical state and moderate climate change (RCP 4.5), but decreased under stronger warming (RCP 8.5). Under RCP 4.5, F_{MSY} for striped red mullet did not change much, but it was associated with higher MSY. Reference points for horse mackerel showed very little evolution under climate change, whatever the scenario considered.

To explore the evolution of reference points globally under climate change, relative changes of MSY and F_{MSY} compared to historical values were displayed on a biplot for each species (**Figure 3**). For most cases (79% i.e., for 22 cases in the 28 combinations of species and RCP scenarios), a decrease of F_{MSY} was projected under climate change. Except for squids under RCP 4.5 (for which the catch-F curve showed a plateau and might provide less reliable estimates), no situation associated an increase of F_{MSY} with a decrease of MSY. However, the opposite can be true, i.e., for sole, striped red mullet, dragonet for both scenarios but also for sardine and mackerel under RCP 4.5, climate change induced a decrease of F_{MSY} associated with an increase of MSY. It is worth noting that evolution of reference points under RCP 8.5 was not always a stronger evolution than the one simulated for RCP 4.5, and changed sometimes in the opposite direction. For instance, F_{MSY} for mackerel decreased under RCP 4.5 but increased under RCP 8.5, MSY of lesser spotted dogfish increased strongly between RCP 4.5 and historical level, but decreased between RCP 4.5 and RCP 8.5.

When considering the potential link between F status and evolution of reference points (**Figure 3A**), we found that for both overexploited species climate change induced a decrease of MSY and F_{MSY}, but only under RCP 8.5 for plaice. For moderately exploited species such as whiting, a decrease of both reference points was also observed. However, for lightly exploited species, various directions of change of reference points were observed, from a decrease of both MSY and F_{MSY} for herring to an increase of MSY but decrease of F_{MSY} for striped red mullet and to an increase of both reference points (lesser spotted dogfish). The analysis of reference points evolution according to T° status (**Figure 3B**) showed that for cold water species (high negative T° status) both reference points decreased under global warming. Conversely, warmer water species (with high positive T° status) seemed to display a small increase of MSY under climate change, and no clear direction for F_{MSY} (small increase for sardine, small decrease for dragonet). No clear pattern emerged from species with intermediate values of T° status. Finally, the consideration of species TL (**Figure 3C**) did not allow identifying trophic groups for which reference points would behave the same, but conversely illustrated some balance within the ecosystem: when reference points of predators North Sea cod and whiting decreased, reference points of another predator (lesser spotted dogfish) increased. Similar balance was observed for planktivorous species (sardine and herring, TL < 3). For intermediate TL species, this pattern was dampened, probably due to the numerous complex interactions linking the species at the center of the food web.

DISCUSSION

The expected evolution of reference points under climate change is not mono-directional and depends on species considered.

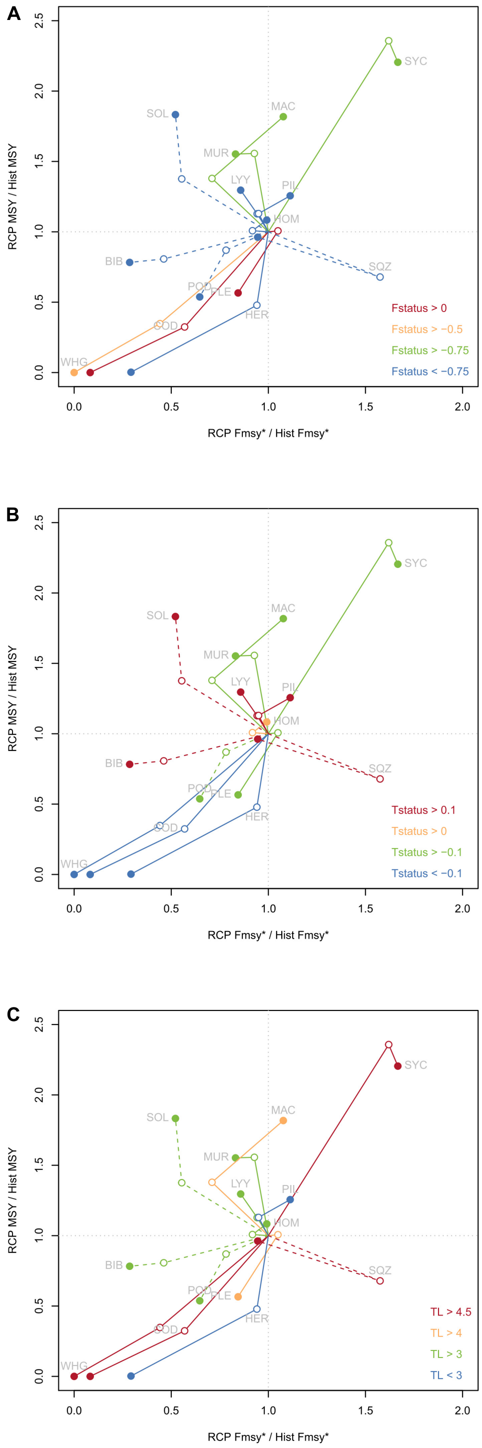

FIGURE 3 | Evolution of reference points under climate change scenarios compared to historical values of reference points. Relative MSY is plotted on the *y*-axis. Relative $F_{MSY}{}^*$ corresponds to relative F_{MSY} for most species and to relative F_{95MSY} for species displaying a plateau in their catch-F curve, and is displayed on *x*-axis. Dashed lines indicate those species. Historical references points are situated at coordinates (1,1) by construction, references points under RCP 4.5 are indicated by open dots and reference points under RCP 8.5 are indicated by filled dots. Colors are associated to species characteristics, either F status **(A)**, T° status **(B)** or TL **(C)**.

MSY evolution appears to be strongly linked to species biomass evolution, which cannot be derived *a priori* from temperature preference of fish species. Indeed, climate change is applied on several processes within OSMOSE (Genu, 2017; **Supplementary Material S2**) and the representation of the full life cycle coupled with the multiple and flexible trophic links between fish individuals allows simulations of both direct and indirect effects of climate change, leading to unpredictable species biomass evolution. This results in expected decrease of MSY under climate change for half of the modeled species. Both directions of change of MSY have been reported with observed increasing temperature and have been projected under climate change scenarios. When analyzing the evolution of MSY with historical temperature for 235 populations worldwide, Free et al. (2019) showed that MSY increased for nine populations and decreased for 19 populations. This decrease was particularly observed for populations inhabiting the North Sea, a neighbor ecosystem to the EEC, and for species that had experienced overfishing, warming and were located at the warm ends of their thermal niches (Free et al., 2019). Another time series analysis realized in the North Sea emphasized that MSY of five planktivorous species have been halved between the late 1970s and the most recent period, illustrating this time a common decrease of forage fish productivity probably induced by a precedent shift in plankton community (Clausen et al., 2018) that have been linked to temperature (Beaugrand et al., 2003). Complementary to time series analysis, studies using projections of ecosystem under climate change give also contrasting results. Cheung et al. (2010) showed that the projected maximum catch potential (computed from estimated species MSY) under Special Report on Emissions Scenarios (SRES) scenarios was highly variable across regions and ranges from −20% for Indonesia EEZ to +45% for Norway EEZ, with almost no change for United Kingdom EEZ which includes part of the EEC. From projections under four recent RCP scenarios, total global MSY from almost a thousand stocks worldwide did not change markedly by 2100 on average, but showed enormous variation across stocks as 53% of stocks' MSY decreased under RCP 4.5 and 91% under RCP 8.5 (Gaines et al., 2018).

Determining generalities of reference points' response to climate change would be helpful for managers, as it would provide information required for anticipating future changes in their operational tool. From the relatively small amount of species modeled with OSMOSE it seems that cold-water species will undergo a decrease in both reference points, but for temperate species no pattern can be identified. Exploitation status might have a role as well, as overexploited species also undergo a decrease in both reference points. Even with a limited number of species considered this study shows that overexploited cold-water species are likely to have both their reference points declining with climate warming. This result concurs with conclusions from Free et al. (2019) concerning MSY only. Additional general patterns involving both reference points were not evidenced in this study, especially regarding temperate species. However, conversely to the diversity of MSY responses to climate change, F_{MSY} projections considered alone show more consistent decreasing pattern in the EEC under RCP scenarios. The few cases (20%) in which F_{MSY} was found to increase concern lesser spotted dogfish, mackerel and sardine, which are moderately exploited and temperate to warm species. Consistent decrease of F_{MSY} with increasing temperature was also observed from time series analysis of five planktivorous fish in the adjacent North Sea (Clausen et al., 2018). When studying possible response of North Sea cod reference points to warming, Kell et al. (2005) illustrated that F_{MSY} was expected to decrease as temperature increases. These studies combined to our results reinforced the main pattern obtained here, that fishing reference point F_{MSY} is expected to decrease under global warming for a variety of stocks.

Climate-induced decrease of F_{MSY} constitutes a big risk for managers and sustainability of stocks. Even if this fishing reference point is currently used as a management target in EU and supposedly reached by 2015 (European Union [EU], 2013), current fishing mortality rate remains higher than F_{MSY} for 64% of the 397 stocks in EU therefore indicating their overexploitation (Froese et al., 2018). This percentage goes down to 44% when considering only the greater North Sea ecoregion (45 stocks) to which the EEC pertains, a value still illustrating that sustainable exploitation of this ecosystem is not reached yet. In this context, the risk for managers is that the fishing reference points they are targeting (and having difficulties to reach) when reducing fishing pressure will decrease under climate change, and therefore will prevent the sustainable exploitation of stocks. Positive expected consequences of fishing at F_{MSY} such as highest average yield fishers can expect would not be observed as warming would have change the reference values, and might discourage effort to further reducing the fishing pressure. To ensure sustainable fisheries, managers need to be proactive regarding effects of climate change, and should start targeting fishing mortalities smaller than F_{MSY}. Such recommendations have already been proposed, but for other objectives. Targeting only a "pretty good yield", i.e., corresponding to 80% of MSY as proposed by Hilborn (2010), allows reasonably high yields for fishers and other beneficial outputs linked to the multiple objectives of most fisheries management. This is particularly true for mixed-fisheries, i.e., when several species are caught together and their respective MSY cannot be reach concomitantly (Rindorf et al., 2017; Ulrich et al., 2017). Using the F_{MSY} reference points as a limit rather than a target, i.e., aiming at keeping the fishing mortality rate lower than F_{MSY}, or targeting a reference point lower than F_{MSY} would be precautionary both in case of technical interactions between stock (mixed fisheries) and in case of climate change anticipation.

Mechanistic multispecies model such as OSMOSE represent a useful framework to explore response of management tools such as F_{MSY} to different modalities of ecosystem state usually considered constant in stock assessment models. The model provided good estimates of relative reference points when compared to stock assessment output. The occurrence of a plateau in the yield to fishing mortality curve for four species tempered the overall good representation of stocks dynamics, even though a plateau is also observed sometimes using stock assessment models. Typically, fishing selectivity curve affects the shape of the yield to fishing mortality curve (and the values of reference points), and asymptotic selectivity can result in the presence of a plateau (Scott and Sampson, 2011). In the present study, two main hypotheses can explain the occurrence of a plateau. First, growth depends on food availability, and under abundant food conditions, some individuals can reach maturity size long before reaching recruitment age. These individuals would have time to reproduce before being caught by fishing, preventing population collapse under high fishing mortality rates. Second, fishing pressure was modeled in a simple way, with a knife-edge selectivity and therefore a constant fishing mortality rate applied to all individuals older than the specified age at recruitment. Further developments implementing several fishing fleets and associated size selectivity curves would allow identifying if a plateau would persist under more realistic modeling choices, and would be useful for integrating technical interactions in the exploration of MSY behavior to climate change. Here we used a monospecific procedure to estimate MSY reference points, even if we used a multi-species model with predation interactions, because they correspond to the target of the CFP (European Union [EU], 2013). However, alternatives could be studied, such as the concomitant estimation of MSY for a set of interacting species (Nash equilibrium between F_{MSY} reference points, Thorpe et al., 2017) and/or multispecies MSY (MMSY) or other system-wide reference points (Moffitt et al., 2016). Because they integrate part of the complexity of marine system, ecosystem models are useful to investigate how fishing and climate change combined themselves when impacting fish communities, and if one increases the sensitivity of marine ecosystems to the other (Perry et al., 2010). Moving toward more sustainable and ecosystem-based management of fisheries can rely on ecosystem models to better anticipate changes to come and ensure the pertinence and reliability of reference points used in management. Considering uncertainty attached to model results is the next step in this direction as it would increase transparence, credibility and therefore usefulness of ecosystem models for fisheries advice (Lehuta et al., 2016). Identifying which parameters are the most influential on model output allows prioritizing research toward reduction of model uncertainty (e.g., more accurate estimation of model parameters) and better understanding of model structure and error propagation (Bracis et al., 2020; Xing et al., 2020).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation to any qualified researcher.

AUTHOR CONTRIBUTIONS

MT-T designed the study, ran the model, and analyzed and interpreted the results. PB, MG, LV, and YV contributed to the results analysis and interpretation. MG provided parameters related to climate change scenarios. LV helped to running the MSY estimation procedure. MT-T led the drafting of the manuscript with the contributions and revisions from all the authors. All authors contributed to the article and approved the submitted version.

FUNDING

This work has been partially funded by the BiodivErsA and Belmont Forum project SOMBEE (BiodivScen programme, ANR contract n°ANR-18-EBI4-0003-01), and by the French Government and the region Hauts-de-France under the framework of the project CPER 2014-2020 MARCO. We acknowledged the "Pôle de Calcul et de Données Marines" (PCDM, http://www.ifremer.fr/pcdm) for providing DATARMOR storage and computational resources. The POLCOMS-ERSEM projections under RCP scenarios were produced with funding from the European Union Horizon 2020 Research and Innovation Programme under grant agreement no. 678193 (CERES, Climate Change and European Aquatic Resources).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.568232/full#supplementary-material

REFERENCES

Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature* 426, 661–664. doi: 10.1038/nature02164

Bracis, C., Lehuta, S., Savina-Rolland, M., Travers-Trolet, M., and Girardin, R. (2020). Improving confidence in complex ecosystem models: the sensitivity analysis of an Atlantis ecosystem model. *Ecol. Model.* 431:109133. doi: 10.1016/j.ecolmodel.2020.109133

Briton, F., Shannon, L., Barrier, N., Verley, P., and Shin, Y.-J. (2019). Reference levels of ecosystem indicators at multispecies maximum sustainable yield. *ICES J. Mar. Sci.* 76, 2070–2081. doi: 10.1093/icesjms/fsz104

Brochier, T., Ecoutin, J. M., de Morais, L. T., Kaplan, D. M., and Lae, R. (2013). A multi-agent ecosystem model for studying changes in a tropical estuarine fish assemblage within a marine protected area. *Aquat. Living Resour.* 26, 147–158. doi: 10.1051/alr/2012028

Butenschön, M., Clark, J., Aldridge, J. N., Allen, J. I., Artioli, Y., Blackford, J., et al. (2016). ERSEM 15.06: a generic model for marine biogeochemistry and the ecosystem dynamics of the lower trophic levels. *Geosci. Model Dev.* 9, 1293–1339. doi: 10.5194/gmd-9-1293-2016

CERES (2018). *Deliverable Report 1.3: Projections of Physical and Biogeochemical Parameters and Habitat Indicators for European Seas, Including Synthesis of Sea Level Rise and Storminess. Kay S (main author), Andersson H, Catalán IA, Drinkwater KF Eilola K, Jordà G, Ramirez-Romero E (main contributors).* Boston, MA: CERES.

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., Zeller, D., et al. (2010). Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Glob. Change Biol.* 16, 24–35. doi: 10.1111/j.1365-2486.2009.01995.x

Clausen, L. W., Rindorf, A., van Deurs, M., Dickey-Collas, M., and Hintzen, N. T. (2018). Shifts in North Sea forage fish productivity and potential fisheries yield. *J. Appl. Ecol.* 55, 1092–1101. doi: 10.1111/1365-2664.13038

Coppin, F, Giraldo, C., and Travers-Trolet, M. (1988). *CGFS: Channel Ground Fish Survey*. Available online at: https://doi.org/10.18142/11

European Commission (2017). Commission decision (EU) 2017/848 of 17 May 2017 laying down criteria and methodological standards on good environmental status of marine waters and specifications and standardised methods for monitoring and assessment, and repealing Decision 2010/477/EU. *Off. J. Eur. Union* 125, 43–74.

European Union [EU] (2013). Regulation (EU) No 1380/2013 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002 and (EC) No 639/2004 and Council Decision 2004/585/EC. *Off. J. Eur. Union* 354, 22–61.

Food and Agriculture Organization [FAO] (1995). *Code of Conduct for Responsible Fisheries*. Rome: FAO.

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., and Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science* 363, 979–983. doi: 10.1126/science.aau1758

Froese, R., and Quaas, M. (2013). Rio+20 and the reform of the common fisheries policy in Europe. *Mar. Policy* 39, 53–55. doi: 10.1016/j.marpol.2012.10.007

Froese, R., Winker, H., Coro, G., Demirel, N., Tsikliras, A. C., Dimarchopoulou, D., et al. (2018). Status and rebuilding of European fisheries. *Mar. Policy* 93, 159–170. doi: 10.1016/j.marpol.2018.04.018

Fu, C., Shin, Y.-J., Perry, R. I., King, J., and Liu, H. (2012). "Exploring climate and fishing impacts in an ecosystem model of the Strait of Georgia, British Columbia," in *Global Progress in Ecosystem-based Fisheries Management*, eds K. L. Cochrane and H. I. Browman (Fairbanks: University of Alaska Fairbanks), 65–85. doi: 10.4027/gpebfm.2012.04

Fu, C., Travers-Trolet, M., Velez, L., Grüss, A., Bundy, A., and Shannon, L. J. (2018). Risky business: the combined effects of fishing and changes in primary productivity on fish communities. *Ecol. Model.* 368, 265–276. doi: 10.1016/j.ecolmodel.2017.12.003

Gaines, S. D., Costello, C., Owashi, B., Mangin, T., Bone, J., and Molinos, J. G. (2018). Improved fisheries management could offset many negative effects of climate change. *Sci. Adv.* 4:eaao1378. doi: 10.1126/sciadv.aao1378

Genu, M. (2017). *Relative Importance of Different Mecanisms Underlying Fish Response to Climate Change*. Master's thesis, The Higher Institute of Agronomic, Agri-food, Horticultural and Landscape Sciences, Lisboa.

Grüss, A., Harford, W. J., Schirripa, M. J., Velez, L., Sagarese, S. R., Shin, Y.-J., et al. (2016). Management strategy evaluation using the individual-based, multispecies modeling approach OSMOSE. *Ecol. Model.* 340, 86–105. doi: 10.1016/j.ecolmodel.2016.09.011

Grüss, A., Schirripa, M. J., Chagaris, D., Drexler, M., Simons, J., Verley, P., et al. (2015). Evaluation of the trophic structure of the West Florida Shelf in the 2000s using the ecosystem model OSMOSE. *J. Mar. Syst.* 144, 30–47. doi: 10.1016/j.jmarsys.2014.11.004

Guo, C., Fu, C., Forrest, R. E., Olsen, N., Liu, H., Verley, P., et al. (2019). Ecosystem-based reference points under varying plankton productivity states and fisheries management strategies. *ICES J. Mar. Sci.* 76, 2045–2059. doi: 10.1093/icesjms/fsz120

Halouani, G., Ben Rais Lasram, F., Shin, Y.-J., Velez, L., Verley, P., Hattab, T., et al. (2016). Modelling food web structure using an end-to-end approach in the coastal ecosystem of the Gulf of Gabes (Tunisia). *Ecol. Model.* 339, 45–57. doi: 10.1016/j.ecolmodel.2016.08.008

Heino, M., Baulier, L., Boukal, D. S., Ernande, B., Johnston, F. D., Mollet, F. M., et al. (2013). Can fisheries-induced evolution shift reference points for fisheries management? *ICES J. Mar. Sci.* 70, 707–721. doi: 10.1093/icesjms/fst077

Hilborn, R. (2010). Pretty Good Yield and exploited fishes. *Mar. Policy* 34, 193–196. doi: 10.1016/j.marpol.2009.04.013

ICES (2011a). *Catches in FAO Area 27 by Country, Species, Area and Year. Source: Eurostat/ICES database on catch statistics - ICES 2011, Copenhagen. Format: Archived dataset in .xls and .csv format. Version 30-11-2011*. Lowestoft: ICES.

ICES (2011b). *Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK) (No. ICES CM 2011/ACOM:13)*. Lowestoft: ICES.

ICES (2012). *Report of the Working Group on Widely Distributed Stocks (WGWIDE) (21 - 27 August 2012 No. ICES CM 2012/ACOM:1 5)*. Lowestoft: ICES.

ICES (2016). *ICES Advice Basis*. Lowestoft: ICES, 15.

ICES (2017). *Report of the Working Group on Assessment of Demersal Stocks in the North Sea*. Lowestoft: ICES.

ICES (2019). *General Context of ICES Advice*. Lowestoft: ICES.

IPCC (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]*. Geneva: IPCC.

Kell, L. T., Pilling, G. M., and O'Brien, C. M. (2005). Implications of climate change for the management of North Sea cod (*Gadus morhua*). *ICES J. Mar. Sci.* 62, 1483–1491. doi: 10.1016/j.icesjms.2005.05.006

Kielbassa, J., Delignette-Muller, M. L., Pont, D., and Charles, S. (2010). Application of a temperature-dependent von Bertalanffy growth model to bullhead (*Cottus gobio*). *Ecol. Model.* 221, 2475–2481. doi: 10.1016/j.ecolmodel.2010.07.001

Le Goff, C., Lavaud, R., Cugier, P., Jean, F., Flye-Sainte-Marie, J., Foucher, E., et al. (2017). A coupled biophysical model for the distribution of the great scallop Pecten maximus in the English Channel. *J. Mar. Syst.* 167, 55–67. doi: 10.1016/j.jmarsys.2016.10.013

Lehuta, S., Girardin, R., Mahévas, S., Travers-Trolet, M., and Vermard, Y. (2016). Reconciling complex system models and fisheries advice: practical examples and leads. *Aquat. Living Resour.* 29:208. doi: 10.1051/alr/2016022

Marzloff, M., Shin, Y.-J., Tam, J., Travers, M., and Bertrand, A. (2009). Trophic structure of the Peruvian marine ecosystem in 2000–2006: insights on the effects of management scenarios for the hake fishery using the IBM trophic model Osmose. *J. Mar. Syst.* 75, 290–304. doi: 10.1016/j.jmarsys.2008.10.009

Mesnil, B. (2012). The hesitant emergence of maximum sustainable yield (MSY) in fisheries policies in Europe. *Mar. Policy* 36, 473–480. doi: 10.1016/j.marpol.2011.08.006

Moffitt, E. A., Punt, A. E., Holsman, K., Aydin, K. Y., Ianelli, J. N., and Ortiz, I. (2016). Moving towards ecosystem-based fisheries management: options for parameterizing multi-species biological reference points. *Deep Sea Res. II Top. Stud. Oceanogr. Understand. Ecosyst. Process. Eastern Bering Sea IV* 134, 350–359. doi: 10.1016/j.dsr2.2015.08.002

Oliveros-Ramos, R., Verley, P., Echevin, V., and Shin, Y.-J. (2017). A sequential approach to calibrate ecosystem models with multiple time series data. *Prog. Oceanogr.* 151, 227–244. doi: 10.1016/j.pocean.2017.01.002

Perry, R. I., Cury, P., Brander, K., Jennings, S., Möllmann, C., and Planque, B. (2010). Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. *J. Mar. Syst. Impact Clim. Variabil. Mar. Ecosyst. Comp. Approach* 79, 427–435. doi: 10.1016/j.jmarsys.2008.12.017

Rindorf, A., Cardinale, M., Shephard, S., De Oliveira, J. A. A., Hjorleifsson, E., Kempf, A., et al. (2017). Fishing for MSY: using "pretty good yield" ranges without impairing recruitment. *ICES J. Mar. Sci.* 74, 525–534. doi: 10.1093/icesjms/fsw111

Salomon, M., Markus, T., and Dross, M. (2014). Masterstroke or paper tiger – The reform of the EU×s common fisheries policy. *Mar. Policy* 47, 76–84. doi: 10.1016/j.marpol.2014.02.001

Scheffers, B. R., Meester, L. D., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., et al. (2016). The broad footprint of climate change from genes to biomes to people. *Science* 354:aaf7671. doi: 10.1126/science.aaf7671

Scott, R. D., and Sampson, D. B. (2011). The sensitivity of long-term yield targets to changes in fishery age-selectivity. *Mar. Policy* 35, 79–84. doi: 10.1016/j.marpol.2010.08.005

Shin, Y.-J., and Cury, P. (2001). Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. *Aqu. Living Resour.* 14, 65–80. doi: 10.1016/S0990-7440(01)01106-8

Shin, Y.-J., and Cury, P. (2004). Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Can. J. Fish. Aquat. Sci.* 61, 414–431. doi: 10.1139/f03-154

Shin, Y.-J., Houle, J. E., Akoglu, E., Blanchard, J. L., Bundy, A., Coll, M., et al. (2018). The specificity of marine ecological indicators to fishing in the face of environmental change: a multi-model evaluation. *Ecol. Indic.* 89, 317–326. doi: 10.1016/j.ecolind.2018.01.010

Thorpe, R. B., Jennings, S., and Dolder, P. J. (2017). Risks and benefits of catching pretty good yield in multispecies mixed fisheries. *ICES J. Mar. Sci.* 74, 2097–2106. doi: 10.1093/icesjms/fsx062

Travers, M., Shin, Y.-J., Jennings, S., Machu, E., Huggett, J. A., Field, J. G., et al. (2009). "Two-way coupling versus one-way forcing of plankton and fish models to predict ecosystem changes in the Benguela," in *Proceedings of the Ecological Modelling, Selected Papers from the Sixth European Conference on Ecological Modelling - ECEM '07, on Challenges for ecological modelling in a changing world: Global Changes, Sustainability and Ecosystem Based Management, November 27-30, 2007*, Trieste, 3089–3099. doi: 10.1016/j.ecolmodel.2009.08.016

Travers, M., Shin, Y.-J., Shannon, L., and Cury, P. (2006). Simulating and testing the sensitivity of ecosystem-based indicators to fishing in the southern Benguela ecosystem. *Can. J. Fish. Aquat. Sci.* 63, 943–956. doi: 10.1139/f06-003

Travers-Trolet, M., Coppin, F., Cresson, P., Cugier, P., Oliveros-Ramos, R., and Verley, P. (2019). Emergence of negative trophic level-size relationships from a size-based, individual-based multispecies fish model. *Ecol. Model.* 410:108800. doi: 10.1016/j.ecolmodel.2019.108800

Travers-Trolet, M., Shin, Y.-J., and Field, J. G. (2014a). An end-to-end coupled model ROMS-N2P2Z2D2-OSMOSE of the southern Benguela foodweb: parameterisation, calibration and pattern-oriented validation. *Afr. J. Mar. Sci.* 36, 11–29. doi: 10.2989/1814232X.2014.883326

Travers-Trolet, M., Shin, Y.-J., Shannon, L. J., Moloney, C. L., and Field, J. G. (2014b). Combined fishing and climate forcing in the southern benguela upwelling ecosystem: an end-to-end modelling approach reveals dampened effects. *PLoS One* 9:e94286. doi: 10.1371/journal.pone.0094286

Ulrich, C., Vermard, Y., Dolder, P. J., Brunel, T., Jardim, E., Holmes, S. J., et al. (2017). Achieving maximum sustainable yield in mixed fisheries: a management approach for the North Sea demersal fisheries. *ICES J. Mar. Sci.* 74, 566–575. doi: 10.1093/icesjms/fsw126

Vanhoutte-Brunier, A., Fernand, L., Ménesguen, A., Lyons, S., Gohin, F., and Cugier, P. (2008). Modelling the Karenia mikimotoi bloom that occurred in the western English Channel during summer 2003. *Ecol. Model.* 210, 351–376. doi: 10.1016/j.ecolmodel.2007.08.025

Xing, L., Chen, Y., Zhang, C., Li, B., Tanaka, K. R., Boenish, R., et al. (2020). Evaluating impacts of imprecise parameters on the performance of an ecosystem model OSMOSE-JZB. *Ecol. Model.* 419:108923. doi: 10.1016/j.ecolmodel.2019.108923

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 25 November 2020
doi: 10.3389/fmars.2020.567841

Determinism of Temporal Variability in Size at Maturation of Sardine *Sardina pilchardus* in the Bay of Biscay

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Specialty section:
This article was submitted to
Marine Fisheries, Aquaculture
and Living Resources,
a section of the journal
Frontiers in Marine Science

Received: *30 May 2020*
Accepted: *19 October 2020*
Published: *25 November 2020*

Citation:
Véron M, Duhamel E,
Bertignac M, Pawlowski L, Huret M
and Baulier L (2020) Determinism
of Temporal Variability in Size
at Maturation of Sardine Sardina
pilchardus in the Bay of Biscay.
Front. Mar. Sci. 7:567841.
doi: 10.3389/fmars.2020.567841

Age and size at maturation appear as key parameters governing the dynamics of a population as they affect growth rate, fecundity, and survival. The expression of such life history traits is determined by genetic make-up and modulated by environmental factors mainly through phenotypic plasticity. Moreover, fishing, besides decreasing population size and changing demographic composition can alter allelic frequencies through fisheries-induced evolution by selecting for some particular traits. In the Bay of Biscay, a decreasing trend in both sardine body condition and size-at-age has recently been pointed out at the population level. The Probabilistic Maturation Reaction Norm (PMRN) approach was applied to help disentangle phenotypic plasticity and genetic changes. Based on the analysis of sardine spawning seasonality, PMRN was estimated by considering body condition as additional life-history state variable to predict the onset of maturation. The resulting PMRN was then used to investigate temporal trends in reaction norm midpoints to test whether changes in length at maturation can be explained by plastic and/or evolutionary adaptive change. Overall, our results emphasize for the first time that including sardine body condition as explanatory variable improves predictions of maturation probability. We found that better individual condition increases maturation probability. The assessment of temporal changes in length at maturation confirms the low plasticity in this trait for a species maturing mostly at age-1 and advocates for the use of a monthly time scale when investigating PMRNs for this species. Beside environmental variables included in this analysis (water temperature, chlorophyll-*a*, and population biomass) that only show a weak correlation with PMRN midpoints, our results reveal no evidence for recent fisheries-induced evolution in the sardine stock of the Bay of Biscay. They suggest that the short-term variability in length at maturation is strongly dependent upon individual growth which is likely driven by environmental factors. For sardine fisheries management, our study highlights the need to consider both the length-composition data and the seasonality within a stock assessment model. Finally, we discuss the fact that considering individual growth trajectories should improve our understanding of the relationship between environmental variability and changes in maturation for sardine.

Keywords: fisheries-induced evolution, body condition, phenotypic plasticity, maturation, growth, *Sardina pilchardus*, bay of biscay

INTRODUCTION

Understanding mechanisms that regulate a stock's reproductive potential is of fundamental importance for marine fisheries management as it corresponds to the ability of a fish population to produce a viable offspring, which in turn conditions the future recruitment (Trippel, 1999). Reproductive potential is itself influenced by stock productivity, which has declined for a wide range of commercially exploited fish species over the past decades (Christensen et al., 2003; Myers and Worm, 2003). Concomitant to those declines, several studies emphasized drastic changes in life history traits and, in particular, a decrease in both age and size at which fish start to reproduce [e.g., reviewed by Rijnsdorp (1993), Trippel (1995), and Jorgensen et al. (2007)]. Such adaptive changes may result from evolutionary and/or plastic responses, the relative importance of which are difficult to distinguish in exploited fish populations (Rijnsdorp, 1993; Law, 2000). However, since lifetime reproductive success and therefore stock productivity are closely linked to both age and size at maturation (Bernardo, 1993), it becomes essential to identify which underlying processes can induce changes in the maturity of those populations.

Maturation is a costly and complex physiological process that constitutes a key event in fish life history. Its schedule is determined by the individual genetic pool, which reflects selective pressures to which the population has been subjected to, and by environmental conditions that the individual experiences during maturation or at an earlier stage when the onset of the maturation process is triggered (abbreviated maturation "decision" in the following text) (Wright, 2007). Although it has long been described as dependent on size thresholds, a large corpus of knowledge underlines that environmental variations may also play a critical role through the modification of the individual's growth and energetic status at particular times of the life cycle (Thorpe et al., 1998; Wright, 2007; Tobin and Wright, 2011). Following initial growth, age- and size-at-maturation are determined by both the ability of fish to store energy and how they will allocate it between growth and other functions. Considering such dependence implies that external factors play an important role in the process of maturation either through phenotypic plasticity or evolutionary changes.

Among the potential drivers of these changes, several studies highlighted the role of water temperature (Grift et al., 2003; Kraak, 2007) and food availability (Trippel, 1995; Law, 2000) which may affect the probability of maturing either directly [e.g., Tobin and Wright (2011) for temperature], or indirectly by increasing growth rates (Sinclair et al., 2002) and body condition (Morgan, 2004; Grift et al., 2007). The social structure and the size composition of a fish population have also been pointed out as factors that may influence the probability of maturing at a given age and size (Diaz Pauli and Heino, 2013). Superimposed on the effects of environment, fishing is commonly known as a factor also affecting fish maturation. Fishing induces changes in the demographic structure of exploited populations (Law, 2000) and may finally lead to both phenotypically plastic (e.g., faster growth rates resulting from lower density-dependent effects) and genetic changes. Moreover, beside decreasing population sizes (Law, 2000) that may alter intra- and inter-specific competition, fishing may also induce direct or indirect (e.g., through habitat modification) changes in food availability (Rijnsdorp and Van Leeuwen, 1996) and cause evolutionary change by selecting for genotypes less affected by fishing (Law, 2000). Although the observed trends toward earlier maturation in fish population have been described as the result of a single factor or the combination of multiple factors (Marshall and McAdam, 2007), it remains unclear to what extent these changes are due to phenotypic plasticity on the one hand or evolutionary change on the other. Due to their different response time-scales, ranging from changes within a single generation (phenotypic plasticity) to those taking several generations before becoming detectable (evolutionary responses), disentangling genetic and plastic influences on maturation is of primary importance for the sustainability of marine resources.

The age and length at which an individual matures are variable and because of this variation at the individual level, maturation must usually be considered probabilistically: at a particular combination of age and size, some fish may mature while others do not. In this context, Probabilistic Maturation Reaction Norms (PMRNs), introduced by Heino et al. (2002b), are commonly used to describe the probability of maturation as a function of age and size and possibly other life history traits such as body condition (Grift et al., 2003, 2007; Barot et al., 2004; Mollet et al., 2007; Marty et al., 2014). Thus, using this method and providing some assumptions, one can estimate maturation probability independently of the influence of survival and growth (Dieckmann and Heino, 2007).

The European sardine, *Sardina pilchardus*, is a small pelagic fish widely distributed along the Northeast Atlantic shelf, from the English Channel to Mauritania, and in the Mediterranean Sea (Parrish et al., 1989). This species, which has an observed lifespan of up to 14 years, is a multiple egg batch spawner and is characterized by a fast growth and an early maturation. Several studies emphasized an extended spawning activity for sardine in the Bay of Biscay, from autumn to spring with two spawning peaks occurring in April and in October (Coombs et al., 2006;

Stratoudakis et al., 2007), and individuals mostly maturing during their first 2 years of life and in particular as 1 year old.

Over the last two decades, changes in life history traits of sardine have been brought to light in several regions of European waters (Silva et al., 2006, 2013; Doray et al., 2018; Saraux et al., 2019). In particular, Doray et al. (2018) highlighted a decreasing trend in both body length and weight for the Bay of Biscay sardine stock without emphasizing any correlations either with local changes in environmental conditions or with fishing intensity. Analyzing this decrease in details, Véron et al. (2020) recently noticed a concomitant decline in body condition at the population level. Moreover, recent analyses also suggest a decreasing trend in the proportion of mature individuals at age one which could be related to changes in sardine growth and/or maturation (Véron, 2020). Based on those observations, it becomes essential to identify if changes in the maturation of sardine have occurred over the last decades and which could be the underlying processes in the Bay of Biscay.

Despite a recent increase in fishing mortality rate (Ages 2–5) toward a value stabilized above both natural mortality (0.44 yr^{-1}) and F_{MSY} [0.51 yr^{-1}; ICES (2019)], fishing mortality in this stock has remained historically relatively low (ICES, 2019). Consequently, based on the life history characteristics of this species and the relatively low exploitation rate for this stock over the study period, we do not expect recent fisheries-induced evolutionary changes in maturation.

Since the maturation process is strongly linked to spawning seasonality and because the duration of a population's spawning season plays a critical role in reproductive success and can be negatively impacted by the age truncation effects of fishing (Anderson et al., 2008; Wright and Trippel, 2009), we first investigated if temporal changes in sardine spawning seasonality occurred within the population over the period 2003–2018. With this first step we identified months that permitted accurate investigation of the sardine maturation process in the Bay of Biscay. Then, we used the PMRN approach to analyze the sardine maturation schedules in the Bay of Biscay and to disentangle genetic and plastic changes in these schedules. We focused on two aspects of the maturation process: we first investigated the relative importance of body length and condition in sardine maturation, and then we further examined the effects of environmental variables that could influence sardine maturation through growth-independent phenotypic plasticity. Subsequent to this analysis, the unexplained part of variability in sardine maturation process would potentially be attributed to genetic variability since this factor was not accounted for.

MATERIALS AND METHODS

Biological Data Collection

We used biological data collected both by research vessels (pelagic and demersal trawlers) and commercial fleets (mainly purse seiners) within the European Data Collection Framework (*DCF*). Both spring and autumn surveys, [Pelagiques Gascogne survey, PelGas; Doray et al., 2017 and EVHOE survey (Evaluation des Ressources Halieutiques de l'Ouest de l'Europe; Duhamel et al., 2014), respectively] are yearly conducted by Ifremer aboard R/V Thalassa since 2000 and 1997, respectively. Since these surveys entirely cover the Bay of Biscay, the samples are assumed to be representative of the whole spawning fraction of the sardine population in this area. The design of the PelGas survey, especially dedicated to monitor the pelagic ecosystem on the continental shelf of the Bay of Biscay in springtime, makes it the main source of data used in this study. This dataset was complemented with fish market samples collected in the fishing harbors for sardine mainly located in the northern part of the Bay of Biscay (southwest Brittany). Finally, the dataset used in this study includes morphometric and physiological characteristics of sardine throughout the year from more than 24,000 individuals collected over the period 2003–2018 (**Table 1**). Independently of the season considered, the distribution of these morphometric characteristics was assumed representative of the whole population.

For each fish, standard measurements were taken including total body length, weight, sex, and maturity stage. Length and weight were rounded down to the nearest 0.5 cm and the lower gram, respectively. Sex and maturity status were determined following ICES guidelines (ICES, 2008) through macroscopic inspection of the gonads. The maturity scale was based on a six-stage key defined as follows: (1) immature, (2) developing, (3) pre-spawning, (4) spawning, (5) partial post-spawning, and (6) post-spawning (ICES, 2008). Following the macroscopic inspection of gonads and the extraction of otoliths, age determination was carried out visually by binocular microscopy at the "Laboratory of Technology and Fisheries Biology" of Ifremer (Lorient, France) using the number of winter rings and considering January 1st as the nominal birthday.

Because of a limited number of samples in our dataset, we decided to pool males and females together in this analysis in order to reduce uncertainty in model estimates. This is not expected to create temporal changes in PMRN since sex ratio in the samples was relatively stable over the study period (**Table 1**). Moreover, we only considered individuals of length between 7.0 and 21 cm to reduce the number of length classes with only mature or immature individuals and therefore ensure model convergence and increase the goodness of fit around $p = 0.5$. In order to have enough individuals for each cohort, analyses were carried out for cohorts from 2002 to 2017. Since macroscopic observation of gonads does not allow distinguishing upcoming spawners from other individuals when the "decision" to mature takes place, maturity status was therefore used to separate individuals within the population. Individuals that had reached maturity stage 2 were considered mature while those in stages 3–5 were assumed to be spawning.

Consideration of Body Condition

The effect of body condition on sardine maturation was investigated using the relative condition index (Le Cren, 1951). This index, identified as one of the best morphometric indicators of fish condition in marine ecosystems (ICES, 2016), corresponds to the ratio between the measured weight of an individual and its predicted weight from a length-weight relationship. To account for variations in the weight of mature individuals within the

TABLE 1 | Summary of monthly available morphometric data included in the analyses (study period: 2003–2018).

Month	Years	*N*	Mean sex ratio (% of females)	Mean % of Age 0 and 1
1	2006–2008	189	64	3
2	2006–2008	198	69	1
3	2003, 2006–2008, 2015, 2016	181	59	16
4	2004, 2006–2015, 2017	3,090	49	30
5	2003–2018	13,847	49	27
6	2003, 2006–2007, 2015, 2016	525	46	23
7	2003, 2005–2008, 2012–2016	518	59	42
8	2003–2009, 2012–2016, 2018	970	53	42
9	2003–2016, 2018	1,094	56	34
10	2003–2018	1,579	53	45
11	2003–2008, 2010–2012, 2015–2018	1,303	53	45
12	2003–2007, 2009, 2013	648	54	38

N corresponds to the total individual number for each month.

spawning season, which might result from both feeding cycle and spawning activity, observed weights of mature individuals of different maturity stages were standardized as if they had all been collected when in maturity stage 2 (gonad developing stage), accounting for both endogenous characteristics of individuals (length, sex, and maturity stage) and year. The resulting corrected weight (termed W_{corr}) was obtained by adding to the observed weight the difference between observed weight and predicted weight for an individual with the same length but with maturity stage 2 in the same year. The Le Cren condition index was then computed as follow:

$$Kn_{i,s} = \frac{Wcorr_{i,s}}{\hat{W}_{i,s}}, \; \hat{W}_{i,s} = \alpha_{m_s} \times L_{i,s}^{\beta_{m_s}} \tag{1}$$

where $\hat{W}_{i,s}$ is the predicted body weight of an individual i, of a given length $L_{i,s}$ obtained from a sex-specific length-weight relationship for sex s. A detailed description regarding the computation of the sex specific length-weight relationship used in this study is provided in Véron et al. (2020).

Application of the Probabilistic Maturation Reaction Norm

While maturity ogives describe the fraction of mature individuals within a population at a given age and/or size in a given year, maturation ogives refer to the probability that an immature individual, which has survived and grown until a certain age and size, sexually matures during a given time interval (Heino et al., 2002b). Maturity ogives therefore describe a population "state" without distinguishing between first-time spawners and repeat spawners whereas maturation ogives are more related to the process itself (Heino and Dieckmann, 2008). In this study, maturation propensity has been investigated through the PMRN approach which assumes that mature and immature individuals have the same growth and survival rates within age class and cohort.

For sardine, newly mature individuals (first time spawners) and repeat spawners cannot be distinguished through visual examination of the gonads. Age and maturity status are therefore the only information that can be used to separate those individuals within a population. Taking into account that sardine maturation takes place during the first 2 years, with almost all individuals maturing within their first reproductive season (i.e., as age 0 or young age 1) and given that these individuals constitute the bulk of sardine spawning biomass in the Bay of Biscay (ICES, 2019), maturity ogives appear relevant to deduce sardine maturation probabilities. For age 0, maturation ogives can be approximated by maturity ogives. This assertion can be extended to age 1, as only a minority of sardine mature at age 0 and the contribution of repeat spawners at age 1 can be considered negligible.

Contrary to most studies investigating fish maturation process, the reaction norm approach applied to sardine here only considers length and condition as explanatory variables. The procedure for statistical analysis of sardine maturation probabilities in the Bay of Biscay involves the five following steps: (A) data selection and estimation of spawning ogives, (B) estimation of maturity ogives, (C) computation of the reaction norm midpoints and estimation of confidence limits, (D) analysis of differences between the two spawning seasons, and (E) testing the significance of trends in reaction norm midpoints. Each step of this procedure is described in detail below.

(A) Spawning ogives and data selection

Because data collected just prior to or during the spawning period are needed to analyze fish maturation, the sampling period used to compute sardine maturation probabilities was based on the analysis of sardine spawning seasonality. The probability of spawning of Atlantic sardine was modeled using generalized additive models (GAMs, as implemented in the R-package mgcv, 1.8-17, Wood, 2011). GAMs with a binomial error distribution and *logit* link function were fitted to the probability of spawning as an anisotropic bivariate function of fish length and month:

$$logit\ (Sp) = f(L,\ m), \tag{2}$$

where Sp is the probability of spawning, L corresponds to the length class and m is the month. Because Véron et al. (2020) emphasized changes in both body condition and body length over the study period and as those variables are known to influence spawning (Lowerre-Barbieri et al., 2011), we investigated potential changes in sardine spawning seasonality over the study period by fitting four models to the data. The first one considered the whole study period (2003–2018) while the other three were fitted to each period identified in Véron et al. (2020), based on the decreasing trend of body condition (2003–2006; 2007–2011 and 2012–2018).

Since schedules for the start of vitellogenesis can differ among individuals of a given population and may depend upon length-class, differences in spawning seasonality within the population were assessed using these models to predict the probability of spawning for three length-classes throughout the year. These length-classes were assumed to correspond to young, medium and old individuals within the population. The outcomes of this analysis highlighted the existence of two spawning peaks within the year (end of April and mid October) which were used as a basis to analyze sardine maturation probabilities.

(B) Maturity ogives

Statistical analyses were conducted separately for each spawning season previously identified. Since maturity status can be reduced to a binary response variable (mature or maturing vs. immature), the fraction of mature fish (O) was estimated by means of logistic regression (using generalized linear models assuming a binomial error structure), with the proportion of mature individuals as the dependent variable and cohort and length (Eq. 3) or cohort, length and condition (Eq. 4) as independent variables. The linear predictor was linked to the fraction of mature individuals (i) using a *logit* link function [$logit\,(O) = \ log_e(^{O}/_{(1-O)})$]:

$$logit\,(O_i) = \ \alpha_{0,c_i} \ + \alpha_{1,c_i}\, L_i, \tag{3}$$

$$logit\,(O_i) = \alpha_{0,c_i} \ + \alpha_1\, L_i + \alpha_2\, Kn_i + \alpha_{3,c_i} L_i + \alpha_{4,c_i} Kn_i, \tag{4}$$

where length (L) and condition (Kn) are treated as continuous variables while cohort (c) is a factor. For both models, the α values correspond to the parameter estimates. In order to comprehensively assess the effects of cohort, length, and body condition on sardine maturation, performances of both models in explaining the fraction of mature individuals were compared by computing both a likelihood ratio-test and the Akaike Information Criterion.

(C) Reaction norm midpoint and confidence limits

Equation (5) was used to estimate $L_{p_{50}}$, defined as the midpoint of the Probabilistic Maturation Reaction Norm. This particular point, which corresponds to the length at which an immature fish has a 50% probability of sexually maturing, was used to summarize the reaction norm. For each cohort, $L_{p_{50}}$ estimates were obtained by solving the equation of model (4) for length with a probability O equal to 50%. An increase in $L_{p_{50}}$ will indicate an increase in length at first maturity. The reaction norm width, here defined as the interval between the lengths that correspond to maturation probabilities of 25% and 75% ($L_{p_{25}}$ and $L_{p_{75}}$, respectively) was also considered to investigate the strength of the link between body length and maturation "decision." The narrower this width is the stronger the influence of length on maturation probabilities.

Because the estimation of sardine maturation probabilities relies on several successive steps, confidence intervals for $L_{p_{50}}$ were estimated by bootstrapping data (Barot et al., 2004). Individuals in the original data set were resampled 2000 times with replacement, with stratification by cohort, to generate distributions of $L_{p_{50}}$. Confidence intervals were then derived using the 2.5–97.5 percentiles of the bootstrap distribution.

(D) Trend analysis and differences between spawning seasons

Temporal trends in maturation probability were assessed with a linear regression of the PMRN midpoints ($L_{p_{50}}$) against cohort (c) as a continuous variable:

$$L_{p_{50,c}} = \ \alpha_0 + \ \alpha_1 c + \ \varepsilon_c, \tag{5}$$

where ε is a normally distributed error term. The estimated midpoints were weighted with the inverse of the variance of each midpoint in order to lower the influence of imprecise estimates on the regression. Variance estimates were obtained from the bootstrap output.

Furthermore, differences in reaction norm midpoints between spawning seasons were investigated using the following simple linear model, also weighted by the inverse of the variance of bootstrapped estimates of $L_{p_{50}}$,

$$L_{p_{50,s}} = \ \alpha_{0,s} + \ \varepsilon_s, \tag{6}$$

where s corresponds to the spawning season (spring or autumn), treated as a categorical variable and ε is a normally distributed error term. The comparison of the envelope widths between spawning seasons was also considered to test for potential differences in the strength of the influence of body length on sardine maturation between spawning seasons.

(E) Environmental impacts on reaction norm midpoints

When a linear temporal trend in reaction norm midpoints was found, growth-independent plasticity of sardine maturation was investigated considering the effect of environmental factors that may potentially affect sardine maturation. Sea surface temperature [*SST* (°C), *averaged over the first 30 m*] and chlorophyll-*a* [Chl-*a* ($mg.m^{-3}$), used as an indicator of food abundance] were extracted from the Copernicus Marine Service[1] and came from the Atlantic Iberian Biscay Irish (IBI) model and satellite data, respectively. These variables were averaged by intervals of 3 months over the continental shelf of the Bay of Biscay (Bathymetry < 330 m). Population abundances were considered as indicators of intra- and inter-specific competition that may affect sardine maturation. Long-term trends in sardine maturation process were investigated considering explanatory variables showing a significant temporal trend.

Since anchovy and sardine are commonly found together in the Bay of Biscay and feed on a similar wide variety of

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

plankton organisms, abundance estimates for these two species obtained during the spring PelGas survey were considered in the analysis. The effect of abundance on maturation reaction norm midpoints was considered using two time series describing the total abundance of both species for the current year and the previous years.

Using separate linear models for each spawning season, $L_{p50,s,c}$ were regressed against environmental factors $e_{k,s,\Delta}$, abundance $a_{s,c-d}$, and cohort c as continuous variables,

$$L_{p50,s,c} = \alpha_{0,s} + \alpha_{1,s}c + \sum_{k} \sum_{\Delta \epsilon \mathrm{M}} \alpha_{\mathrm{k,s,\Delta}}\ \mathrm{e}_{\mathrm{k,s,\Delta}} + \sum_{\mathrm{d}=0}^{1} \alpha_{\mathrm{s,d}}\ \mathrm{a}_{\mathrm{s,c-d}} + \varepsilon_{\mathrm{s,c}}, \qquad (7)$$

where k identifies the environmental factor considered, Δ is the time lag in months from the set of lags considered M (3 *or* 6 months before the peak of the given spawning season) and $c - d$ is the year when abundance is estimated, with a time lag d (0 or 1 year). Similarly to previous models, $\varepsilon_{s,c}$ corresponds to the normally distributed error term. In order to account for non-growth-mediated phenotypic plasticity in sardine maturation, before investigating possible evolutionary trends when analyzing long term trends in $L_{p_{50}}$, the cohort was only included after the selection of all other significant explanatory variables. Then, for each explanatory variable showing a significant effect on reaction norm midpoints over the study period, the absolute magnitude of change in $L_{p_{50}}$ attributable to this effect was calculated as the product of the linear rate of change over time of this explanatory variable, the regression coefficient of $L_{p_{50}}$ according to this variable and the number of years in the time interval.

Finally, since short-term fluctuations in both environmental conditions and population abundance may induce short-term variations in maturation propensity, fluctuations around the trend in $L_{p_{50}}$ were investigated using Eq. (7). For each spawning season, we regressed the $L_{p_{50}}$ [or its residuals from Eq. (5) if a long-term trend has been found] against explanatory variables for which the potential long-term trend was also removed (using residuals from regression of each explanatory variables against time).

For both analyses (long-term trend and short-term fluctuations), a stepwise procedure was implemented to remove non-significant variables with a threshold set at p-value = 0.05 (ANOVA; Zuur, 2009). The estimated reaction norm midpoints were weighted with the inverse of the variance obtained from the bootstrap procedure.

RESULTS

Spawning Modeling

Whatever the time period considered, our models described sardine spawning seasonality well as shown by the explained deviance ranging from 43.9 to 59.6% (**Table 2**).

TABLE 2 | Summary description of fitted GAMs to sardine spawning probabilities (Sp) for the whole period and for the three periods identified in Véron et al. (2020).

Model:	***logit* $(Sp) = f(L,\ m)$**			
Period	**Explained deviance (%)**	***n***	**χ^2**	***p*-value**
Whole	52.9	24,142	5,655	<2e-16
P1 (2003–2006)	43.9	5,074	1,324	<2e-16
P2 (2007–2011)	53.9	7,193	1,610	<2e-16
P3 (2012–2018)	59.6	11,875	2,759	<2e-16

Percentage of deviance explained, individual number for each period (n), Chi-square and p-value are noted.

Because we wanted to investigate sardine maturation probabilities and since sardine mostly matures at 1 year old (represented here by the 16 cm length-class), the extent of spawning seasons has been delimited using a minimum threshold of 25% of individuals being spawning in the lower size-class. Based on this threshold, sardine spawning activity appears to be composed of two spawning seasons within the year with a first one extending from January to June and a second one occurring between September and December (**Figure 1**). Independently of the size-class, sardine exhibited a maximum spawning activity with a first peak in April–May and the second one in October–November. The magnitude of the spawning activity appeared size-dependent with small individuals showing both a shorter spawning season and a lower percentage of spawning individuals when compared with larger ones, in particular in autumn and early winter (**Figure 1**). Even if patterns in spawning seasonality showed no major difference across periods, our results suggested a slight shift toward latter and longer spring spawning season at the end of the study period (P3: 2012–2018). However, due to the small number of individuals collected in summer as reflected by the wide confidence interval (**Figure 1**), this predicted increase in the duration of the spring spawning season should be considered cautiously.

Overall, our results do not show strong temporal shifts either in the peak or in the spawning activity pattern of sardine over the study period. Based on these outcomes, we characterized sardine spawning seasonality in the Bay of Biscay as being composed of two spawning seasons defined as follows: the first one during winter/springtime (from January to June, referred to as spring spawning season) and a second one occurring in autumn (from September to December). These seasons were used to derive maturity ogives at two different times of the year.

Maturity Ogives

For both seasons, models fitted the data well as indicated by the percentage of explained deviance. The fraction of mature individuals was better explained in springtime than in autumn with models accounting for around 60% and 35% of the deviance, respectively (**Table 3**). Cohort, size, and condition, as well as the 2-way interactions, significantly affect the probability of being mature when incorporated within the same model. As expected, whatever the season and the maturation model considered (length- or length and condition- based), body length was the best variable explaining sardine maturation (explained deviance ranging from 24 to 55.7%). Moreover, behind its strong dependence upon body length, sardine maturation process fluctuates among cohorts (explaining 5% and 7% of the total

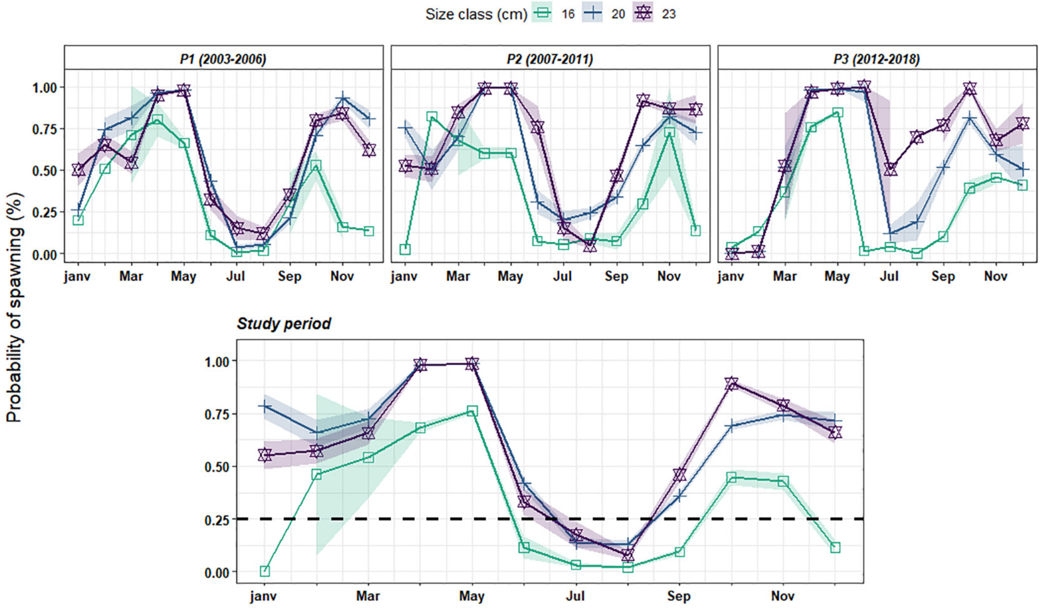

FIGURE 1 | Estimated probability of spawning for three length classes [16 cm (green), 20 cm (blue), and 23 cm (purple)] corresponding to the mean length at ages 1, 3, and 6 over the study period. The first three panels correspond to prediction considering the three identified periods in Véron et al. (2020) (P1: 2003–2006; P2: 2007–2011 and P3: 2012–2018) while the last one represents prediction considering the whole study period.

deviance in spring and autumn, respectively) with a relationship between maturation and length that appeared cohort-dependent for both seasons, as indicated by the significant interaction between length and cohort.

Models in which sardine body condition was included performed significantly better than the model without it only in springtime, as shown by lower AIC (Akaike Information Criterion, significance based in chi-square test for likelihood-ratio test statistic, $p < 0.001$). However, including body condition in addition to length resulted in a limited increase in predictive power (0.9% of the explained deviance in springtime). The significant interaction between condition and cohort reveals that the relationship between maturation and body condition is cohort-dependent for both spawning seasons and accounts for 0.5% and 0.76% of the deviance in spring and autumn, respectively.

Although only a small proportion of the deviance was accounted for by body condition, its positive effect on the probability to mature, in addition to size, remains statistically significant. Results are presented for one selected cohort in springtime only (**Figure 2**). In that case, there was a clear increase in the estimated probability of becoming sexually mature with an increase in body condition. Obviously, this increase remains strongly dependent on body length with an earlier increase for large individuals when compared with smaller ones (**Figure 2A**). While small individuals (13 cm length-class) do not exhibit drastic changes in the proportion of mature individuals under a "threshold" value of body condition (around 1.4), an increase of 0.4 units in body condition leads to a significant increase in the proportion of mature individuals in the 16 cm length-class (from around 25 to 75%, for condition values ranging from 0.7 to 1.1). When this proportion is estimated as a function of length for a small range of body condition (**Figure 2B**; 0.7, 0.9, and 1.1) corresponding to the median values of body condition observed during the three identified periods (P3, P2, and P1; respectively) in Véron et al. (2020), our results show a small increase in the proportion of mature individuals with increasing body condition which corresponds to a small decrease in length at maturation with an increase in condition.

"Spring" and "Autumn" Maturation Reaction Norms

Variability in maturation process between spawning season was investigated through the comparison of PMRN midpoints from models considering body condition. Our results show significant differences between seasons with higher average reaction norm midpoints in autumn than in spring indicating that at the same length, spring-spawning sardines have a higher maturation probability than autumn-spawning ones (ANOVA, F-value = 33.2, p = *2.44e-6*; **Figure 3A**). On average, spring spawning sardines reached sexual maturity at 14.3 cm while in autumn $L_{p_{50}}$ was 15.6 cm.

Envelope widths were significantly different between autumn and spring (two-sided paired Student's t-test: $p = 0.003$). While the average distance between L_{p25} and L_{p75} was around 4 cm for the former, it was less than 2 cm in springtime (**Figure 3B**). Moreover, contrary to the spring reaction norm width which appears relatively stable over time, our analyses emphasize a larger variability in this envelope for autumn-spawners (one-sided Fisher's F-test: $p = 5.6\ 10^{-9}$; **Figure 3B**). Altogether, these results highlight a stronger link between maturation "decision"

TABLE 3 | Results from generalized linear models showing the effect of body condition on sardine maturation probabilities for the two spawning seasons.

Spring spawning season		**Model (1) – Equation (3)**				**Model (2) – Equation (4)**		
		Residual deviance	***P*-value (χ^2)**	***R^2* (%)**		**Residual deviance**	***P*-value (χ^2)**	***R^2* (%)**
	Null	9.201			Null	9.201		
	Length	4.078	<2.2e-16	55.7	Length	4.078	<2.2e-16	55.7
	Cohort	2.630	<2.2e-16	4.9	Condition	3.991	<2.2e-16	0.9
	Length × Cohort	3.548	3.2e-ll	0.9	Cohort	3.561	<2.2e-16	4.7
					Length × Cohort	3.481	6.3e-ll	0.9
					Condition × Cohort	3.439	2.5e-4	0.5
	Total deviance			61.5				62.7
	AIC			3.612				3.535
	Log Lik – df			−1,774 (df = 32)				−1,719 (df = 48)
Autumn spawning season		**Residual deviance**	***P*-value (χ^2)**	***R^2* (%)**		**Residual deviance**	***P*-value (χ^2)**	***R^2* (%)**
	Null	3.496			Null	3.499		
	Length	2.659	<2.2e-16	24.0	Length	2.659	<2.2e-16	24.0
	Cohort	2.418	<2.2e-16	6.9	Condition	2.658	0.44	0.02
	Length × Cohort	2.285	<2.2e-16	3.8	Cohort	2.417	<2.2e-16	6.9
					Length × Cohort	2.284	<2.2e-16	3.8
					Condition × Cohort	2.258	0.03	0.8
	Total deviance			34.7				35.5
	AIC			2.349				2.353
	Log Lik – df			−1,143 (df = 32)				−1,128 (df = 48)

R^2 corresponds to the explained deviance (in %) and AIC is the Akaike Information Criterion. Total explained deviance and log-likelihood (with df) of each model are indicated.

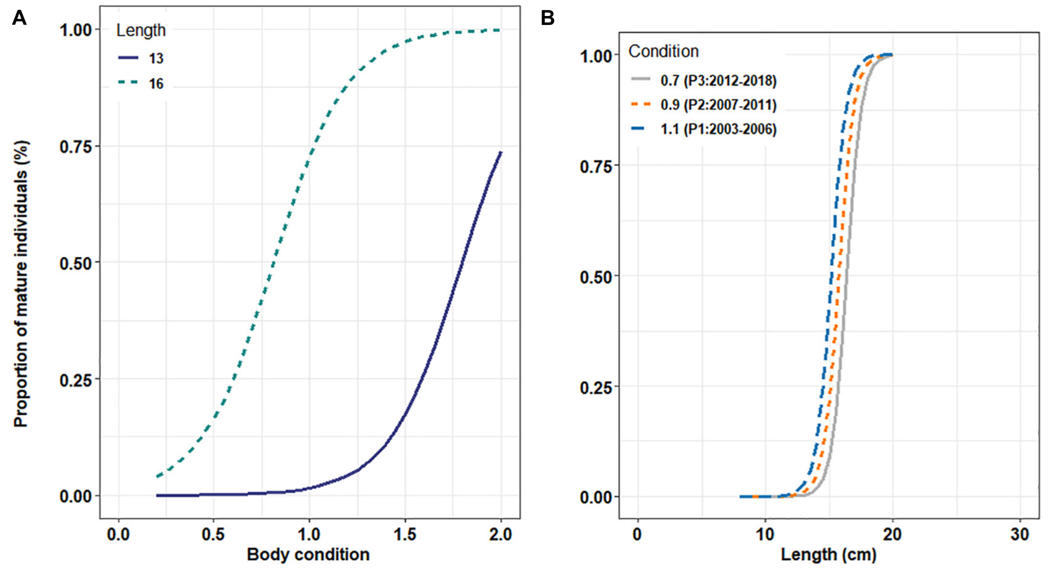

FIGURE 2 | (A) Predicted proportion of mature individuals using parameter estimates from the model (2) in springtime for two length classes (13 and 16 cm corresponding to the mean length-at-age 0 and 1, respectively) and across the observed range of body condition. **(B)** Estimated proportion of sardine mature at length for three levels of body condition corresponding to the median condition observed during the three periods considered (0.7 for P3; 0.9 for P2 and 1.1 for P1). Results are presented for the 2008 cohort in springtime.

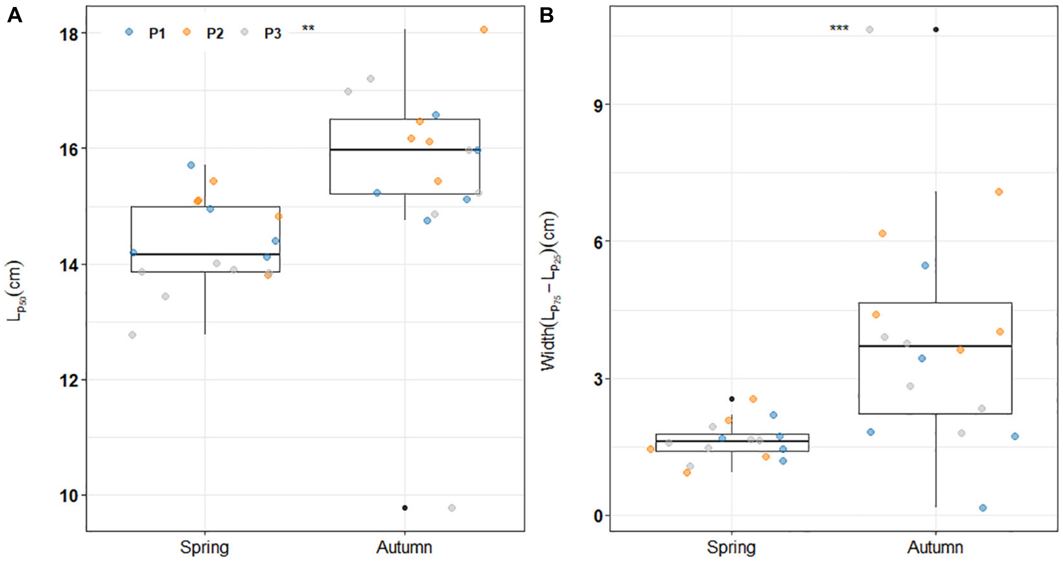

FIGURE 3 | Global distribution of all **(A)** estimated maturation reaction norm midpoints and **(B)** corresponding envelope widths (difference between L_{p75} and L_{p25}) for both seasons over the study period. For both panels, stars indicate significant differences between Spring and Autumn in **(A)** average PMRNs (**) and **(B)** both variance and average envelope widths (***). P1; P2 and P3 refer to the three identified period in Véron et al. (2020).

and body length in spring than in autumn underlying a more size-dependent probability to mature in spring than in autumn when sardine have lower and more variable tendencies to mature at a given size. While regression analyses of trends in maturation reaction norms (Eq. 5) do not show evidence for temporal trends in autumn $L_{p_{50}}$, a significant decreasing trend was found in spring reaction norms (midpoint: $p < 0.01$, width: $p < 0.02$; **Figure 4A**). The magnitude of the changes over the study period was quite substantial: from 2002 to 2018, $L_{p_{50}}$ shifted from more than 15 cm to less than 14 cm.

Reaction Norm Midpoints and Environmental Effect

Among all explanatory variables tested in this analysis (temperature, chlorophyll-*a*, and fish abundance), significant

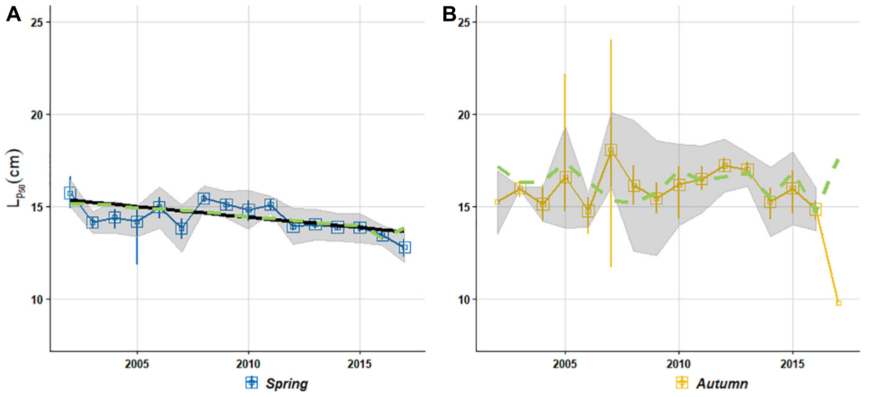

FIGURE 4 | Time series of PMRN midpoints L_{p50} for both spring **(A)** and autumn **(B)** spawning season. Vertical bars give the bootstrap 95% confidence limits for all cohorts. The gray polygon represents the reaction norm widths ($L_{p25} \rightarrow L_{p75}$) and indicates the length where the probability of maturing equals 25% and 75% (lower and upper part, respectively). Solid lines are regression lines of reaction norm midpoints against cohort, weighted by the inverse of variance estimates from the bootstrap analysis, whenever significant. Dashed lines give the predicted L_{p50} from Eq. (8) investigating either long-term trend (only significant for spring PMRN) or short-term fluctuations (only significant for autumn PMRN) and including abundance, environmental effects and cohort for long-term trend analysis.

trends over the study period were only found in both series of fish abundance (**Figure 5**; $p < 0.036$ for both series). These variables were consequently selected as potential factors affecting long-term trends in sardine spring maturation. No significant trend was found in series of temperature or chlorophyll-*a*, which were therefore only considered to investigate short term trends in both seasonal maturation reaction norms.

In contrast with autumn L_{p50} which do not display any temporal trend, the long term decrease in spring L_{p50} was significantly related to the total population abundance (anchovy and sardine) estimated the year prior to the observation of the maturity status (**Table 4** and **Figure 4A**). Moreover, the inclusion of this variable explained enough of the variation in L_{p50} to make the subsequently added cohort effect insignificant. From cohort 2002 to 2017, the rising population abundance experienced the year before maturation accounts for 15% of the decrease in L_{p50}. Despite being non-significant, the cohort effect accounted for a reduction of 1.44 cm in spring sardine L_{p50} corresponding to 69% of the downward trend in maturation reaction norm midpoints.

In contrast to spring, short term fluctuations in autumn L_{p50} could be partly explained by short term variations in both the sea surface temperature and the chlorophyll-*a* 6 months before the spawning peak, and by total population abundance the year preceding the computation of the reaction norm (**Table 4** and **Figure 4B**). The probability to mature at a given size in autumn increased significantly ($p < 0.03$) with an increase of both Chl-*a* and SST 6 months before the spawning peak and an increase in spring abundance the previous year.

DISCUSSION

The present study reveals no evidence that the recently observed decrease in length at maturity of sardine in the Bay of Biscay can be attributed to fisheries-induced evolution. Instead, our results suggest that this decrease can be, at least, partly ascribed to an increase in the combined biomass of sardine and anchovy the year before. To our knowledge, this paper is the first to analyze sardine maturation processes in the Bay of Biscay by considering both spawning schedule and fish body condition. Overall, we show a significant increase in the estimated probability of becoming sexually mature with an increase in body condition. Our results serve to better understand the origin of the marked changes in the proportion of mature individuals at age 1 over the past decade.

Sardine Reproductive Period

Our results are consistent with the reproductive pattern described in the literature for the sardine population in the Bay of Biscay (Arbault and Lacroix, 1971, 1977; Coombs et al., 2006; Gatti, 2016). They confirm the extended reproductive period of sardine in the North East Atlantic and emphasize a synchronicity within the population with two spawning peaks occurring in spring and autumn (April–May and October–November, respectively). Taking into account both the key role of energy reserves in the reproductive process (Lloret et al., 2013) and the significant decline in sardine body condition over the last decades (Véron et al., 2020), the duration of the reproductive period was expected to be negatively impacted at the end of the study period. However, our results do not exhibit temporal shifts either in the duration of the spawning season or in the peak, which suggests that the investment toward the reproduction function has been kept constant over the study period.

The probability of spawning was both length- and season-dependent. In particular, smaller individuals exhibited lower probabilities of spawning than larger ones (whatever the season) and a shorter reproductive period. Thus, 1-year-old sardines maturing in spring appear to be smaller than those

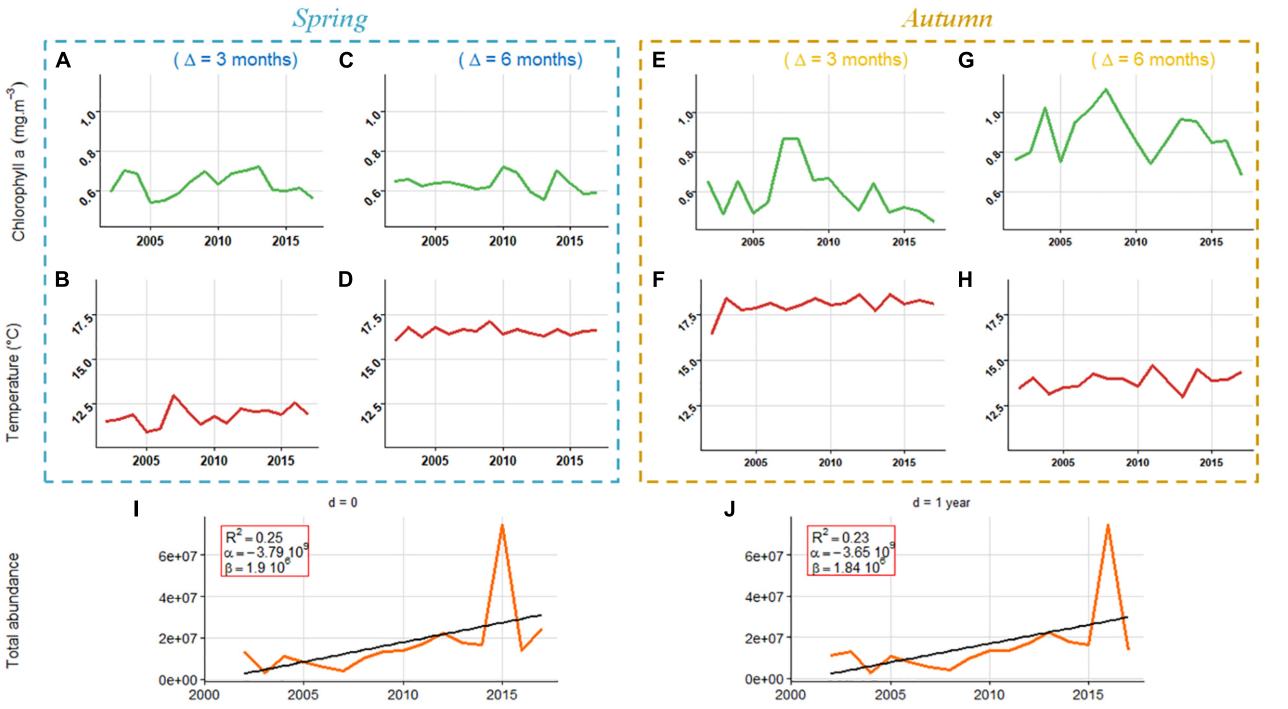

FIGURE 5 | Time series of environmental factors and abundance. The blue box show chlorophyll *a* and temperature considered for spring time analysis with a lag of three (Δ = 3 months) or six (Δ = 6 months) months before the spawning peak **(A–D)** while the yellow box correspond to those variables used when analyzing autumn reaction norm midpoints **(E–H)**. **(I,J)** correspond respectively to the total fish abundance the year and the year prior to the computation of reaction norm. Black lines are regression lines whenever a significant time trend at the 5% α-risk is found.

TABLE 4 | Regression coefficients and their standard errors (SE) obtained from Eq. (7).

	Spring	**Effect**	**Coefficient (SE)**	***F***	***p*-value *(F)***	**Δ Lp50**
Long-term trend		Cohort	-9.03×10^{-2} (4.40×10^{-2})	4.29	0.06	−1.44
		Abundance (*d* = 0)	$\mathbf{-1.03 \times 10^{-8}}$ **($\mathbf{9.36 \times 10^{-9}}$)**	1.22	0.29	−0.31
		Abundance (*d* = 1)	$\mathbf{-1.03 \times 10^{-8}}$ **($\mathbf{9.57 \times 10^{-9}}$)**	**6.42**	**0.02**	**−0.30**
	Autumn	**Effect**	**Coefficient (SE)**	***F***	***p*-value *(F)***	
Short-term fluctuations		Abundance	$\mathbf{-3.63 \times 10^{-8}}$ **($\mathbf{1.00 \times 10^{-8}}$)**	**13.13**	**<0.01**	
		Temperature (Δ = 6 months)	**−1.06 5 ($\mathbf{3.70 \times 10^{-1}}$)**	**8.16**	**0.01**	
		Chlorophyll *a* (Δ = 6 months)	**−5.72 (2.31)**	**6.13**	**0.03**	

Results are only presented for seasonal PMRN midpoints showing either long-term trend or short-term fluctuations. For each coefficient, F-statistic value (F) and associated p-value are given. Regarding the long-term trend analysis, the change in L_{p50}, ΔL_{p50} *(cm), that is attributable to each effect is also provided. Significant variables are shown in bold.*

maturing in autumn (**Figure 3**), the average difference in body length being 1.3 cm.

Impact of Body Condition on Maturation Process

Our analysis confirms that good condition has a significant positive effect on sardine maturation in the Bay of Biscay. These results are in line with the conclusions of various studies involving other fish species (Rowe et al., 1991; Marteinsdottir and Begg, 2002; Bromley, 2003; Morgan, 2004; Grift et al., 2007). Since energy allocation involves trade-offs between growth, reproduction and maintenance (Stearns and Koella, 1986), individuals exhibiting a higher body condition may devote more energy to reproduction making them able to make the "decision" to mature at a smaller size.

The influence of body condition on maturation was more substantial for sardine spawning in spring than those spawning in autumn. This is illustrated by a wider maturation envelope in autumn. Contrary to the autumn period when sardines have benefited from both spring and summer periods to store energy reserves (McBride et al., 2015), sardines emerge at the end of the overwintering period with, on average, a very low body condition (Gatti et al., 2018; Véron et al., 2020). The maturation envelope represents most of the combinations of size and condition at which sardine maturation can occur (Heino and Dieckmann, 2008) and the autumn maturation envelope could represent the strong variability in both growth rates and ability of individuals to store reserves. Alternatively, the size of the autumnal maturation envelope may be a consequence of the mixing of newly mature individuals (including both ages 0 and 1) and those that have already spawn. Assuming that the ability of an individual to enter sexual maturity relies on an energetic threshold value (Thorpe et al., 1998; Morita and Fukuwaka, 2006; Diaz Pauli and Heino, 2013), the amount of available energy in the beginning of the spring reproductive period will greatly influence the maturation of individuals. Such hypothesis is in agreement with several studies on salmonids which have pointed out how the accumulation of energy stores may act as a triggering signal for determining the onset of puberty (Rowe et al., 1991; Hutchings and Jones, 1998; Metcalfe, 1998).

The effect of body condition on maturity ogives appears furthermore dependent upon cohort and, to a large extent, on years considered over the study period. Indeed, when compared with the beginning of the study period (2002–2006), when individuals exhibited a relatively good body condition (Véron et al., 2020), the lower body condition observed in recent years may have a stronger effect on sardine maturation propensity. This assumption is also supported by the observed difference between seasons in the significance of the cohort-dependent effect of body condition on maturation in Eq. (4). Indeed, the stronger significance of this interaction term in spring could mostly be explained by the fact that sardine enter the overwintering period with a lower body condition and thus a smaller amount of energy reserves than at the beginning of the time series (Véron et al., 2020), potentially resulting in a higher dependence of maturation upon individual condition.

Although we found that body condition has an effect on maturation, our results also show that this effect is lower than the effect of body length, which accounts for a much higher proportion of the explained deviance of maturation probability. Such outcome is in agreement with other studies showing similar results for other species (Marteinsdottir and Begg, 2002; Morgan, 2004; Grift et al., 2007). Predicted differences in the Lp_{50} were relatively small over the observed range of body condition (0.7–1.1). This may indicate that despite the lower energy reserves observed in recent years the sardines have maintained their average size at maturation. Moreover, these results are in good agreement with a general prediction from the life-history theory that if fish are facing high mortality, selection will not only favor earlier reproduction but also higher reproductive effort at age and therefore length, at the expense of body growth and/or survival (Heino and Kaitala, 1999).

Differences in Maturation Lengths Between Reproductive Periods

Our results suggest that spring-spawning sardines had a significantly greater probability of maturing than autumn-spawning sardines of equivalent length (**Figure 3**). There are several reasons that may explain such differences. First, as confirmed in this study, sardine exhibit two spawning peaks throughout the year that occur before and after the main growth and energy storage season for sardines in the Bay of Biscay (spring and summer, McBride et al., 2015). Therefore and since sardine maturation takes place during the first 2 years of life, with most individuals maturing in their first year of life, individuals born in springtime and becoming mature in spring are more likely to be smaller when they arrive at their first reproductive period (age-1 fish) than those which will become mature in the following autumn (age-1.5 fish), after the productive planktonic season. Second, several studies emphasized the ability of fish to skip spawning if they have not reached both size and condition threshold values required at the time to make the "decision" to mature (Wright, 2007; Lowerre-Barbieri et al., 2011; Diaz Pauli and Heino, 2013). Therefore, taking into account that both body condition and growth have strongly declined over the study period (Véron et al., 2020), we hypothesized here that some small individuals skip their first spawning opportunity to increase their energy reserves in favor of both growth and postponed reproduction. As the "decision" to mature is made long before the maturation (Wright, 2007), and since it has been emphasized that the decrease in sardine body condition is mainly supported by both summer and autumn periods (Véron et al., 2020), such hypothesis could be relevant if the first reproductive period is in spring. This may partly explain the higher $L_{p_{50}}$ highlighted by our results for the autumn spawning season.

Understanding Variability of Sardine Maturation in the Bay of Biscay

Temporal Trends in Reaction Norm Midpoints

While changes in the proportion of young sardine mature individuals from cohort 2002 to 2017 have been detected (not shown), our analysis does not conclude in drastic changes in the PMRNs over time. We highlighted a quantitative decrease in spring $L_{p_{50}}$ and no evidence for long term changes in autumn reaction norm midpoints has been found. As it has been underlined by several studies using PMRNs to disentangle the effect of phenotypic plasticity from the effect of genetic change (Heino et al., 2002a; Grift et al., 2003; Engelhard and Heino, 2004; Barot et al., 2005; Olsen et al., 2005), the cohort effect highlighted in this study could support the existence of evolutionary changes in spring maturation process. However, after including in the analysis a set of environmental variables capable of generating growth-independent plasticity in maturation, the effect of cohort on the spring reaction norm midpoints was no longer significant. The variability of environmental conditions affecting growth during the period between the date of the maturation "decision" and the date at which the maturity status is assessed appears as the most likely candidate to explain a major part of the inter-annual variability in $L_{p_{50}}$. The deviation from the assumption that negligible somatic growth occurs between these two dates is here too strong and the methodology carried out here does not allow to capture all growth-related variability in the maturation probability. This result has two implications. First, although genetic selection generated by fishing is commonly known as a potential factor contributing to changes in fish maturation (Trippel, 1995; Law, 2000; Wright, 2007), it suggests that temporal modifications in sardine maturity ogives do not result from such process over the period considered here. This is expected for a fish population that has not been subject to intense harvesting over the past decades. Second, it strengthens the need to consider environmental factors as additional explanatory variables that can drive plastic variation in PMRNs (Kraak, 2007; Marshall and McAdam, 2007), and in particular those impacting fish juvenile stages.

Phenotypic Plasticity of Sardine Maturation Process

Several studies emphasized that the onset of maturation may be affected by environmental factors such as temperature (Grift et al., 2003; Yoneda and Wright, 2005; Tobin and Wright, 2011), food availability or trends in abundance which may alter social structures (Kraak, 2007; Diaz Pauli and Heino, 2013). Moreover, these factors have been suspected to affect PMRN midpoints through their impacts during juvenile stages or more months/years prior to the maturation process (Mollet et al., 2007). Potential plastic responses of sardine maturation to environmental fluctuations were assessed at the population level by correlating PMRN midpoints with environmental variables (temperature, chlorophyll-*a* and total abundance of anchovy and sardine).

Analyzing long-term trends in spring reaction norm midpoints, our results emphasized a negative correlation between $L_{p_{50}}$ and the spring abundance experienced the year prior to reaching sexual maturity. This indicates that abundance may have an effect on sardine maturation, driving individuals to mature earlier at a smaller size if population densities experienced during the critical "decision" phase are high. This counter-intuitive outcome is most likely another consequence of the deviation from the major assumption of negligible somatic growth between the time the "decision" is made and the observation of maturation, made in the PMRN approach. An increase in population abundance during the time interval between the "decision" to mature and maturation may have led to a decrease in growth rates, after the "decision" to mature, due to higher competition for food. Such process is in line with potential density-dependence effects that have already been suggested to occur within nursery grounds in the Bay of Biscay (Doray et al., 2018; Véron et al., 2020). Moreover, this result strengthens the idea that probabilistic maturation reaction norm approach for this case study might not completely account for growth-related plasticity (Morita and Fukuwaka, 2006; Dieckmann and Heino, 2007; Wright, 2007; Heino and Dieckmann, 2008) and in particular that occurring during the juvenile stages (Mollet et al., 2007; Diaz Pauli and Heino, 2013), when growth is very variable.

At shorter time scales, abundance seems to have a similar effect on the fluctuations in reaction norm midpoints. Our results emphasize that population densities experienced during springtime have a positive effect on the probability to mature in the following autumn reproductive period. Moreover, they also emphasized that short term fluctuations in autumn reaction norm midpoints could partly be explained by short term variations in water temperature and chlorophyll-*a*. Temperature (Charnov and Gillooly, 2004) and food availability are known to impact early life history stages, as they may affect age at maturity through their effect on juvenile growth rates. However, and as already highlighted by several studies (Grift et al., 2003; Dhillon and Fox, 2004; Mollet et al., 2007; Tobin and Wright, 2011), our results suggest potential effects of these environmental factors on maturation process at relatively short term. Since temperature has been demonstrated as a potential factor accelerating developmental rates other than through growth (Fuiman et al., 1998), the onset of maturation might therefore be affected by temperature in early life. However, like several studies which have examined the relationship between reaction norm midpoints and temperature (Grift et al., 2003; Kraak, 2007; Mollet et al., 2007; Morita et al., 2009), we cannot conclude whether temperature is having a direct effect on sardine maturation or is a proxy for other factors.

Toward New Perspectives to Improve Our Approach

Several of our findings should be interpreted with caution owing to the assumptions underlying the approach and the availability of data as potential explanatory factors.

First, a corpus of literature emphasized that the "decision" to mature relies on specific physiological threshold traits during the period of maturation (Thorpe et al., 1998; Wright, 2007; Tobin and Wright, 2011). Among them, fish energetic status before and during the critical phase of the developmental "decision to spawn" seems to play a critical role. Here, we used the relative condition index to account for the effect of sardine body condition on maturation process. Even if our results are in good agreement with those from several studies showing a positive effect of body condition on the probability to mature (Grift et al., 2007; Mollet et al., 2007; Diaz Pauli and Heino, 2013), they also emphasize that the decrease in sardine body condition over the study period cannot explain the whole temporal trend in maturation. Here, we highlight two main reasons for this. First, the timing of observations has been suggested as a potential source of misunderstanding of maturation process using the PMRN approach (Wright, 2007; Diaz Pauli and Heino, 2013). Since the developmental "decision to spawn" takes place long before spawning actually happens, the state of individuals when the initial maturation "decision" is made does not match the observed state in field-data. In particular, Wright (2007) highlighted that changes in energy status around the time of maturation "decision" cannot be accounted for in PMRN approach. In this context, Diaz Pauli and Heino (2013) notably suggested that the initiation of maturation stage for guppies (*Poecilia reticulata*) was closer to the maturation "decision" than to its completion. The authors argue that differences between initiation and completion of maturation might result from differential allocation of resources into growth and reproduction at the different stage and therefore conclude that PMRN defined around the initiation stage could better represent maturation schedule than that considering completion stage. Therefore, and since it has been suggested that maturation is controlled by successive inhibition through lipid-regulated switches during the critical period (Thorpe, 2007), we suggest here the use of those biochemical indices to identify the beginning of maturation in order to help understanding of maturation process. A second explanation of our results relies on the properties of the body condition index itself. In this study, data used to compute PMRN were selected during the identified spawning seasons. Since gonad development increases body weight at the time of spawning, it results (due to calculation process) in a higher body condition index. Such effect could therefore contribute to the positive effect of condition on the probability of maturation. This supports the difficulty to interpret the role of condition in the maturation process because with this in mind, a higher condition index can therefore be the consequence of maturation rather than the cause.

Second, our results confirm the existence of two spawning peaks for sardine in the Bay of Biscay. Moreover, they highlight significant differences in the reaction norm midpoints between the two reproductive seasons, with higher and more variable $L_{p_{50}}$ in autumn than in spring. Those differences may be explained by the fact that sardines are multiple batch spawners and simple visual examination of the gonads or histological analyses do not allow distinguishing between first time spawners and individuals that have already spawned. Therefore, we could hypothesize that the higher PMRN midpoints may result from a mix between newly mature individuals and those that have already spawned in spring, grown during summer and skipped spawning on the second opportunity of the year, just before the autumn reproductive period, due to deficient diet and poor nutritional condition (Lowerre-Barbieri et al., 2011; Rideout and Tomkiewicz, 2011). With this result in mind, we suggest that the back-calculation of monthly growth trajectories from scales and otoliths of sardine may help to first set individuals on their own growth trajectory according to their birth season and second determine at which time they made the “decision” to mature through the identification of the shift in energy allocation between growth and reproduction.

This kind of back-calculation, that has already been used for some species (Engelhard et al., 2003; Baulier and Heino, 2008), may also help to better account for phenotypic plasticity in growth trajectories that can lead to the same age-size combination and which therefore constitutes a limit of the PMRN approach (Morita and Fukuwaka, 2006; Heino and Dieckmann, 2008; Diaz Pauli and Heino, 2013). Here we highlighted that consequence of such plasticity may be more important for species maturing mostly in their first year of life (old age 0 and young age 1). Indeed, as shown by Morita and Fukuwaka (2006), our results strengthen the idea that growth condition just before the initiation of maturation, here individual growth trajectories between the larval stage and age one, considerably influences maturation probabilities.

Finally, even if we considered a set of environmental factors that can influence sardine maturation process through growth-independent effects, the question remains as to what extent both the timing and the spatial windows were adequate with our analysis. This issue is strongly linked with the previous limit of our approach. In particular, Wright (2007) emphasized that temperature is likely to have the greatest direct influence during the “decision” period and therefore suggested that it should be examined when an individual initiates its maturation. In our case, we therefore recommend collecting individuals on nursery grounds some months before the spawning season in order to be able to understand the effect of environmental variables on sardine maturation process. Furthermore, due to the lack of data, our analysis was not spatially explicit. However, recent analyses of sardine population dynamics suggest different growth trajectories between the north and the south of the Bay of Biscay. Such a spatial pattern in growth may induce spatial patterns in the maturation process for sardine and could therefore involves strong repercussions on the dynamics of this stock and consequently its management if not accounted for.

Toward a Better Understanding of Stock Population Dynamics

This study clearly demonstrates that the strong phenotypic plasticity in sardine maturation process is tightly linked to variability in growth rates. Such variability originates from multiple sources among which environmental conditions play a prominent role and can consequently have a strong impact on both spawning stock biomass and population productivity (Dutil and Brander, 2003). Indeed, considering the current warming of sea surface temperature, climate change may lead to an increase in growth rate during the juvenile phase that may result in a decrease in the length at first maturation which in turn might impact adults growth since available energy has been routed toward reproduction at smaller size (Heino et al., 2002b). Moreover, even though a shift toward earlier maturation will positively affect spawning stock biomass, its consequences on the oncoming recruitment will not necessarily be as positive since fecundity and egg viability are positively linked with maternal size and condition (Trippel and Neil, 2011).

With all of this in mind, our results support the need to develop modeling tools allowing for the consideration of both temporal variations in biological processes and their relationships with biotic and abiotic drivers to better understand stock population dynamics. In the case of sardine, our study leads us to suggest the use of a length-based stock assessment model as a first step to account for both the variability in sardine maturation process and the spawning seasonality which may lead to several recruitments throughout the year and therefore strongly impact its population dynamics. Furthermore and more generally, considering that climate variation will impact fish biological processes such as maturation, a better understanding of its influence as well as its incorporation within fish stock assessment models will clearly help evaluate management options for sustainable fisheries under climate change (Hollowed et al., 2009). A future key step would therefore be to identify and quantify more precisely the environmental drivers of the maturation process in order to ultimately increase the predictive power of stock assessment models.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MV analyzed the data and wrote the manuscript. MB and LP designed the study. MH, ED, and LP contributed to the data collection. LB, MH, and ED gave guidance on analyses. All authors commented on the analysis, interpretation, and presentation of the data.

FUNDING

This study was supported by a Ph.D. grant funded by the Brittany Region and the "Federation des Industries des Aliments Conservés" (FIAC, Adépale). The morphometric data used in this study were collected during scientific programs and surveys. Fish sampling was mostly funded by the European Common Fisheries Policy and Ifremer.

ACKNOWLEDGMENTS

We are grateful to the crews and onboard scientific teams of R/V "Thalassa," who made data collection possible during the PelGas and EVHOE surveys. We thank the team of the national CAPTAIN project funded by France Filière Pêche, as well as the technicians and fisheries professionals involved in the sampling made at fish markets and during the Sentinelle and JUVAGA surveys. The authors would also like to thank the two reviewers as well as the Editor for their helpful comments and suggestions.

REFERENCES

Anderson, C. N. K., Hsieh, C., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., et al. (2008). Why fishing magnifies fluctuations in fish abundance. *Nature* 452, 835–839. doi: 10.1038/nature06851

Arbault, S., and Lacroix, N. (1971). Aires de ponte de la sardine, du sprat et de l'anchois dans le golfe de gascogne et sur le plateau celtique resultats de 6 annees d'etude. *Rev. Trav. Inst. Pêch. Marit.* 35, 35–56. doi: 10.1111/j.1502-3885.1974.tb00665.x

Arbault, S., and Lacroix, N. (1977). Oeufs et larves de clupéidés et engraulidés dans le Golfe de Gascogne (1969-1973):,distribution des frayères, Relation entre les facteurs du milieu et la reproduction. *Rev. Trav. Inst. Pêch. Marit.* 41, 227–254.

Barot, S., Heino, M., Morgan, M. J., and Dieckmann, U. (2005). Maturation of Newfoundland American plaice (*Hippoglossoides platessoides*): long-term trends in maturation reaction norms despite low fishing mortality? *ICES J. Mar. Sci.* 62, 56–64. doi: 10.1016/j.icesjms.2004.10.004

Barot, S., Heino, M., O'Brien, L., and Dieckmann, U. (2004). Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. *Evol. Ecol. Res.* 6, 659–678.

Baulier, L., and Heino, M. (2008). Norwegian spring-spawning herring as the test case of piecewise linear regression method for detecting maturation from growth patterns. *J. Fish Biol.* 73, 2452–2467. doi: 10.1111/j.1095-8649.2008.02088.x

Bernardo, J. (1993). Determinants of maturation in animals. *Trends Ecol. Evol.* 8, 166–173. doi: 10.1016/0169-5347(93)90142-C

Bromley, P. (2003). The use of market sampling to generate maturity ogives and to investigate growth, sexual dimorphism and reproductive strategy in central and south-western North Sea sole (*Solea solea* L.). *ICES J. Mar. Sci.* 60, 52–65. doi: 10.1006/jmsc.2002.1318

Charnov, E. L., and Gillooly, J. F. (2004). Size and temperature in the evolution of fish life histories. *Integr. Comp. Biol.* 44, 494–497. doi: 10.1093/icb/44.6.494

Christensen, V., Guenette, S., Heymans, J. J., Walters, C. J., Watson, R., Zeller, D., et al. (2003). Hundred-year decline of North Atlantic predatory fishes. *Fish Fish.* 4, 1–24. doi: 10.1046/j.1467-2979.2003.00103.x

Coombs, S. H., Smyth, T. J., Conway, D. V. P., Halliday, N. C., Bernal, M., Stratoudakis, Y., et al. (2006). Spawning season and temperature relationships for sardine (*Sardina pilchardus*) in the eastern North Atlantic. *J. Mar. Biol. Assoc. U.K.* 86, 1245–1252. doi: 10.1017/S0025315406014251

Dhillon, R. S., and Fox, M. G. (2004). Growth-independent effects of temperature on age and size at maturity in Japanese medaka (*Oryzias latipes*). *Copeia* 2004, 37–45. doi: 10.1643/CI-02-098R1

Diaz Pauli, B., and Heino, M. (2013). The importance of social dimension and maturation stage for the probabilistic maturation reaction norm in *Poecilia reticulata. J. Evol. Biol.* 26, 2184–2196. doi: 10.1111/jeb.12215

Dieckmann, U., and Heino, M. (2007). Probabilistic maturation reaction norms: their history, strengths, and limitations. *Mar. Ecol. Prog. Ser.* 335, 253–269. doi: 10.3354/meps335253

Doray, M., Petitgas, P., Huret, M., Duhamel, E., Romagnan, J. B., Authier, M., et al. (2018). Monitoring small pelagic fish in the Bay of Biscay ecosystem, using indicators from an integrated survey. *Prog. Oceanogr.* 166, 168–188. doi: 10.1016/j.pocean.2017.12.004

Doray, M., Petitgas, P., Romagnan, J. B., Huret, M., Duhamel, E., Dupuy, C., et al. (2017). The PELGAS survey: ship-based integrated monitoring of the Bay of Biscay pelagic ecosystem. *Prog. Oceanogr.* 166, 15–29. doi: 10.1016/j.pocean.2017.09.015

Duhamel, E., Salaun, M., and Pawlowski, L. (2014). EVHOE 2014 cruise, Thalassa R/V. doi: 10.17600/14002000

Dutil, J.-D., and Brander, K. (2003). Comparing productivity of North Atlantic cod (*Gadus morhua*) stocks and limits to growth production. *Fish. Oceanogr.* 12, 502–512. doi: 10.1046/j.1365-2419.2003.00243.x

Engelhard, G., and Heino, M. (2004). Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? *Mar. Ecol. Prog. Ser.* 272, 245–256. doi: 10.3354/meps272245

Engelhard, G. H., Dieckmann, U., and Godø, O. R. (2003). Age at maturation predicted from routine scale measurements in Norwegian spring-spawning herring (*Clupea harengus*) using discriminant and neural network analyses. *ICES J. Mar. Sci.* 60, 304–313. doi: 10.1016/S1054-3139(03)00017-1

Fuiman, L. A., Poling, K. R., and Higgs, D. M. (1998). Quantifying developmental progress for comparative studies of larval fishes. *Copeia* 1998, 602–611. doi: 10.2307/1447790

Gatti, P. (2016). *Une Approche Bioénergétique Pour la Comparaison des Traits D'histoire de vie de L'anchois et de la Sardine du Golfe de Gascogne*. Ph.D. thesis, Université de Rennes, Rennes.

Gatti, P., Cominassi, L., Duhamel, E., Grellier, P., Le Delliou, H., Le Mestre, S., et al. (2018). Bioenergetic condition of anchovy and sardine in the Bay of Biscay and English Channel. *Prog. Oceanogr.* 166, 129–138. doi: 10.1016/j.pocean.2017.12.006

Grift, R., Heino, M., Rijnsdorp, A., Kraak, S., and Dieckmann, U. (2007). Three-dimensional maturation reaction norms for North Sea plaice. *Mar. Ecol. Prog. Ser.* 334, 213–224. doi: 10.3354/meps334213

Grift, R., Rijnsdorp, A., Barot, S., Heino, M., and Dieckmann, U. (2003). Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Mar. Ecol. Prog. Ser.* 257, 247–257. doi: 10.3354/meps257247

Heino, M., and Dieckmann, U. (2008). Detecting fisheries-induced life-history evolution: an overview of the reaction-norm approach. *Bull. Mar. Sci.* 83, 69–93.

Heino, M., Dieckmann, U., and Godø, O. R. (2002a). Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. *ICES J. Mar. Sci.* 59, 562–575. doi: 10.1006/jmsc.2002.1192

Heino, M., Dieckmann, U., and Godø, O. R. (2002b). Measuring probabilistic reaction norms for age and size at maturation. *Evolution* 56, 669–678. doi: 10.1111/j.0014-3820.2002.tb01378.x

Heino, M., and Kaitala, V. (1999). Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *J. Evol. Biol.* 12, 423–429. doi: 10.1046/j.1420-9101.1999.00044.x

Hollowed, A. B., Bond, N. A., Wilderbuer, T. K., Stockhausen, W. T., A'mar, Z. T., Beamish, R. J., et al. (2009). A framework for modelling fish and shellfish responses to future climate change. *ICES J. Mar. Sci.* 66, 1584–1594. doi: 10.1093/icesjms/fsp057

Hutchings, J. A., and Jones, M. E. (1998). Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.* 55, 22–47. doi: 10.1139/d98-004

ICES (2008). *Report of the Workshop on Small Pelagics (Sardina pilchardus, Engraulis encrasicolus) Maturity Stages (WKSPMAT)*. ICES No. CM2008/ACOM:40. Mazara del Vallo: ICES.

ICES (2016). *Report of the Workshop on Fish Condition*. ICES WKFICON Report 2016. Girona: ICES, 33.

ICES (2019). Working group on Southern horse mackerel, anchovy and sardine (WGHANSA). *ICES Sci. Rep.* 1, 544–653.

Jorgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., et al. (2007). Ecology: managing evolving fish stocks. *Science* 318, 1247–1248. doi: 10.1126/science.1148089

Kraak, S. (2007). Does the probabilistic maturation reaction norm approach disentangle phenotypic plasticity from genetic change? *Mar. Ecol. Prog. Ser.* 335, 295–300. doi: 10.3354/meps335295

Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57, 659–668. doi: 10.1006/jmsc.2000.0731

Le Cren, E. D. (1951). The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *J. Anim. Ecol.* 20, 201–219. doi: 10.2307/1540

Lloret, J., Shulman, G., and Love, R. M. (2013). *Condition and Health Indicators of Exploited Marine Fishes: Lloret/Condition and Health Indicators of Exploited Marine Fishes*. Oxford: John Wiley & Sons. doi: 10.1002/9781118752777

Lowerre-Barbieri, S. K., Ganias, K., Saborido-Rey, F., Murua, H., and Hunter, J. R. (2011). Reproductive timing in marine fishes: variability, temporal scales, and methods. *Mar. Coast. Fish.* 3, 71–91. doi: 10.1080/19425120.2011.556932

Marshall, C., and McAdam, B. (2007). Integrated perspectives on genetic and environmental effects on maturation can reduce potential for errors of inference. *Mar. Ecol. Prog. Ser.* 335, 301–310. doi: 10.3354/meps335301

Marteinsdottir, G., and Begg, G. (2002). Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* 235, 235–256. doi: 10.3354/meps235235

Marty, L., Rochet, M.-J., and Ernande, B. (2014). Temporal trends in age and size at maturation of four North Sea gadid species: cod, haddock, whiting and Norway pout. *Mar. Ecol. Prog. Ser.* 497, 179–197. doi: 10.3354/meps10580

McBride, R. S., Somarakis, S., Fitzhugh, G. R., Albert, A., Yaragina, N. A., Wuenschel, M. J., et al. (2015). Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish Fish.* 16, 23–57. doi: 10.1111/faf.12043

Metcalfe, N. B. (1998). The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 55, 93–103. doi: 10.1139/d98-005

Mollet, F., Kraak, S., and Rijnsdorp, A. (2007). Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea*. *Mar. Ecol. Prog. Ser.* 351, 189–199. doi: 10.3354/meps07138

Morgan, M. (2004). The relationship between fish condition and the probability of being mature in American plaice (*Hippoglossoides platessoides*). *ICES J. Mar. Sci.* 61, 64–70. doi: 10.1016/j.icesjms.2003.09.001

Morita, K., Fukuwaka, M. (2006). Does size matter most? the effect of growth history on probabilistic reaction norm for salmon maturation. *Evol*, 60:1516. doi: 10.1554/06-007.1

Morita, K., Tsuboi, J., and Nagasawa, T. (2009). Plasticity in probabilistic reaction norms for maturation in a salmonid fish. *Biol. Lett.* 5, 628–631. doi: 10.1098/rsbl.2009.0290

Myers, R. A., and Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283. doi: 10.1038/nature01610

Olsen, E. M., Lilly, G. R., Heino, M., Morgan, M. J., Brattey, J., and Dieckmann, U. (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 62, 811–823. doi: 10.1139/f05-065

Parrish, R. H., Serra, R., and Grant, W. (1989). The monotypic sardines, *Sardina* and *Sardinops*: their taxonomy, distribution, stock structure, and zoogeography. *Can. J. Fish. Aquat. Sci.* 46, 2019–2036. doi: 10.1139/f89-251

Rideout, R. M., and Tomkiewicz, J. (2011). Skipped spawning in fishes: more common than you might think. *Mar. Coast. Fish.* 3, 176–189. doi: 10.1080/19425120.2011.556943

Rijnsdorp, A. (1993). Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia* 96, 391–401. doi: 10.1007/bf00317510

Rijnsdorp, A. D., and Van Leeuwen, P. I. (1996). Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. *ICES J. Mar. Sci.* 53, 1199–1213. doi: 10.1006/jmsc.1996.0145

Rowe, D. K., Thorpe, J. E., and Shanks, A. M. (1991). Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) Parr. *Can. J. Fish. Aquat. Sci.* 48, 405–413. doi: 10.1139/f91-052

Saraux, C., Van Beveren, E., Brosset, P., Queiros, Q., Bourdeix, J.-H., Dutto, G., et al. (2019). Small pelagic fish dynamics: a review of mechanisms in the Gulf of Lions. *Deep Sea Res. II Top. Stud. Oceanogr.* 159, 52–61. doi: 10.1016/j.dsr2.2018.02.010

Silva, A., Faria, S., and Nunes, C. (2013). Long-term changes in maturation of sardine, *Sardina pilchardus*, in Portuguese waters. *Sci. Mar.* 77, 429–438. doi: 10.3989/scimar.03852.03A

Silva, A., Santos, M., Caneco, B., Pestana, G., Porteiro, C., Carrera, P., et al. (2006). Temporal and geographic variability of sardine maturity at length in the northeastern Atlantic and the western Mediterranean. *ICES J. Mar. Sci.* 63, 663–676. doi: 10.1016/j.icesjms.2006.01.005

Sinclair, A. F., Swain, D. P., and Hanson, J. M. (2002). Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. *Can. J. Fish. Aquat. Sci.* 59, 372–382. doi: 10.1139/f02-014

Stearns, S. C., and Koella, J. C. (1986). The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40, 893–913. doi: 10.2307/2408752

Stratoudakis, Y., Coombs, S., de Lanzós, A. L., Halliday, N., Costas, G., Caneco, B., et al. (2007). Sardine (*Sardina pilchardus*) spawning seasonality in European waters of the northeast Atlantic. *Mar. Biol.* 152, 201–212. doi: 10.1007/s00227-007-0674-4

Thorpe, J. (2007). Maturation responses of salmonids to changing developmental opportunities. *Mar. Ecol. Prog. Ser.* 335, 285–288. doi: 10.3354/meps335285

Thorpe, J. E., Mangel, M., Metcalfe, N. B., and Huntingford, F. A. (1998). Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evol. Ecol.* 12, 581–599. doi: 10.1023/A:1022351814644

Tobin, D., and Wright, P. J. (2011). Temperature effects on female maturation in a temperate marine fish. *J. Exp. Mar. Biol. Ecol.* 403, 9–13. doi: 10.1016/j.jembe.2011.03.018

Trippel, E., and Neil, S. (2011). Maternal and seasonal differences in egg sizes and spawning activity of northwest Atlantic haddock (*Melanogrammus aeglefinus*) in relation to body size and condition. *Can. J. Fish. Aquat. Sci.* 61, 2097–2110. doi: 10.1139/f04-125

Trippel, E. A. (1995). Age at maturity as a stress indicator in fisheries. *BioScience* 45, 759–771. doi: 10.2307/1312628

Trippel, E. A. (1999). Estimation of stock reproductive potential: history and challenges for Canadian Atlantic gadoid stock assessments. *J. Northw. Atl. Fish. Sci.* 25, 61–81. doi: 10.2960/j.v25.a6

Véron, M. (2020). *Variabilité de Traits d'Histoire de Vie et Implications Pour la Modélisation des Dynamiques de Population: Application au Stock de Sardines du Golfe de Gascogne*. Brest: Universite de Bretagne Occidentale.

Véron, M., Duhamel, E., Bertignac, M., Pawlowski, L., and Huret, M. (2020). Major changes in sardine growth and body condition in the Bay of Biscay between 2003 and 2016: temporal trends and drivers. *Prog. Oceanogr.* 182:102274. doi: 10.1016/j.pocean.2020.102274

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models: estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 73, 3–36. doi: 10.1111/j.1467-9868.2010.00749.x

Wright, P. (2007). Understanding the maturation process for field investigations of fisheries-induced evolution. *Mar. Ecol. Prog. Ser*. 335, 279–283. doi: 10.3354/meps335279

Wright, P. J., and Trippel, E. A. (2009). Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. *Fish Fish.* 10, 283–304. doi: 10.1111/j.1467-2979.2008.00322.x

Yoneda, M., and Wright, P. J. (2005). Effect of temperature and food availability on reproductive investment of first-time spawning male Atlantic cod, *Gadus morhua. ICES J. Mar. Sci.* 62, 1387–1393. doi: 10.1016/j.icesjms.2005.04.018

Zuur, A. F. (ed.). (2009). *Mixed Effects Models and Extensions in Ecology with R, Statistics for Biology and Health*. New York, NY: Springer.

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 08 December 2020
doi: 10.3389/fmars.2020.578717

The Celtic Sea Through Time and Space: Ecosystem Modeling to Unravel Fishing and Climate Change Impacts on Food-Web Structure and Dynamics

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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: *01 July 2020*
Accepted: *03 November 2020*
Published: *08 December 2020*

Citation:
Hernvann P-Y, Gascuel D, Grüss A, Druon J-N, Kopp D, Perez I, Piroddi C and Robert M (2020) The Celtic Sea Through Time and Space: Ecosystem Modeling to Unravel Fishing and Climate Change Impacts on Food-Web Structure and Dynamics. Front. Mar. Sci. 7:578717. doi: 10.3389/fmars.2020.578717

Both trophic structure and biomass flow within marine food webs are influenced by the abiotic environment and anthropogenic stressors such as fishing. The abiotic environment has a large effect on species spatial distribution patterns and productivity and, consequently, spatial co-occurrence between predators and prey, while fishing alters species abundances and food-web structure. In order to disentangle the impacts of the abiotic environment and fishing in the Celtic Sea ecosystem, we developed a spatio-temporal trophic model, specifically an Ecopath with Ecosim with Ecospace model, for the period 1985–2016. In this model, particular attention was paid to the parameterization of the responses of all trophic levels to abiotic environmental changes. Satellite remote sensing data were employed to determine the spatial distribution and annual fluctuations of primary production (PP). Spatial and temporal changes in the habitat favorable for zooplankton were predicted with a novel ecological-niche approach using daily detection of productivity fronts from satellite ocean color. Finally, functional responses characterizing the effect of several abiotic environmental variables (including, among others, temperature, salinity and dissolved oxygen concentration, both at the surface and at the bottom) on fish species groups' habitat suitability were produced from the predictions of statistical habitat models fitted to presence-absence data collected by multiple fisheries-independent surveys. The dynamic component of our model (Ecosim) was driven by time-series of fishing effort, PP, zooplankton habitat suitability and abiotic environmental variables, and was fitted to abundance and fisheries catch data. The spatial component of our model (Ecospace) was constructed, for specific years of the period 1985–2016 with contrasted abiotic environmental conditions, to predict the variable distribution of the biomass of all functional groups. We found that fishing was the main driver of observed ecosystem changes in the Celtic Sea over the period 1985–2016. However, the integration of the environmental variability into the model and the subsequent improvement of the fit of the dynamic Ecosim component highlighted (i) the control of the overall pelagic production by PP and (ii) the influence of temperature on the productivity of several trophic levels in the Celtic Sea, especially on trophic groups with warm and cold water affinities. In addition, Ecospace predictions indicated that the spatial distributions of commercial fish species may have substantially changed over the studied period. These spatial changes mainly appeared to be driven by temperature and may, therefore, largely impact future fisheries given the continuity of climatic changes.

Keywords: Celtic Sea, ecosystem modeling, habitat model, environment, Ecopath with Ecosim and Ecospace, primary production, fishing impact

INTRODUCTION

Food webs govern the structure and functioning of marine ecosystems (Libralato et al., 2014) and are, therefore, typically modeled using trophodynamic models. However, marine ecosystems are far from being spatially homogeneous and the productivity of species at the base of the trophic network and prey-predator interactions can vary largely over space (Polis et al., 1997). This spatial variability determines the characteristics of food webs, including their stability and persistence (Huxel and McCann, 1998; Melian and Bascompte, 2002; Gravel et al., 2011).

The main driver of the spatial heterogeneity in prey-predator interactions in marine ecosystems is the abiotic environment (hereafter simply referred to as the "environment"). Environmental variables such as salinity, temperature and chlorophyll-*a* govern species distributions by defining their "environmental niche" (Hutchinson, 1957; Chase and Leibold, 2003). Hence, by regulating the degree of overlap between species niches, the environment largely influences species interactions and shapes communities and food-web structure along gradients (Pellissier et al., 2013; Kortsch et al., 2019). In addition, topography and the structural habitat play an essential role in the spatial variability of marine food webs. In particular, water depth greatly influences exchanges between the pelagic and benthic compartments of ecosystems through food accessibility (Giraldo et al., 2017; Agnetta et al., 2019). Seabed features (including substrate composition) and water column characteristics also mediate species interactions within marine ecosystems by influencing the accessibility of potential prey items to predators (Gardner, 1981), by providing refugia to the prey (e.g., Menge and Lubchenco, 1981) or by facilitating predation through aggregation (Le Fèvre, 1987).

The complexity of marine food webs is enhanced by the responses of predators to their prey, and by competition (Hunsicker et al., 2011). The feeding rate of any predator on a given prey depends on the abundance of that prey (Holling, 1959) and the relative preference of the predator for other co-occurring prey items (Murdoch, 1969). The spatial distribution of a predator can be substantially affected by the spatial distribution of its potential prey (Logerwell and Hargreaves, 1996; Torres et al., 2008), and vice versa (Barnett and Semmens, 2012), as well as by the spatial distribution of the other predators that compete for those prey (Hansson, 1984; Ward et al., 2001). Therefore, identifying the relative role of the drivers of the structure and functioning of marine ecosystems and their changes requires spatially-explicit ecosystem models where the spatial patterns of species biomass depend on both a specific environment and trophic interactions.

Spatially-explicit ecosystem models such as Atlantis (Fulton et al., 2004; Audzijonyte et al., 2019), OSMOSE (Shin and Cury, 2001) and Ecopath with Ecosim and Ecospace (Pauly et al., 2000; Christensen et al., 2014) simulate food-web functioning while representing the spatial distribution patterns of all ecosystem components. These spatially-explicit ecosystem models are powerful tools to disentangle the intricate effects of trophic relationships, the environment and anthropogenic stressors, e.g., fishing, on species distribution patterns and biomass flows within marine ecosystems. In the context of climate change, spatially-explicit food-web models that integrate predictions from statistical habitat or niche modeling approaches are particularly useful to predict how ecosystems may respond to future modifications in environmental conditions (Pellissier et al., 2013; Moullec et al., 2019a). However, such spatial food-web models are currently relatively scarce and these models have often difficulty to comprehensively represent heterogeneous spatial processes.

The Celtic Sea represents a large portion of the Western European continental shelf, and extends from the Western English Channel to the Celtic break delimiting Porcupine Sea Bight and the South-West of Ireland (**Figure 1**). This ecosystem has a complex spatial organization since it encompasses a broad range of depths and a diversity of substrate types, resulting in a variety of benthic habitats that host a wide diversity of species assemblages (Le Danois, 1948; Ellis et al., 2013, 2002; Martinez et al., 2013). This diversity of species assemblages is conducive to complex trophic interactions (Trenkel et al., 2005). In addition, the Celtic Sea is located at the interface of the Lusitanian and Boreal provinces, therefore defining the northern or southern limit of the distribution range of many species (Dinter, 2001). The presence of pelagic mesoscale structures such as productivity fronts (Pingree, 1980; Pingree et al., 1982) is another source of spatial heterogeneity in the Celtic Sea ecosystem. Ultimately, spatial heterogeneity in Celtic Sea fish communities is reflected by the highly mixed fisheries that operate in the Celtic Sea region (Sharples et al., 2013; Mateo et al., 2017; Dolder et al., 2018; Moore et al., 2019). Fishing has been identified as the primary driver of changes in the Celtic Sea ecosystem since 1950 and this pressure has culminated in the late 1990s (Gascuel et al., 2016;

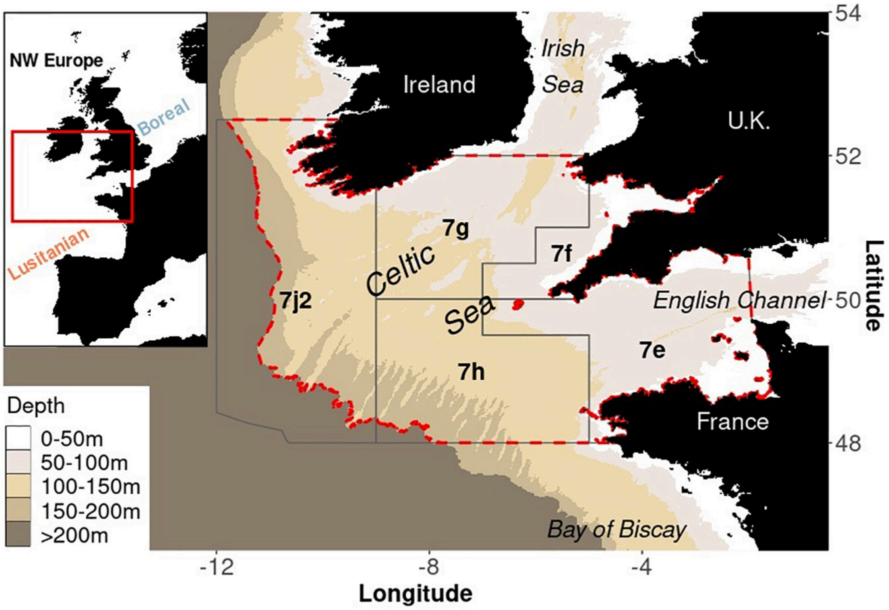

FIGURE 1 | General location of the Celtic Sea (top left corner) and delimitation of the study area regarding physical and management boundaries. The Celtic Sea is located at the border between Lusitanian and Boreal provinces. The Celtic Sea EwE and Ecospace model (red dashed contour) is developed for the shelf area shallower than 200 m depth matching ICES divisions (polygons) 7.e (Western English Channel), 7.f (Bristol Channel), 7.g (Celtic Sea North), 7.h (Celtic South) and 7.j.2 (Southwest of Ireland- East belonging to the NE Atlantic Fisheries Commission regulatory area).

Hernvann and Gascuel, 2020; Mérillet et al., 2020). Nonetheless, long-term variability in hydro-climatic conditions has also largely affected the Celtic Sea ecosystem (Beaugrand et al., 2000; Hernvann and Gascuel, 2020) and the ongoing climate change may greatly impact the basal ecosystem production (McGinty et al., 2011), fish populations (Brunel and Boucher, 2007), and entire communities (ter Hofstede et al., 2010; Simpson et al., 2011) of the Celtic Sea.

In this study, we analyzed the interdependent impacts of fishing and climate change on the structure and functioning of marine ecosystems using the Celtic Sea as a regional case study. We developed a spatially-explicit trophic model for the Celtic Sea to represent the effects of the environment on the distribution and productivity of functional groups, from phytoplankton to top predators. Multiple data types were considered for this aim. Spatio-temporal dynamics of plankton groups were represented in the spatially-explicit trophic model using the predictions of remote sensing based models. The responses of higher trophic level functional groups to changes in the environment were represented using the predictions of statistical habitat models, which were fitted to data from large scale survey and environmental databases. This overall information was used to calibrate the trophic model and determine how changes in primary production, zooplankton habitat and temperature may have interacted with fishing to shape the Celtic Sea food-web dynamics over the period 1985–2016. Then, the spatial structure and functioning of the Celtic Sea food web were analyzed for contrasted years in terms of environmental conditions to better understand the processes of changes in the Celtic Sea ecosystem over the studied decades.

MATERIALS AND METHODS

The EwE Framework in a Nutshell and General Approach to Model the Trophic Functioning of the Celtic Sea

The EwE Modeling Framework in a Nutshell

Our approach relies on the Ecopath with Ecosim (EwE) framework (Pauly et al., 2000; Christensen and Walters, 2004). Hereafter, we only briefly summarize the EwE modeling steps since more details about the EwE framework and its main equations can be found in Christensen and Walters (2004) and are summed up in **Supplementary Appendix SA**.

Ecopath is the basal component of EwE, and provides a snapshot of the ecosystem of interest for a given period, i.e., generally a specific year. Ecopath represents the ecosystem of interest through functional groups (i.e., groups of species/taxa that have similar trophic and ecological niches and life-history characteristics) that exchange matter and energy through trophic relationships while the mass balance between the production of each functional group and all consumptions is assumed.

Ecosim is the dynamic module of EwE that allows for hindcast or forecast of changes in functional group biomasses. Ecosim predator-prey dynamics (under top-down or bottom-up control) are determined based on the foraging arena theory (Ahrens et al., 2012) whereby vulnerability coefficients modulate the proportion of prey biomass accessible to predators by altering predator consumption rates. Vulnerability coefficients can be estimated by fitting Ecosim to observed biomass, abundance or catch time-series. The response of the ecosystem to stressors

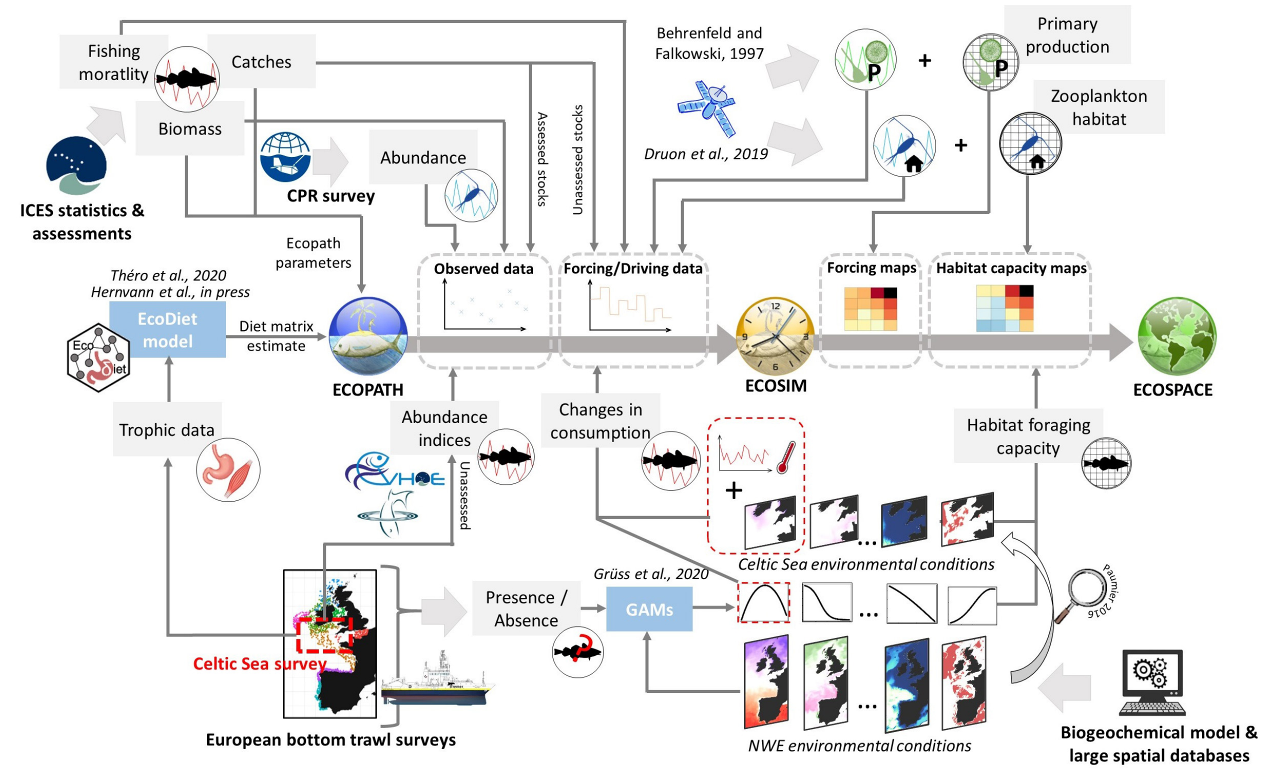

FIGURE 2 | Schematic of the data integration framework used to build and calibrate the Ecopath with Ecosim (EwE) with Ecospace model. Gray rectangles represent data or EwE input. Blue rectangles correspond to statistical model runs to estimate EwE inputs from data.

can be simulated in Ecosim: (1) time-series of fishing effort or fishing mortalities can, respectively, drive exploited groups dynamics through top-down processes; (2) time-series of primary production can drive phytoplankton dynamics controlling bottom-up the food-web; and (3) environmental time-series can affect the consumption rates of predators according to linear response of following specific user-defined functional responses.

Ecospace is the spatial component of EwE, which predicts the spatial distribution of functional group biomasses over a horizontal 2-D grid (Walters, 1999; Pauly et al., 2000). The most recent version of Ecospace includes an habitat foraging capacity model that determines the suitability of each model grid cell for a functional group as the relative proportion of the cell over which the group can feed (Christensen et al., 2014). Each grid cell's capacity is calculated as the product of functions that reflect the preferences of the group of interest for specific environmental parameter values.

General Approach of Integrated Trophic Modeling in the Celtic Sea

The Celtic Sea ecosystem was previously modeled by Moullec et al. (2017) using the Ecopath and Ecosim modules of EwE to represent its dynamics and fishing impact between 1980 and 2013. However, this model relied on a limited amount of fieldwork data and did not investigate the effect of any environmental driver and their spatial heterogeneity on ecosystem structure and functioning over this period. To improve the ecological realism of the Celtic Sea food-web model, we develop an integrated trophic modeling approach consisting in successively (i) updating the Ecopath model and integrating local trophic data to define trophic relationships, (ii) exploring spatio-temporal changes in the dynamic of plankton groups, (iii) investigating the environmental drivers of high trophic levels, including temperature, and studying their spatio-temporal changes, and (iv) integrating fishing and changes in temporal variation in environmental drivers of functional groups in the fit of the Ecosim model over the period 1985–2016 and using their spatial distribution to build the Ecospace model. The different steps of this integrated trophic modeling framework are displayed in **Figure 2**.

Updating and Improving the Pre-existing Celtic Sea Ecopath Model

We updated the pre-existing Ecopath models for 2013 and 1980 (Moullec et al., 2017) and built a new Celtic Sea Ecopath model for the year 1985. The species composition of a few functional groups was refined for a greater coherence in the diet of the species they contain (see details in **Supplementary Appendix SB**). A major upgrade of the Celtic Sea model was the provision of a new diet matrix for the Ecopath model, estimated using the Bayesian integrated model "EcoDiet" and its R package implementation (Hernvann et al., in press; Théro et al., 2020)[1,2]. EcoDiet allows to simultaneously estimate diet proportions of all functional groups by integrating multiple data types, i.e., stomach content analyses, biotracer analyses and literature knowledge. Here, EcoDiet was applied to trophic analyses conducted on fish collected in the Celtic Sea during a fisheries-independent survey as part of the EATME project (Issac et al., 2017; Rault et al., 2017; Day et al., 2019), and information from an updated bibliographic search. The new model comprised a total of 50 single and multispecies functional groups, including exploited fishes and invertebrates, non-commercial benthic invertebrates (five groups), zoo- and phyto- plankton (four and two groups, respectively), and mammals and seabirds (four groups). Some of these functional groups were further split into younger and older life-stage groups (cod *Gadus morhua*, hake *Merluccius merluccius*, and anglerfish *Lophius* sp.) based on onthogenetic changes in diet identified by stomach content analyses (Issac et al., 2017; Day et al., 2019). Details on the Celtic Sea Ecopath model, its parameters, and the species it represents can be found in **Supplementary Appendix SB**. The validity of the 1985 Ecopath model was analyzed using the standard PREBAL diagnostics (Link, 2010; **Supplementary Appendix SB**).

Representing the Dynamics of Plankton Groups

Spatial-temporal changes in the production of phytoplankton groups (primary production, PP) were taken from the Vertically Generalized Production Model (VGPM, Behrenfeld and Falkowski, 1997) for the period 1998–2016, and from a regional application of hydrodynamic-biogeochemical NEMO-ERSEM to the European shelf (Baretta et al., 1995; Madec, 2008; Edwards et al., 2012; UK Met Office[3]) for the period 1985–1997. The VGPM model uses remote-sensed chlorophyll-*a* data collected by SeaWiFS and MODIS-Aqua to quantify PP over the entire water column (Morel and Berthon, 1989). PP is one of the direct outputs of the NEMO-ERSEM model and was extracted over the entire water column to align with the VGPM outputs. Data products were obtained from the Ocean Productivity website[4] and the E.U. Copernicus Marine Environment Monitoring Service[5] (eu), respectively. Time-series of PP in the Celtic Sea were used to force the productivity of phytoplankton groups in Ecosim (Christensen et al., 2009; Mackinson et al., 2009) while annual maps of primary productivity were used in Ecospace (Steenbeek et al., 2013). PP maps averaged by 5-year periods are provided in **Supplementary Appendix SC**.

The spatio-temporal changes of the suitable feeding habitat of zooplankton (small and large mesozooplankton, macrozooplankton) were estimated for the 1998–2016 period using a niche model of mesozooplankton in the North Atlantic (Druon et al., 2019). This zooplankton suitable habitat (ZSH) model relies on the identification of productivity fronts at mesoscale. Because these fronts persist long enough in the pelagic realm (at least 3 to 4 weeks), they allow the production of elevated biomass of mesozooplankton which, in turn, can sustain higher trophic level organisms. The mesozooplankton habitat model is fitted to data of the Continuous Plankton Recorder (CPR) and relies on remotely-sensed horizontal gradients of chlorophyll-*a* (SeaWiFS and MODIS-Aqua sensors). This habitat model only results of the daily observation of productivity fronts by satellite sensors, therefore the ZSH model is an algorithm that translates chlorophyll-*a* distribution directly into a daily habitat value. Seasonal maps of ZSH in the Celtic Sea are provided in **Supplementary Appendix SC**.

Linking the Dynamics of Higher Trophic Level Organisms to Environment

To characterize the response of higher trophic level organisms to environment, we determined functional relationships for 38 Ecopath groups (over 45 high trophic level groups, excluding mammals and birds, and benthic meiofauna) using the statistical habitat modeling approach developed by Grüss et al. (2020, 2018). This approach involved the following steps: (1) the construction of fisheries-independent survey and environmental databases; (2) the development of generalized additive models (GAMs); and (3) the use of the GAMs to estimate functional relationships.

Construction of Survey and Environmental Databases

For each functional group, presence/absence (encounter/non-encounter) data were collected by 13 International Bottom Trawl Surveys (IBTS; Cronne, 2016) conducted between 1987 and 2017 in European waters (**Supplementary Appendix SD**; ICES database)[6]. We allocated presence/absence data, collected by the surveys (only 3 surveys for 4 low TL benthic invertebrates groups; **Supplementary Appendix SD**), to a 0.125° spatial grid to address the issue of heterogeneity in sampling schemes (Grüss et al., 2020). A set of environmental variables were compiled for all of these grid cells. These environmental variables included time-invariant topographic and habitat variables: bathymetry, distance to the coast, and percentages of seabed substrate types. The environmental variables also included hydro-climatic time-varying variables: surface (first 10 m) and bottom sea temperature, salinity and dissolved oxygen concentration, and surface phytoplankton concentration. Spatial-temporal estimates of these variables for each grid cell at a monthly resolution were obtained from the General Bathymetric Chart of the Oceans (GEBCO)[7], the European Marine Observation and Data Network (EMODnet)[8], and the Copernicus platform. More details are provided in **Supplementary Appendix SD**.

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[1] https://github.com/pyhernvann/EcoDiet

[2] https://cran.r-project.org/web/packages/EcoDiet/index.html

[3] https://www.metoffice.gov.uk/

[4] http://sites.science.oregonstate.edu/ocean.productivity/

[5] https://marine.copernicus.eu/

[6] https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx

[7] https://www.gebco.net/

[8] https://www.emodnet-seabedhabitats.eu/

GAM Fitting

The literature was screened to determine which of the variables included in the environmental database may influence the spatial distribution patterns of each functional group. This list was reduced through a collinearity analysis to avoid the selection of variables that are strongly correlated with one another together or with eastings and northings (longitude and latitude expressed in UTM coordinates) (Grüss et al., 2018). Then, for each functional group, we fitted binomial GAMs of the following form to the presence/absence data from the survey database ("mgcv" package in the R environment Wood, 2017):

$$g(\eta) = te(X, Y) + s(x_1) + s(x_2) + \ldots + s(x_n) + factor(Survey) + factor(Year) \quad (1)$$

where η is the probability of presence of the functional group; g is the logit link function between η and each predictor; *te(X,Y)* is a tensor product smooth fitted to eastings and northings that accounts for spatial autocorrelation at broad scale; x_1, x_2,..., x_n are the predictors from the environmental database; s is a thin plate regression spline fitted to a given predictor and limited to four degrees of freedom for interpretability; and *Survey* and *Year* are treated as fixed-effect factors (Farmer and Karnauskas, 2013; Grüss et al., 2018). Only predictors with a significant effect (statistical criteria detailed in **Supplementary Appendix SE**) were kept in the GAMs, and the models were evaluated using the interactive cross-validation procedure described in Grüss et al. (2018). More details can be found in **Supplementary Appendix SE**.

Production of Preference Functions

Fitted GAMs were utilized to produce preference functions (also called functional reponses below) expressing for the preferences of each functional group for specific environmental parameter values. For each environmental variable *i* integrated in a GAM, predictions were made with the GAM over a vector of values ranging between the minimum and maximum values of environmental variable *i* in the Celtic Sea, while: (1) setting eastings *X* and northings *Y* at their values at the barycenter of the Celtic Sea; (2) keeping the other variables at their mean value from the GAM modeled dataset; and (3) setting the *Survey* and *Year* factors at their mode from the GAM modeled dataset. GAM predictions were then rescaled to provide preferences functions ranging between 0 and 1, which account for the relative effects of each environmental variable on the probability of presence of the functional group of interest. The procedure for rescaling follows Grüss et al., 2018 and is described in **Supplementary Appendix SE**.

Fitting Ecosim and Building Ecospace

Ecosim

The Ecosim model was first fitted to observed biomasses from available ICES stock assessments, abundance indices from scientific surveys for fish (EVHOE; Duhamel et al., 2018; UK-WCGFS, CEFAS), the CPR survey[9] for plankton (Johns, 2019), and catch time-series (Statlant)[10]. Time-series of fishing mortality (for assessed stocks) or catch (for non-assessed stocks) were used as forcing functions. A summary of the time-series used is provided in **Supplementary Appendix SF**. Ecosim calibration was conducted using the stepwise fitting procedure implemented into EwE by Scott et al. (2016) and following the protocol found in Bentley et al. (2019) to determine the most suitable number of predator-prey dynamics parameters (vulnerabilities Vs) to estimate. To assess the relative impacts of fishing and environment on the ecosystem, we adopted an approach similar to the one developed by Mackinson (2014). We applied the fitting procedure, integrating fishing forcing functions only, then integrating the environmental drivers of plankton and fish dynamics, first separately and then simultaneously. PP and zooplankton suitable habitat (ZSH) time-series drove the production of phytoplankton groups (see Christensen et al., 2009) and the consumption of zooplankton (small and large mesozooplankton, macrozooplankton), respectively. More specifically, ZSH time-series were used as multiplier of the arena area for zooplankton-phytoplankton interactions, of zooplankton vulnerability for fish-zooplankton interactions, and of both parameters for zooplankton-zooplankton interactions (see **Supplementary Appendix SF**; Dahood et al., 2019). Temperature variations and corresponding preference functions to the model drove the consumption of fish groups (foraging environmental response; see Bentley et al., 2017; Serpetti et al., 2017; Corrales et al., 2018). In order to avoid any potential confounding effects with temperature-induced changes, that we precisely wanted to quantify in this study, we chose to not use the available information on recruitment anomalies (e.g., from stock assessments) as forcing function of the dynamics of functional groups represented by multiple life-stages. To quantify the relative contribution of each driver, the various fits of the models were compared using the sum of squares between observed and predicted time-series and the bias-corrected Akaike information criterion (AICc) of the model (Akaike, 1974). We addressed the uncertainty in Ecopath input parameters in Ecosim outputs through the Monte Carlo uncertainty routine based on confidence intervals determined from Pedigrees (Heymans et al., 2016; Steenbeek et al., 2018). More details on the fitting procedure can be found in **Supplementary Appendix SF**.

Ecospace

The fitted Ecosim scenario was run over the period 1985–2016, and the "Ecopath model from Ecosim" plug-in (Steenbeek et al., 2016) was employed to generate 6 Ecopath models corresponding to mean conditions over successive 5-year periods (from 1985–1989 to 2005–2010, and 2011–2016 for the last period). Ecospace models were built for each of the 5-year periods to facilitate the comparison of spatial distributions through time and run over a spin-up period of 5 years. The Ecospace models integrated the average maps of PP to force its distribution, those of ZSH to feed the distribution of habitat foraging capacity for zooplankton, and those of environmental variables employed in the GAMs and the

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[9] https://www.cprsurvey.org/

[10] https://www.ices.dk/data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx

associated preference functions of higher TL groups to spatially distribute fish habitat foraging capacities (Coll et al., 2016; Grüss et al., 2018, 2016). Trophic and diversity indicators (**Table 1**) were projected based on functional groups' distributions, partly using the ECOIND plug-in (Coll and Steenbeek, 2017). This approach decoupling temporal and spatial changes will be further discussed in the Discussion section. Parameters of the Ecospace model are given in **Supplementary Appendix SG**.

RESULTS

Improvement of Ecosim Model Fit and Relative Importance of Ecosystem Drivers

The statistically best model was obtained when trophic interactions, fishing, and environment were included together in the model fitting (SS = 340 and AICc = −3365, **Table 2**), hence improving the model fit by 86%. The proportions of each driver in the Sum of Square SS reduction suggest that fishing was the main driver of ecosystem changes, followed by trophic interactions and, with much lower but significant contributions, the environment (**Table 2** and **Figure 3**). Temperature effects on higher trophic levels and overall changes in low trophic levels productivity had similar weight in the fit. Integrated independently from plankton data, temperature forcing especially increased the hindcast quality for species with thermal preferenda at outside the temperature ranged covered in the Celtic Sea (warmer or colder, **Figure 3B**). Conversely, PP and ZHS integration essentially led to a better fit for functional groups belonging to the pelagic pathway.

Predicted Historical Trends for Functional Groups Abundance

Low Trophic Levels

With regard to the basal productivity in the Celtic Sea ecosystem, no clear trend was apparent in the Ecosim model over the period 1985–2016. Despite this relative stability, some differences can be observed in CPR time-series within the phytoplankton community. Most significant changes in observed phytoplankton data occurred during the late 1980s when the abundance of large phytoplankton (diatoms and dinoflagellates) dropped whereas the one of small phytoplankton increased (**Figure 4**). However, the trends for both large phytoplankton and small phytoplankton were not correctly captured by Ecosim and remained overall constant over the entire period 1985–2016 in the model.

Similarly to PP, the ZSH remained stable over the study period, yet, looking at the data, substantial changes were observed within the zooplankton community, mostly during the late 1980s. When PP and ZSH were integrated, Ecosim reproduced the overall observed trend in small mesozooplankton abundance, which substantially declined before 1990 and was still decreasing until the mid-2000s. By contrast, large mesozooplankton abundance tended to increase over the period 1985–2016. Again for this zooplankton group, the trend predicted by Ecosim correctly matched observations both in terms of trend and of amplitude of variations. Both trends and interannual variability in zooplankton abundance were not captured when PP and ZSH were not included in the fit (**Figure 4**). The stability in the predicted phytoplankton time-series precludes us from linking changes in mesozooplankton abundance with changes in primary productivity in the Celtic

TABLE 1 | Indicators used to analyze spatial changes in the Celtic Sea structure over the period 1985–2016.

Acronym	Indicator	Unit	Definition	References
SOI	System Omnivory Index	–	Mean standard deviation of trophic levels in the diets	Libralato, 2013
K	Kempton's diversity index	–	Trophic group's diversity	Ainsworth and Pitcher, 2006
MTL	Mean trophic level	TL	Mean trophic level of the community (TL $\geq$ 2)	Christensen et al., 2008
$B_{TL=x}$	Total biomass at TL threshold x	tones	Total biomass of groups with TL superior or equal to x	Christensen et al., 2008
HTI	High Trophic Indicator	%	Percentage of predators with TL $\geq$ 4 among the consumers	Bourdaud et al., 2016

TABLE 2 | Results of the Ecosim fitting procedure.

Scenario	Vs/Predator	Vs/Predator-Prey	K	minSS	AICc
Baseline	0	0	0	3082	879
Trophic interaction	40	13	53	2195	318
Fishing	0	0	0	1248	−905
Trophic interactions + Fishing	45	7	52	385	−3119
Trophic interactions + Fishing + Plankton forcing	45	8	53	383	−3128
Trophic interactions + Fishing + Temperature	29	14	43	394	−3093
Trophic interactions + Fishing + Plankton forcing + Temperature	**46**	**6**	**52**	**340**	**−3365**

Vs columns indicate the number of vulnerability parameters that have been estimated and whether they have been estimated by predator or by couple predator-prey. K is the total number of parameters estimated by the model, which is equal to the number of Vs estimated as no PP anomaly is estimated. The maximum number for K to avoid overfitting is 56 (Supplementary Appendix SE). The best model in terms of minSS, the sum of squares between observed and predicted values reached at the end of the fit, and AICc is the one including both trophic interactions, fishing, plankton-related data and temperature effect on high trophic level groups. The best model statistically is written in bold.

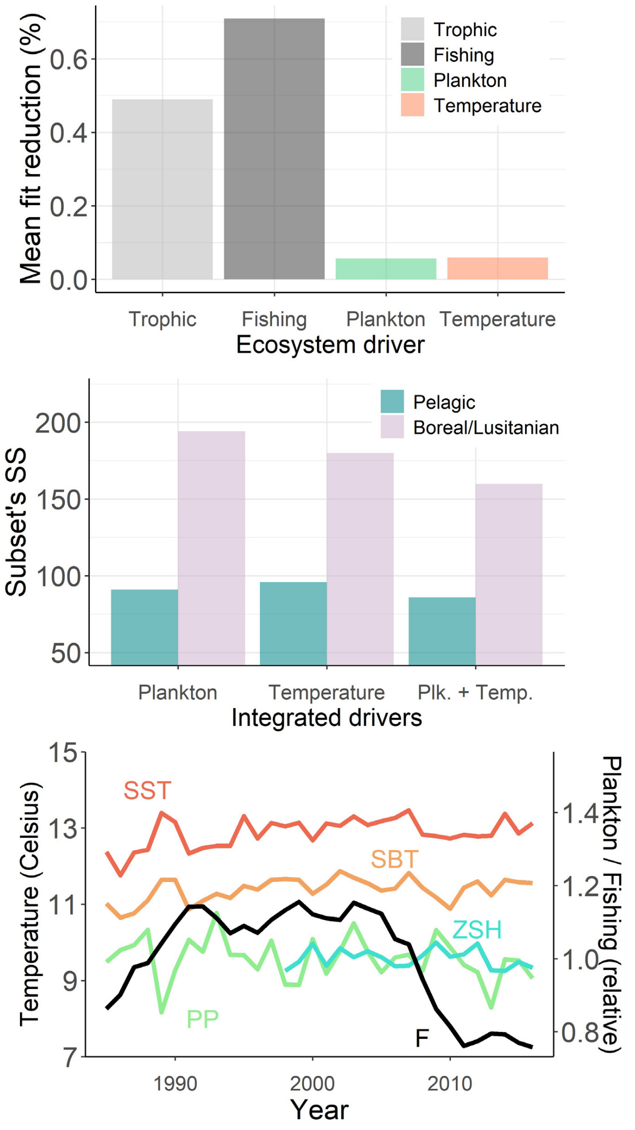

FIGURE 3 | Changes in the temporal fit of the Ecosim model: **(A)** mean gain in the Sum of Square (SS) when integrating each driver in the fitting procedure: "Trophic" when estimating the vulnerabilities, "Fishing" when integrating fishing mortality time-series and forced catches, "Plankton" when integrating primary production (PP) and zooplankton suitable habitat (ZSH), "Temperature" when integrating sea surface temperature (SST) and sea bottom temperature (SBT) – Plankton and Temperature data were integrated only in the models accounting for Trophic interactions and Fitting;. **(B)** Changes in the SS for pelagic species and species with temperature optimum outside the Celtic Sea temperature range according to the different environmental drivers integrated in the fit. **(C)** Trends in the forcing variables – F is the mean fishing mortality time-series for stocks under assessment.

Sea between 1985 and 2016. Although Ecosim was able to correctly predict the overall zooplankton abundance level over the study period, the predictions did not perfectly match the observed patterns, especially at the beginning of the time-series.

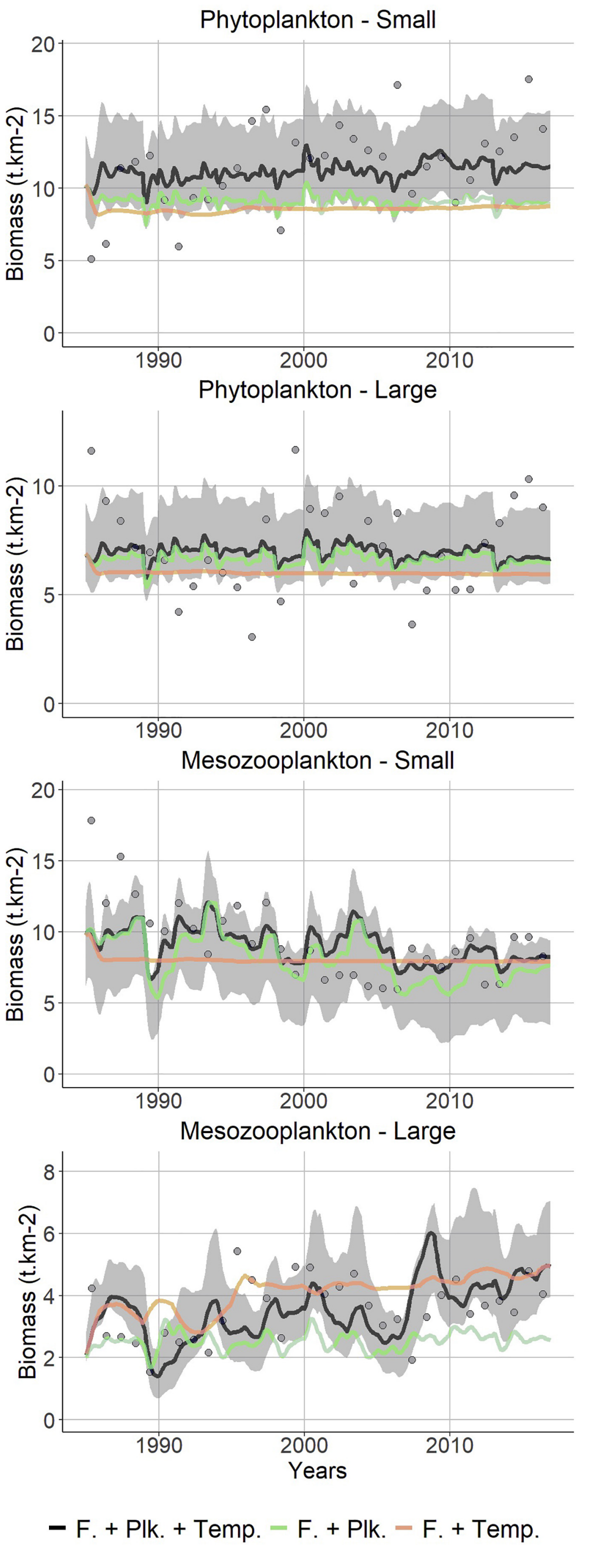

FIGURE 4 | Observed (points; CPR) vs. predicted (lines; Ecosim) changes in the plankton community of the Celtic Sea over the period 1985–2016. Black line: best fitted model, including trophic interactions, fishing, PP, ZSH and temperature; green line: with integration of PP and ZSH but without

(Continued)

FIGURE 4 | temperature forcing; orange line: with integration of temperature forcing but without PP and ZSH. The gray shaded area is delimited by the 95% intervals of the Monte Carlo runs that propagate the uncertainty on Ecopath input parameters to Ecosim. The points correspond to observed time-series used during Ecosim calibration.

Higher Trophic Levels

The observed time-series of biomass, abundance and catch of most of high trophic level groups were satisfactorily reproduced by Ecosim. Overall, Ecosim predictions were better for those single-species groups for which stock assessments are carried out than for multispecific fish groups, and they were less consistent for exploited invertebrate groups.

In 1985, main target species such as large Gadiformes [e.g., hake, cod, whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*)], large flatfish species [i.e., sole (*Solea solea*), plaice (*Pleuronectes platessa*)], anglerfish, megrim (*Lepidorhombus whiffiagonis*), sea bass (*Dicentrarchus labrax*), other large piscivorous demersal fish [e.g., saithe (*Pollachius virens*), ling (*Molva molva*), pollock (*Pollachius pollachius*), turbot (*Psetta maxima*), conger (*Conger conger*)] and forage fish [i.e., herring (*Clupea harengus*), mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*)] were already subject to high fishing mortality that far exceeded natural losses. Driven by an increase in fishing mortality, the biomass of most of these groups declined between 1985 and the mid-2000s while their catches simultaneously stabilized or decreased. In 2005, their fishing mortality decreased and Ecosim predicted a stabilization of their abundance that preceded a progressive recovery from 2010 onward (**Figure 5**).

The pressure exerted on species that were initially less exploited such as smaller flatfish (i.e., endobenthivorous), medium demersal fish (i.e., epibenthivorous), or cephalopods increased after 1985. Concomitantly, the natural mortality exerted on these species decreased as a result of the depletion of highly commercial groups such as large predatory fish (e.g., hake, cod, whiting, megrim). The predicted biomass trends of lower TL fish and invertebrates varied according to their exploitation patterns (**Figure 5**). Dramatic changes in the composition of the pelagic community were also predicted by Ecosim. In parallel to horse mackerel depletion, the biomass of pelagic fishes that feed upon similar ressources such as suprabenthivorous fish, sprat (*Sprattus sprattus*) or boarfish (*Capros aper*) increased, while these pelagic fishes were initially almost absent from the Celtic Sea ecosystem.

The recovery of commercial species in the 2010s is noticeable, particularly the large increases in the biomasses of large predators, including hake (whose biomass increased 5-fold) and a few other species. According to the model, these species recoveries translated into an increase in predation pressure from large predators and a decline in the abundance of cephalopods, small pelagic and small demersal fish.

The rising temperatures resulting from climate forcing had various effects on the different species represented in the model, and they mainly impacted fish productivity during the mid-1990, when a substantial increase in both surface and bottom temperatures was observed. As highlighted by the comparison of model's fit on observed data according to scenarios (**Figures 3B**, **5**), the integration of temperature forcing allowed to better capture the overall trends in the abundance of Boreal and Lusitanian species. The foraging ability of Boreal species, including cod, plaice, whiting, herring and endobenthivorous demersal fish, dropped at the same time that fishing mortality increased, and this accentuated the depletion of the above-mentioned species. Conversely, for Lusitanian species that have warmer thermal preferences, such as sardine, boarfish, hake and cephalopods, increased productivity in the Celtic Sea ecosystem in the 1990s acted antagonistically to the increasing fishing pressure and synergistically with decreasing competition pressure. The differential trends in the productivity of warm and cold water affinity species between the start and the end of the study period were responsible for differences in the recovery capacities of commercial groups in the 2010s. For instance, cod biomass remains quite stable when temperature is not driving productivity, and plaice recovers much slower from fishing pressure release. Conversely, sole depletion in the first part of the time-series is stronger as its recovery is strengthened (**Figure 5**). These variations triggered changes in the fish assemblages. Interannual variability in high trophic level abundance was better reproduced when incorporating PP and ZSH data, especially for pelagic species (**Figure 5**).

Predicted Spatial Distribution of Food-Web Components in the Celtic Sea

Habitat Projection for the Celtic Sea

Evaluation tests suggested that GAMs (**Supplementary Appendix SE**) were good enough to produce yearly foraging habitat maps for the 38 higher trophic level functional groups (year 2016, **Supplementary Appendix SE**). The tests also indicated that GAM fits and predictive capacities were better for monospecific groups than for heterogeneous multispecies groups. The fit was also lower when the sampling gear employed during the surveys was not adapted to a given functional group (e.g., benthic invertebrates). The type of environmental predictors retained in final GAMs varied across functional groups, as their number, ranging from 3 for the non-commercial invertebrate groups to 9 for hake. The preference functions estimated from fitted GAMs exhibited diverse shapes. The retained predictors often included bathymetry (32 groups) and temperature (surface or bottom; 35 groups), two variables of importance in shaping the Celtic Sea environment. Depth in the Celtic Sea drove marked northeast-southwest gradients, while surface temperature led to pronounced latitudinal gradients and bottom temperature resulted in two opposed pools of warm and cold waters in the English and Bristol Channel and in southern Ireland.

Salinity functional responses quantify habitat suitability in the riverine-influenced Bristol Channel. When they were retained in final GAMs, seabed substrate variables resulted in patchy predicted habitats for demersal species. In those instances, it was possible to make a clear distinction between restricted areas of rocky or mixed substrate and large irregular strands of muddy,

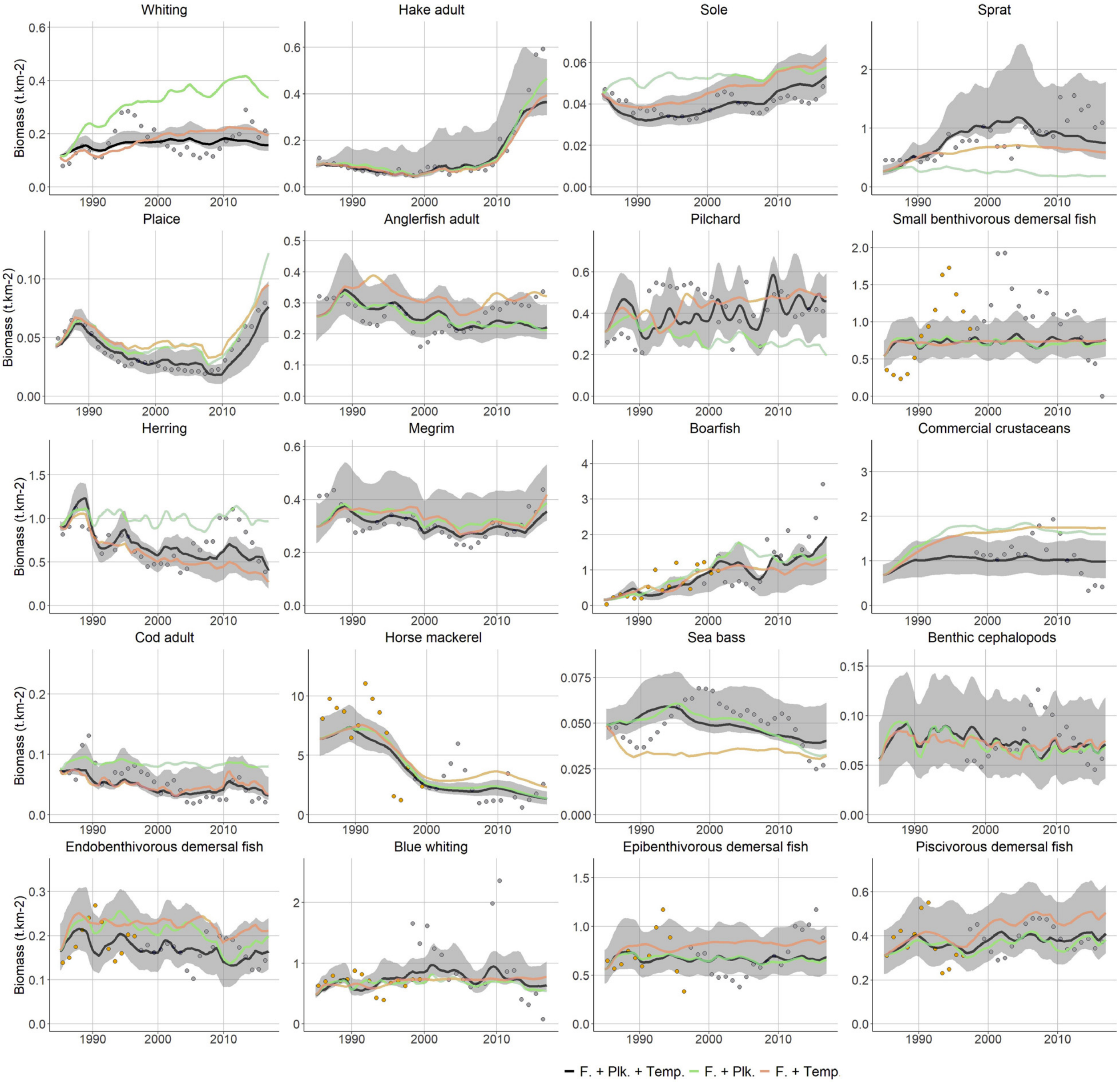

FIGURE 5 | Fitted biomass trends from the Ecosim model for a selection of demersal and pelagic fish species. Black line: best fitted model, including trophic interactions, fishing, PP, ZSH and temperature; green line: with integration of PP and ZSH but without temperature forcing; orange line: with integration of temperature forcing but without PP and ZSH. The gray shaded area is delimited by the 95% intervals of the Monte Carlo runs that propagate the uncertainty on Ecopath input parameters to Ecosim. The color points indicate the different time-series of observed data during Ecosim calibration.

sandy or coarse sediments. The other environmental variables considered in the present study were less frequently retained in final GAMs. Habitat foraging capacity maps for the period 1985–1989 are provided in **Supplementary Appendix SE**.

Predicted Biomass Distributions

The Ecospace model predicted the biomass distribution of all components of the ecosystem, from the phytoplankton to top predators. The biomass distributions of functional groups reflected the overall habitat foraging capacities of these groups, hence their ecological niche, but were also influenced by their trophic interactions with prey, predators and competitors (**Figure 6**).

The distributions of those functional groups for which no GAM was developed were estimated by Ecospace only according to their feeding relationships (birds, mammals, bacteria, benthic meiofauna, large pelagic fish). A wide variety of spatial patterns were exhibited by the functional groups represented in Ecospace. Due to their high mobility in the water column and their eurythermic characteristics, horse mackerel and mackerel were

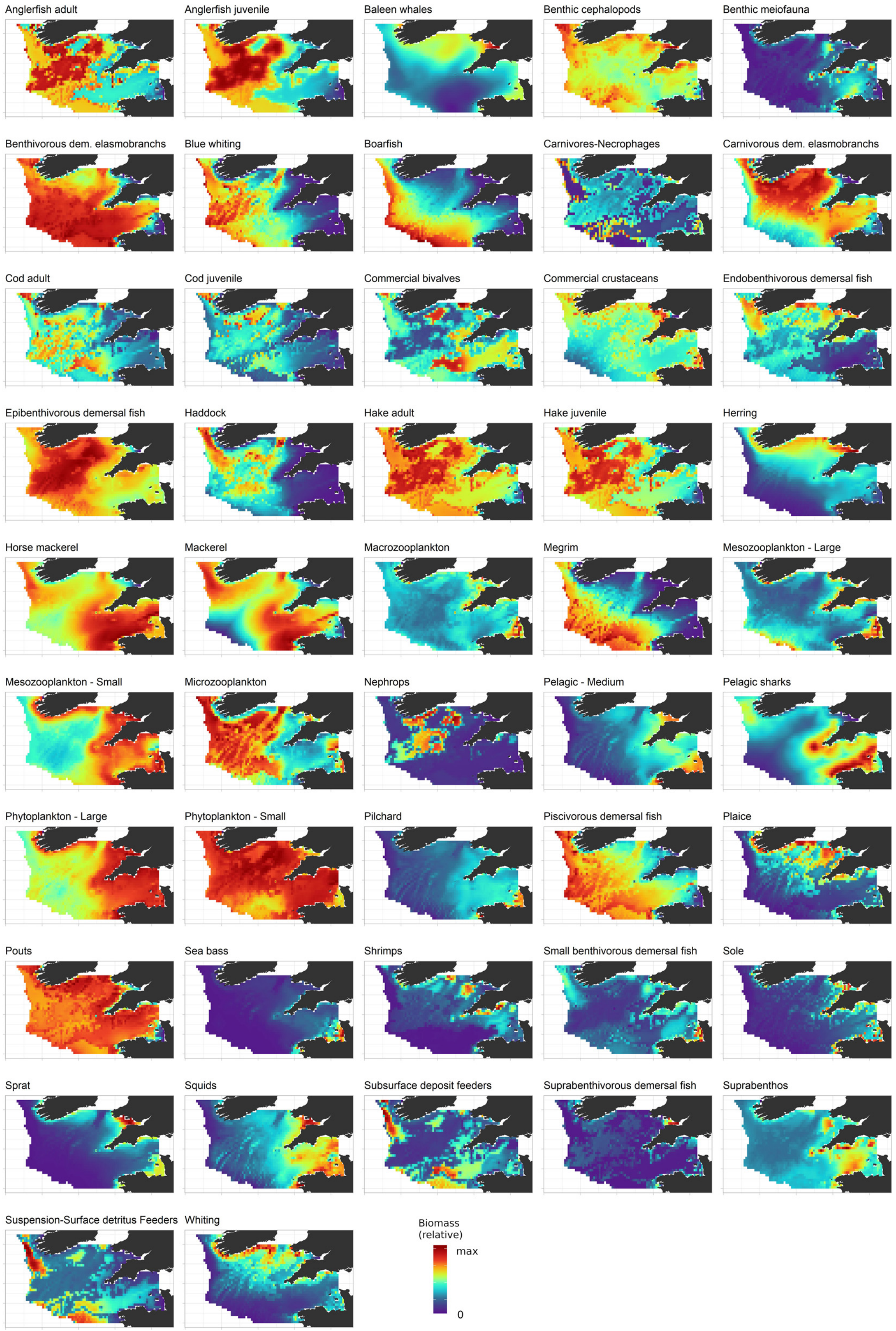

FIGURE 6 | Predicted biomass distribution in 2016 for functional groups for which statistical habitat models (generalized additive models) were developed. Biomass is represented in relative units, i.e., scaled on the highest density predicted in the Celtic Sea. The color scale represents the relative abundance of the considered group, from zero (blue) to the maximum (red).

predicted to be the most widely distributed monospecific groups in the Celtic Sea ecosystem (**Figure 6**). Other fish groups that were predicted to occupy a large fraction of the Celtic Sea were multispecific groups such as benthivorous elasmobranchs, epibenthivorous demersal fish, pouts (*Trisopterus minutus* and *T. luscus*) and benthic cephalopods, which are all made of several species and, therefore, display a broader, composite ecological niche. By contrast, some species were predicted to occupy only a relatively small fraction of the Celtic Sea ecosystem. This was particularly the case for benthic groups, which are highly dependent on the seabed substrate. For instance, the distribution of Norway lobster (*Nephrops norvegicus*) was restricted to muddy patches in the western part of the central Celtic Sea where the species can more easily bury in mud. Ecospace modeling allowed us to distinguish between groups that have similar trophic niches but different environmental niches. Thus, sole and plaice have similar diets but showed limited spatial overlap because of their, respectively, warm and cold water affinities; the same was observed for sardine (*Sardina pilchardus*) and herring. Species that are taxonomically close such as the gadoids cod, haddock and whiting were shown to regularly coexist in the same areas but could also have substantially different distributions: whiting inhabited shallower areas than cod and haddock; both haddock and cod had affinities for muddy areas, but haddock also frequented sandy substrates whereas cod preferred coarse sediments. The distributions of adults and juveniles for hake, anglerfish and cod were comparable yet exhibited some differences (i.e., juveniles showed a greater affinity for muddy substrates), which highlighted the relevance of representing multiple stanzas for some species in Ecospace to better simulate changes in spatial distribution and predation pressure over fish life cycle and the potential for cannibalism.

Species Assemblages

The distribution of functional groups provided a view on fish community assemblages in the Celtic Sea ecosystem. Very coastal areas and bays around Ireland, United Kingdom and France and the inner Bristol Channel were found to be inhabited by functional groups tolerant to low salinities, such as large concentrations of benthic invertebrates, small benthivorous organisms and, upper in the surface, suprabenthivorous and small epipelagic fish (i.e., herring, sardine, sprat). Higher trophic levels in these areas were mainly represented by whiting and sea bass. Also, intense primary and secondary pelagic production took place in these areas. Areas next to the shelf edge, located from the tip of Brittany to southwestern Ireland, were characterized by deeper waters with a steeper slope. Here, abundant populations of megrim, hake, anglerfish and other piscivorous demersal fish were found together with widely distributed pelagic fish species such as boarfish, blue whiting (*Micromesistius poutassou*), mackerel and horse mackerel. Benthic invertebrates in these areas were mainly deposit and suspension feeders. Primary production was observed limited in these areas, but the pelagic habitat was favorable to zooplankton development. In the cold central and northwestern Celtic Sea, the mix of sediment types and the moderate depth was favorable to diverse demersal species, including epibenthivorous demersal fish, hake, anglerfish and three gadoid species, cod, haddock and whiting. Mackerel and horse mackerel were the dominant pelagic species in this area. The density of benthic carnivores and necrophageous invertebrates was especially high in this area. Finally, the Western English Channel and the outer Bristol Channel differed from the other regions of the Celtic Sea by their relatively warm waters and coarse substrate and their higher plankton productivity sustained by mesoscale structures. The Western English Channel and the outer Bristol Channel were characterized by the presence of small benthivorous fish, epibenthivorous fish, pouts, flatfish (plaice and sole), commercial invertebrates (crustaceans and bivalves), cephalopods species, some gadoid species, and a mix of pelagic species including mainly horse mackerel and mackerel but also small epipelagic species.

Temporal Changes in Functional Groups' Distributions

Overall, relative habitat capacity was constant for most functional groups over the study period. Most changes in relative habitat capacity occurred between the late 1980s and the mid-1990s (**Figure 7**). The intensity of changes was variable across functional groups and can be related to the water temperature preferences of functional groups. The fitted GAMs indeed highlighted that temperature, which is the variable most affected by climatic changes in the area, was an ecological niche descriptor common to almost all components of the ecosystem. Thus, changes in the modeled habitats over the studied period were observed for those functional groups with most extreme thermal preferences in the Celtic Sea such as pilchard (*Sardina pilchardus*), sea bass, medium pelagic fish and squids (mainly or exclusively composed of Lusitanian species), as well as cod, haddock, sprat, herring, endobenthivorous fish and whiting (mainly or exclusively composed of Boreal species).

Functional groups dominated by Boreal species illustrate biomass distribution changes related to environment (**Figure 8**). Most changes in the distribution of species that prefer cold waters occurred early in the study period, with a slight contraction of the area occupied by these species in the eastern and southwestern Celtic Sea in response to the more intense warming of already warm bottom waters in those areas. For the remainder of the study period, the relative distribution of biomass of Boreal species remained relatively stable.

Ecosystem Indicators

Primary production in the Celtic Sea (**Figure 9A**) was essentially located in coastal areas, from the southern coast of Ireland to the Western English Channel and western Brittany, and along the southern part of the Celtic Sea shelf break. Differences in primary production between the lowest and the highest productive areas never exceed a factor of four. The biomass of secondary producers (i.e., zooplankton and benthic invertebrates that not carnivorous; **Figure 9B**) was more spread over the shelf and did not display similarly high densities in the center of the Western English Channel. The total biomass of high trophic level groups (i.e., TL ≥ 3; **Figure 9C**) was less variable over space and more patchy. The biomass of primary and secondary producers in the Celtic

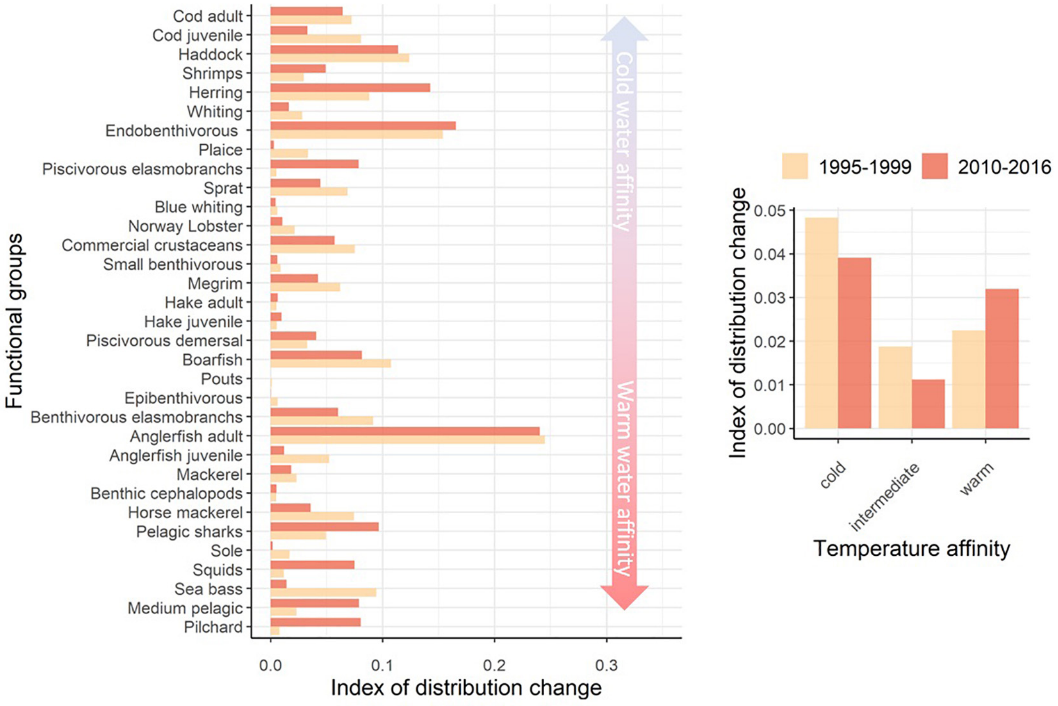

FIGURE 7 | Index of change in the spatial distribution of functional groups' habitat in relation to their thermal preferences between the 1985–1989 and 1995–1999 periods and between the 1985–1989 and 2010–2016 periods: Left: Values by functional group and averages over functional groups according to their temperature preferenda (cold, warm and intermediary corresponding to groups with thermal preferendum lower than, higher than, or within the range of temperatures in the Celtic Sea, respectively). The index is the absolute difference between 1 and the slope of the linear regression between Ecospace model cells' values of relative habitat for the 1985–1989 period and the two other periods. Right: mean index per group of thermal affinity, "cold," "intermediate," and "warm" for species with thermal preferendum, respectively, inferior, within, and superior to the temperature range covered in the Celtic Sea over 1985–2016.

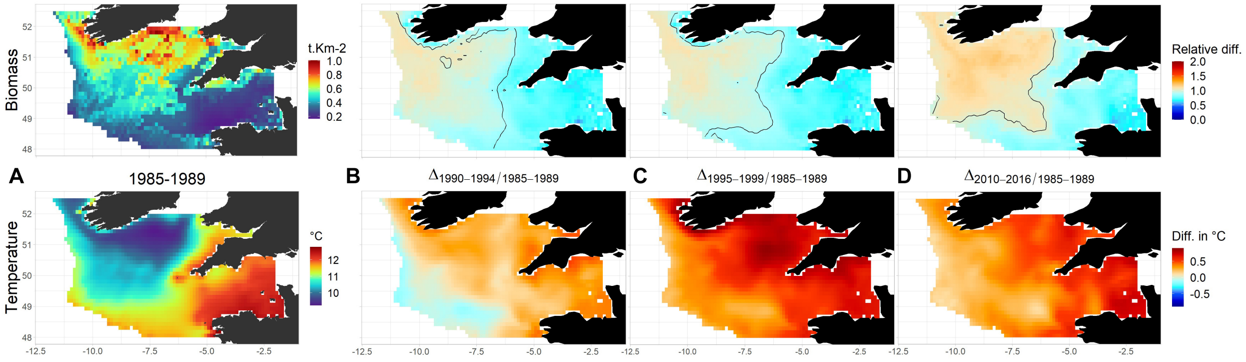

FIGURE 8 | Predicted changes in the total biomass of Boreal demersal species. **(A)** Mean biomass distribution (t.km^{-2}) for the period 1985–1989 and temperature (°C) for the same period. Relative changes of Boreal demersal species biomass are displayed in **(B)** 1990–1994; **(C)** 1995–1999; **(D)**: 2010–2016 and calculated as the ratio between these selected periods and the initial biomass. In **(B–D)** the colors correspond to the ratio of absolute biomass between the predicted biomass and biomass for 1985–1989. The black lines delimit areas for which the fraction in the total Celtic Sea Boreal demersal species biomass increased ("+" area) and decrease ("–" area) compared to 1985–1989.

Sea was concentrated around particular areas, mainly around the coasts and in the English Channel, and this available production is efficiently transferred to higher trophic levels and then likely spread horizontally.

The spatialized mean trophic level (MTL) and high trophic index (HTI) highlighted that higher trophic levels were mainly located in the western Celtic Sea. In particular, high values of the MTL were concentrated in the northwestern Celtic Sea, whereas the HTI is higher in deeper areas along the shelf-break (**Figure 10**, left panel). Areas associated with a high MTL were those areas that were occupied by many medium to large demersal functional group including epibenthivorous and piscivorous fish,

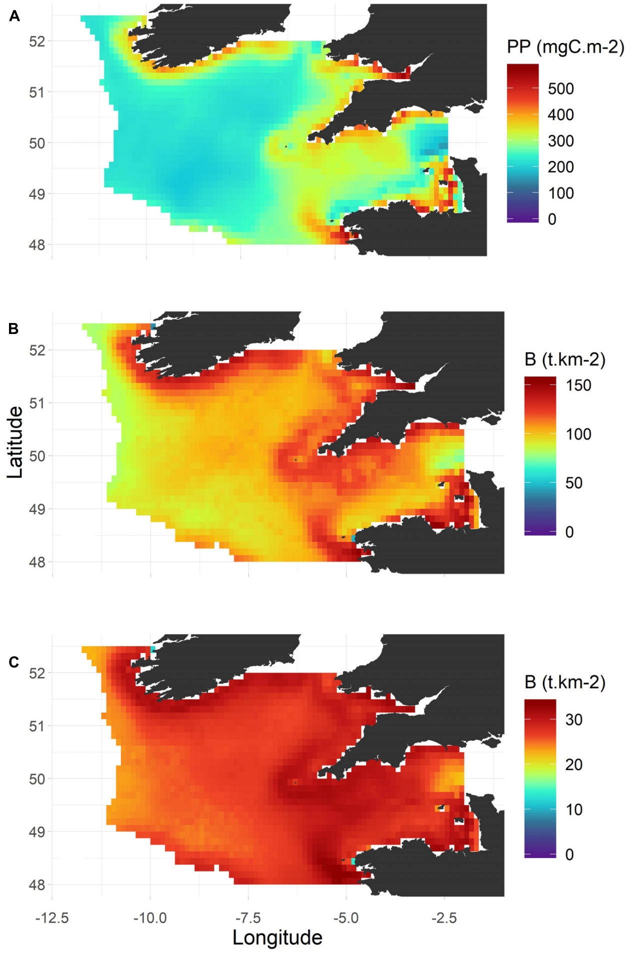

FIGURE 9 | Primary production in the Celtic Sea and biomass for trophic levels 2–3.5 and greater than 3.5 in 1985. **(A)** Primary production; **(B)** total biomass for trophic levels 2–3.5; **(C)** total biomass for tropic levels greater than 3.

elasmobranchs, gadoids, anglerfish and hake. Areas characterized by a high HTI were those where the biomasses of hake, megrim and anglerfish were high. In the eastern part of the Celtic Sea, the MTL was lower, due the large abundance of small demersal fish species feeding on benthic invertebrates (e.g., sole, plaice, small benthivorous fish) in this area, particularly medium and epipelagic species, which dominate in the Western English Channel. In the eastern part of the Celtic Sea, top-predators were mainly represented by large pelagic sharks and sea bass.

The Kempton's index highlighted spatial patterns in functional group diversity. Spatial patterns in functional group diversity were independent from that of biomass levels. For instance, mean values of Kempton's index were found in areas with either low total biomass (shelf-break) or high total biomass (fronts and muddy areas) densities. Functional group diversity was found to be particularly high at the border between the main Celtic Sea regions identified previously. The SOI was similar but not identical to the Kempton's diversity index. It was highest in the northwestern part of the central Celtic Sea, which was inhabited by generalist species and species that can feed on both benthic invertebrates and fish, including gadoids and anglerfish, but not hake which primarily feeds on medium-sized pelagic fish.

All the indicators displayed measurable variations over time and space (**Figure 10**, middle panels). The trends in the HTI and MTL were in opposed directions, which means that the ratio of low trophic level biomass to total biomass increased overall but that, in parallel, the proportion of species with a TL greater than 4 increased. These results were mainly driven by the dramatic changes in horse mackerel and hake abundances that occurred over the study period, while, after a deep depletion, the abundance of most mesopredator in the 2000s returned to levels similar to the 1980s. For the HTI and MTL, the direction of the change was the same among Ecospace cells, partly because the species driving observed changes were widely distributed in the Celtic Sea region. Trophic diversity declined overall over the whole Celtic Sea, especially in coastal areas. While functional groups diversity also declined in the southern Celtic Sea and the English Channel, it increased in the northwestern part of the central Celtic Sea. The standard deviations of the four indices (**Figure 10**, right panels) highlighted a measurable modification of the whole structure of the Celtic Sea ecosystem over the period 1985–2016, yet some specific areas were more affected than others. In particular, the food-web structure of the central Celtic Sea displayed substantial changes between 1985 and 2016, which were reflected by both an increase in MTL and a decrease in HTI and SOI. The standard deviation of spatial indices relative to their mean value also suggests a greater amplitude of changes occurred in the Kempton index.

DISCUSSION

Integrating Multiple Data Types for More Ecological Realism in Trophic Models

The data types integrated in the Celtic Sea EwE model significantly improved its ability to represent the functioning of the Celtic Sea ecosystem by providing a more relevant picture of the food-web structure and by depicting more realistically the drivers that rule its dynamics, and notably the environmental drivers.

Improving the Description of Food-Web Components and Interactions

To ensure that a food-web model correctly represents the temporal and spatial dynamics of an ecosystem, trophic relationships have to be defined as accurately as possible, through the combined use of classical and novel analyses (Pethybridge et al., 2018; McCormack et al., 2019). In this study, the use of outputs of the EcoDiet model (Hernvann et al., in press) applied to the stomach contents and biotracers compiled within the recent and extensive EATME project was advantageous to provide a reliable diet matrix to Ecopath, in better agreement with local data than by the use of literature alone. Additionally, the substantial collection of data compiled for the present study [115 time-series versus 62 in Moullec et al. (2017)] provided new

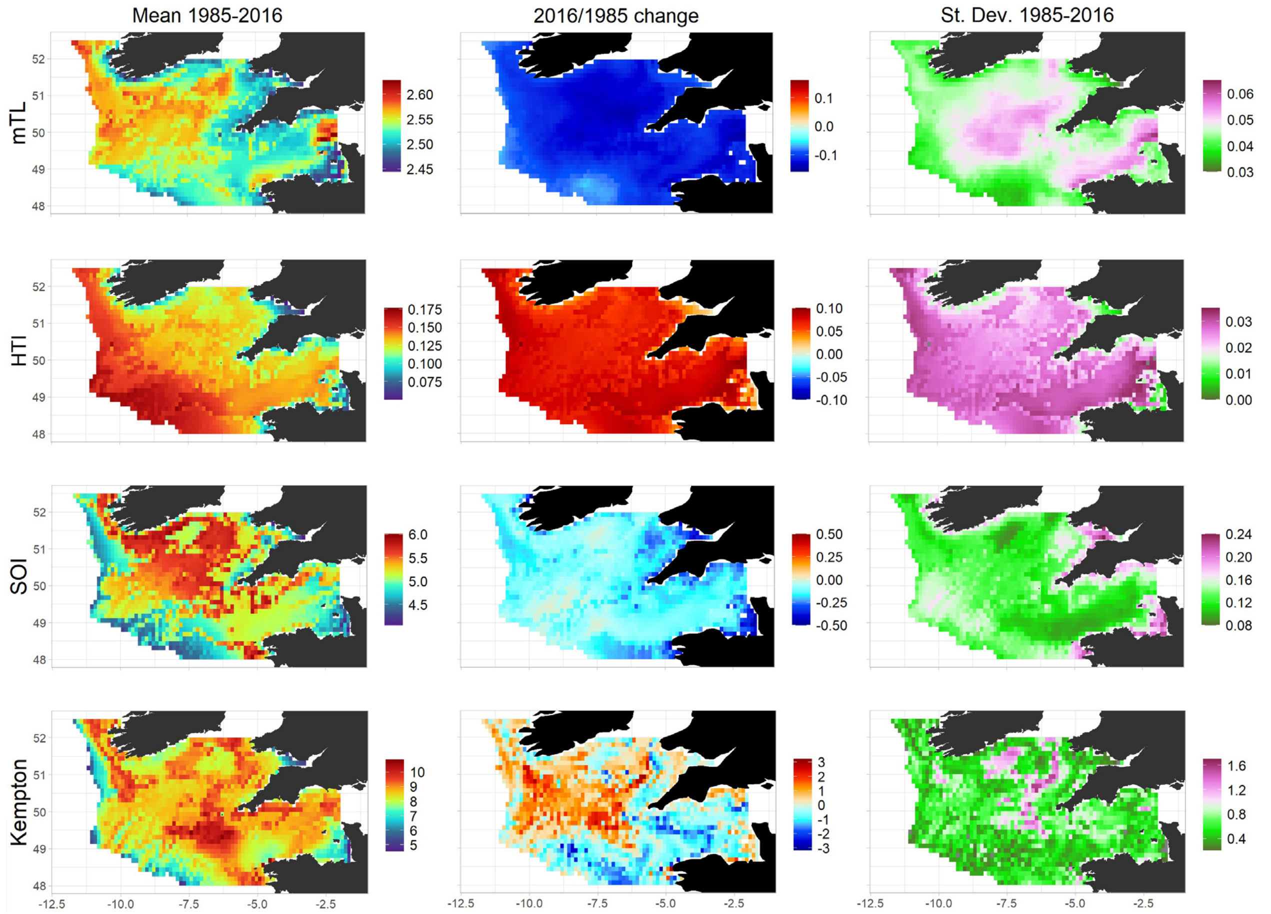

FIGURE 10 | Mean values, change and variability in four ecosystem indicators in the Celtic Sea over the period 1985–2016. Mean trophic level MTL (1st line), high trophic index HTI (2nd line), system omnivory index SOI (3rd line) and Kempton's diversity index (4th line) as spatialized in Ecospace, **(left panels)**, their change (difference) between 1985 and 2016 **(middle panels)**, and their standard deviation calculated over the period 1985–2016 **(right panels)**.

insights on the abundance trends of some food-web components, hence allowing the Celtic Sea EwE model to better capture ecosystem dynamics. Though the integration of abundance time-series for multispecific groups in EwE was informative, the dynamic of these groups remained poorly understood compared to the dynamic groups under stock assessment. Gathering relevant time-series of fishing effort for the period 1985–2016 for multispecific groups would greatly improve the hindcast. However, the large diversity of gears and métiers from many countries operating in the Celtic Sea makes this endeavor particularly challenging.

Primary and Secondary Production

The integration of primary and secondary production related data in EwE only slightly improved the fit of the Ecosim model. The reason for such a low improvement was the absence of clear variation of primary and secondary production in the time-series. This suggested a relative stability of the hydro-climatic conditions in the Celtic Sea between 1985 and 2016 as the main driver of plankton development. PP and ZHS integration allowed a better hindcast for pelagic functional groups, especially for zooplankton and some planktivorous fish, both for trends and interannual fluctuations, while trends in phytoplankton abundance were poorly reproduced. This poor fit for phytoplankton groups illustrates the difficulty to represent plankton prey-predator interactions and zooplankton grazing pressure in EwE models and the consequence this may have on the prediction of higher trophic levels. Here, high productivity and biomass levels of phytoplankton prevent their control by top-down process and limit their variation in abundance to a very low amplitude. Despite this lack of realism on the dynamic of phytoplankton, the information brought on the bottom-up impact of PP and the development conditions for zooplankton well complemented the insight on top-down impact exerced by higher trophic levels on these secondary producers.

Remote sensing data have been increasingly utilized over the last two decades in marine ecology studies (Chassot et al., 2011). The use of satellite-derived PP estimates is relatively common in marine ecosystem modeling (Christensen et al., 2009; Abdou et al., 2016; Grüss et al., 2016) and has the potential to become a routine procedure in new generations of ecosystem models (Lowerre-Barbieri et al., 2019). The main advantages of satellite-derived PP estimates are that they derived from a direct observation and they are accessible at high spatial resolution, given that regional biogeochemical models are not always locally available. However, satellite-derived PP estimates are only available for recent past (the past two decades) and, so far, they have not been calibrated to provide values for different size classes of phytoplankton (Kramer et al., 2018). In particular, CPR data suggested that the phytoplankton community went through measureable changes in the Celtic Sea over the period 1982–2016: The PCI index, proxy of the total standing biomass, increased, while no significant trend was detected in the diatom and dinoflagellate (both included in large phytoplankton group) counts, which suggested an increase in the biomass of nano-phytoplankton between 1985 and 2016.

Despite the relatively short temporal availability of the mesozooplankton niche model of Druon et al. (2019), the endeavor of integrating it in the food-web model turned out to be particularly promising. In particular, estimates from the mesozooplankton niche model allowed us to highlight areas of the Celtic Sea that are favorable to primary production but not to secondary production, and to identify regions with lower food availability for high trophic levels or where the grazing pressure exerted on zooplankton is important. Since the early 2000s, several end-to-end ecosystem models have coupled low and high trophic level models (i.e., have implemented on-line two-way coupling), hence allowing for a better representation of bottom-up and top-down controls within marine ecosystems (Travers et al., 2009, 2007). However, only a few ecosystem modelers have managed to implement an on-line two-way coupling, and it has been more common to develop alternative ways to link low trophic level and high trophic level dynamics (Libralato and Solidoro, 2009; Piroddi et al., 2017), such as forcing the high trophic level model with outputs from a biogeochemical model (e.g., Halouani et al., 2016). In this context, forcing future ecosystem models by observation-based primary productivity and zooplankton habitat would represent a valuable and conservative alternative approach.

Habitat Modeling

The habitat modeling framework adopted in this study that relied on GAMs was used to assess and predict the response of almost all high trophic level groups to warming and to project the abundance and distribution of each group in the Celtic Sea. The habitat-derived functional response to temperature significantly improved the fit of the Ecosim model. Here again, the improvement of model fit was relatively low, as surface and bottom temperatures appeared to be stable over a substantial fraction of the study period. Still, this improvement was substantial for those functional groups that can cope with extreme temperatures, i.e., which have their temperature optimum outside out of the range of temperature values occuring in the Celtic Sea ecosystem (e.g., plaice, cod and sardine).

Despite their interest in predicting past, current, and future species distributions, habitat modeling approaches have still been rarely coupled to ecosystem models (Grüss et al., 2016; Coll et al., 2019; Moullec et al., 2019b). In this study, we successfully integrated the outputs of a statistical habitat model into a spatial trophic model. The limited complexity of the GAM smoothers employed here, together with the choice of modeling probabilities of presence and not abundances with the GAMs, are in line with the ecological niche theory (Citores et al., 2020). The European IBTS survey data employed in this study encompassed a large range of environmental values, hence providing insights into the potential response of species groups to the warmer conditions that could become the norm in the Celtic Sea by the end of the century. The European IBTS survey dataset recently proved to be highly valuable to study species distributions (Baudron et al., 2020; Moriarty et al., 2020) and characterize ecosystem functioning (Maureaud et al., 2019). The methodology developed by Grüss et al. (2018, 2020) can integrate as many variables as desired (e.g., variables measured at different locations of the water column, percentages of different substrate types) and can be applied to any particular representation of functional groups, including multistanza groups. Thus, the approach of Grüss et al. (2020, 2018) is an interesting alternative to the classical and less flexible automatic approach used in Ecospace (Steenbeek et al., 2016) that imports information from AquaMaps (aquamaps.org), with more limited and much less accurate information (Jones et al., 2012).

Note, however, that habitat models quality remained acceptable but limited for multispecies benthic invertebrate groups, for which presence/absence data was limited here to a few French surveys due to the lack of availability and homogeneity for other surveys. This also stresses the need for improving large scale sampling for these compartments.

Are we Still Missing Something?

While calibrating the Ecosim model, several periods of time with a poorer fit were identified for different functional groups. Early changes in phytoplankton and zooplankton abundances were hardly reproduced by the Ecosim model. Ecosim failed to catch the great decline in small mesozooplankton abundance at the beginning of the time-series, as well as the decline in diatom and dinoflagellate abundances and the increase in nanophytoplankton abundance. Although it could be due to wrong trends in PP estimated by the biogeochemical model in the absence of satellite-derived data, this could also be due to uncaptured environmental effects. This would be expected as our study period starts in 1985, only a few years before the occurrence of abrupt changes in the state of the Celtic Sea ecosystem (e.g., in terms of turbulence, temperature, salinity and plankton abundance) that were identified in a previous study (Hernvann and Gascuel, 2020), and as Ecosim is not capable of tackling such ecosystem regime shift dynamics (Walters et al., 1997; Tomczak et al., 2012). As the stability in the plankton-related time-series did not allow us to explain their dynamics, the oceanographic conditions limiting phytoplankton and zooplankton production may not be the main factors of the regime shift. Several hypotheses have been proposed for identifying the main drivers of the severe drop in mesozooplankton abundance that occurred in the Celtic Sea, including climate drivers or changes in ocean circulation, but the mechanisms responsible for these changes (mediating factor of phytoplankton-zooplankton interactions, direct mortality factor of zooplankton, changes in zooplankton species composition, changes in phytoplankton composition, etc.) remain elusive (Pitois and Fox, 2006). In this context, EwE modeling exercises that estimate artificial "primary production anomalies" may improve the fit of our Ecosim model (Mackinson et al., 2009; Araújo and Bundy, 2012; Bentley et al., 2019). The application of this specific procedure to the Celtic Sea EwE model provided an anomaly time-series significantly correlated to the North Atlantic Oscillation (NAO) index. Nevertheless, these developments were not included in this study as: (i) they did not allow us to better reproduce patterns in plankton abundance in the early years of the period 1985–2016; (ii) they may be confounded with environmental factors that may improve, for instance, fish recruitment; and (iii) they did not provide any indications on the mechanisms at stake.

From Temporal and Spatial to a Fully Spatio-Temporal

Note that a novel spatio-temporal framework, that integrates both temporal and spatial dimensions, has been developed by Steenbeek et al. (2013) and included into the EwE software. The present approach relies on the sequential development of temporal rather than spatial food-web model and does not treat both aspects simultaneously in the same framework. Thus, the changes in functional group abundance predicted temporally do not account for eventual mismatch between prey and predators spatial distribution. The consequences on the overall model predictions may remain limited here due to very limited changes in the distribution of functional groups. However, such novel version of Ecopath spatio-temporal framework should be considered to predict long-term changes in the Celtic Sea in a context of climate change, which would imply substantial shifts in species distributions at various rates according to the functional groups.

Spatial Patterns of Species Assemblages and Trophic Functioning in the Celtic Sea

Heterogeneity in Biological Production Influenced by Oceanography

The Ecospace model highlighted the heterogeneous spatial patterns of biological production in the Celtic Sea that are mainly driven by contrasting water mixing conditions over the study region. In coastal areas, inner Bristol and English Channel, well-mixed waters allow for early phytoplankton blooms in spring and high primary production during the year depending on nutrient influx/recycling (Pingree et al., 1976; Pingree, 1980; Jordan and Joint, 1984). The seasonally mixed waters spreading over the shelf of the Celtic Sea lead to lower primary production, which occurs later there and at a lower level than in coastal areas (Pingree, 1980; Hickman et al., 2012; Giering et al., 2019). Note however, that PP can be locally enhanced offshore by the combined effects of topography and tidally-induced vertical mixing (through internal waves at the shelf break; Sharples et al., 2007 and water current shear stress in shallow waters of the shelf). The resulting shelf-break front is well developed in South-West Celtic Sea and finer along the western shelf (Holligan and Groom, 1986; Druon et al., 2001; Joint et al., 2001). In shallower waters, the Ushant front (Pingree et al., 1982) occurs at the interface between the well-mixed and stratified waters of the shelf from the Brittany tip to the Western Channel while the Celtic Sea front (Simpson, 1976) lies between the Bristol Channel and the Irish Sea. According to literature, the most productive areas, and especially productivity fronts, were predicted to concentrate biomass over several trophic levels up to top-predators (Pade et al., 2009; Scales et al., 2014; Druon et al., 2019). Specific functional groups inhabiting the water column displayed aggregated biomass at their location such as mesozooplankton, mackerel and pelagic sharks, as observed at the Ushant front. As about 80% (upwelling) to 90% (oceanic waters) of the PP is transferred to detritus (Raymont, 1980; Joint and Williams, 1985; Parker, 1991), spatial patterns in PP would also affect benthic compartments. The low level of information on benthos in the present study however, prevents any conclusions about these aspects.

The spatial structuration induced by primary production was shown to propagate through the food web. However, except for the above-mentioned functional groups, the spatial contrast in productivity in the Celtic Sea generally dampens with increasing trophic level. The mismatch between higher trophic level species niche and highest primary productivity areas is more important for predators than for prey. In other words, trophic flows progressively operate a biomass transfer from restricted productive areas to lower productive areas in the Celtic Sea. Biomass transfers across the shelf are mainly operated through functional groups characterized by wide ecological niches and large dispersal rates (one input parameter of Ecospace; Romagnoni et al., 2015) such as medium pelagic species mackerel, horse mackerel, pouts and large piscivorous predators in the Celtic Sea. For such functional groups, Ecospace enables the representation of locally enhanced biomass production due to a higher availability of resources when accounting for dispersal toward more suitable environments (Christensen et al., 2014). Thus, through this modeling framework, we highlighted that high fish densities could be maintained in low productive areas of the Celtic Sea through subsidization by prey and predators movements (Polis et al., 1997, 1996) and transport through residual tidal currents.

Spatial Variation in Functional Groups Assemblages

In agreement with previous *in situ* studies, the functional groups' distributions predicted by the Ecospace model highlighted the existence of different species assemblages in the Celtic Sea. The species assemblages of the inner Bristol Channel and coastal areas corresponded to those described by Ellis et al. (2000); Kaiser et al. (2004) and Martinez et al. (2013), and these assemblages included herring and sprat as dominant pelagic species, flatfish [plaice, sole, dab (*Limanda limanda*)], gadoids whiting and pouts, demersal sharks and rays (e.g., catshark *Scyliorhinus canicula*, rays *Raja* sp.), gurnards (*Eutrigla* sp.), small fish (e.g., dragonets *Callionymus* sp.), large crustaceans (e.g., *Maja squinado*) and small crabs, pagurids and shrimps. The central Celtic Sea assemblages identified in this study match those reported in Ellis et al. (2013) and Martinez et al. (2013) and are characterized by many gadoid species, including whiting, haddock, pouts and cod, as well as by shrimps. As the present study, Ellis et al. (2013) and Martinez et al. (2013) also characterized the demersal assemblage of the Celtic Sea shelf-edge as being comprised of hake, megrim, anglerfish, pouts, mesopelagic species such as *Argentina sp*., and benthic cephalopods. The large abundances of pelagic species such as mackerel, horse mackerel, boarfish and blue whiting on the Celtic Sea shelf-edge that were also predicted in this study are consistent with the findings of Reid (2001) and Trenkel et al. (2014).

In agreement with Rees (1999), we found that the Western English Channel displays a particularly diverse benthic assemblage that includes large crustaceans and commercial bivalves [Kaiser et al., 1998; e.g., king scallop (*Pecten maximus*), queen scallop (*Aequipecten opercularis*)], as well as suprabenthos (Vallet and Dauvin, 1998). The preponderant community of pelagic species in the Western English Channel has been carefully screened for decades (Southward et al., 1988; Hawkins et al., 2003). The spatial patterns of abundance of most demersal species predicted in this study were consistent with those derived from English Celtic Sea groundfish survey data (Warnes and Jones, 1995; Tidd and Warnes, 2006), even though the latter were not employed for statistical habitat modeling in this study.

Heterogeneous Species Assemblages Result in Different Local Food Webs

The different species assemblages of the Celtic Sea identified in this study provided some new insights to the possible spatial structure of the food web in the Celtic Sea region. While some functional groups are widely distributed, some others are only present in some specific areas of the Celtic Sea and their absence or negligible biomass at particular locations may be interpreted as reflecting local reorganizations of the food web. Thus, the complex Celtic Sea food-web structure could be interpreted as a meta food web made of local, environmentally-driven, food webs connected through space by functional groups with larger dispersion capacities (Kortsch et al., 2019, 2015). Ecospace reveals to be a useful tool to understand the spatial structure of food webs as a complement to more qualitative approaches for characterizing the trophic structure of marine ecosystems (Albouy et al., 2014; Pellissier et al., 2018; Kortsch et al., 2019). Spatial indicators can be produced with Ecospace to determine the spatial structure of the food web in relation to the environment. Our results suggest that shallowest and least saline (affected by rivers) waters of the Celtic Sea, together with the deepest waters of the region, are characterized by a low number of compartments and groups with relatively low variability in terms of TL. The two above-mentioned areas are, however, radically different in terms of functioning. The latter is dominated by a specific trophic pathway where top-predators (i.e., hake, megrim) in high density feed on abundant pelagic species (i.e., blue whiting, boarfish). The former, in deeper environments, is essentially represented by low trophic level benthic and pelagic functional groups with non-diversified diets. The distinction made between the two areas does not exclude the existence of important benthic-pelagic coupling in both areas, but this coupling may be due to the reliance on pelagic primary production rather than to exchanges between upper trophic level species. Intermediate-depth areas of the Celtic Sea were found to be dominated by pelagic functional groups, yet they displayed large concentrations of benthopelagic fish feeding on the benthos and pelagos. Finally, the central Celtic Sea was found to be dominated by predatory and generalist functional groups that feed on both pelagic and benthic compartments, which may render this specific area more stable than the rest of the Celtic Sea. Spatialized indicators highlighted that boundaries between these different areas constituted ecotones, characterized by higher functional group and trophic diversity as they suited to a wider range of species.

The Limited Perception of the Mean Annually-Averaged Ecosystem Functioning

The spatio-temporal dynamic model of this study represents the trophic functioning of the Celtic Sea ecosystem averaged over a year. We proceeded this way because of data availability for model calibration (i.e., survey-derived abundance indices, stock assessment products, and catch statistics). Averaging trophic interactions can be questionable, as trophic functioning over the year is strongly related to seasonal variations in plankton production. These variations are mainly associated with hydrographic features and water mixing processes. In addition, seasonal movements, and subsequent changes in spatial distributions and local abundances have been highlighted for both pelagic [widely distributed pelagic fish (Trenkel et al., 2014) and coastal to a lower degree (Brophy, 2002)] and demersal communities (Dunn and Pawson, 2002; Persohn et al., 2009; Neat et al., 2014). These movements can notably be related to feeding, spawning and overwintering.

Seasonal changes in distributions would explain the variability of fish diets in the Celtic Sea reported in Trenkel et al. (2005) and Chassot et al. (2008). For instance, large Celtic Sea predators consume more blue whiting during the summer and more mackerel during the winter, whereas the consumption of horse mackerel is relatively constant throughout the year. However, modeling changes in fish spatial distributions at a finer temporal scale remains a challenging issue given the data that are available to us.

More Insights Into the Dynamic of a Shelf Ecosystem Under Multiple Environmental and Anthropogenic Pressures

The Celtic Sea Ecosim model best explained the food-web dynamics when it integrated trophic interactions, fishing, environmental conditions controlling plankton production, and warming as a driver of the productivity of higher trophic level groups. The way the Ecosim model fitted to data when different data types were integrated provided a better understanding of the relative impacts of fishing and environmental changes on the Celtic Sea ecosystem during the three last decades.

Fishing on the Frontline

Previous work based on catch and effort reconstruction highlighted the large impacts that fishing has had on the Celtic Sea ecosystem since 1950 (Pinnegar et al., 2002; Guénette and Gascuel, 2012; Hernvann and Gascuel, 2020). In particular, the dramatic increase in fishing pressure that has occurred in the

Celtic Sea region over several decades may have drastically reduced the biomass of large predators and may have triggered the deep alteration of the food-web structure through trophic cascades (Hernvann and Gascuel, 2020). The impacts of fishing in the Celtic Sea ecosystem suggested by the present study concur with the conclusions of previous EwE modeling works in the ecosystem by Bentorcha et al. (2017) and Moullec et al. (2017). At the beginning of our study period, in 1985, the biomass of main large bentho-demersal fish and predator species had already been severely impacted by fishing and pelagic and invertebrate fisheries started developing in the Celtic Sea region. Then, between 1985 and 2016, fishing kept on severely impacting the Celtic Sea ecosystem. Despite the integration of environmental variability in the Ecosim model, our findings suggest that fishing had more profound impacts on the Celtic Sea ecosystem than environmental changes.

Compared to previous versions of the Celtic Sea EwE model, the present Ecosim predictions were more accurate due to the use of new survey data (EVHOE and UK-WCGFS) which allowed for a better description of the indirect effects of fishing in the Celtic Sea EwE model. The divergent abundance time-series for smaller and larger fish groups, which increased and decreased, respectively, over the period 1985–2016, were better identified in this study than in the studies that employed previous versions of the Celtic Sea EwE model. The analysis of the mortality estimates suggested that the driving factor of trends in mortality was predation release on smaller species, due to both the continuously increasing pressure exerted on large predatory fish and the reallocation of fishing effort on medium fish in response to the depletion of to large predators. These results concur with the hypotheses formulated in community size-structure studies (Blanchard et al., 2005; Shephard et al., 2012, 2011). Though this phenomenon was only described for demersal species, the large decline in the biomass of horse mackerel in the beginning of the 1990s predicted in this study (a 6-fold decline within only a 10-year time frame resulting from a large increase in fishing effort on horse mackerel) may have also contributed to the increasing biomass of smaller species. This may probably be the case (horse mackerel leaving a vacant niche) for other small pelagic species, such as boarfish to boom in the early 2000s, as observed by Blanchard and Vandermeirsch (2005) and Coad (2012) and also correlated to changes in the temperature. Thus, fishing appears as the main driver of changes in species assemblages in the Celtic Sea, especially leading to a decrease in the diversity of diets and a general decline in the mean trophic level in the area.

Finally, the biomass recoveries initiated in the Celtic Sea over the recent period were particularly noticeable, and these biomass recoveries seemed to allow for a progressively increasing dominance of demersal species in the Celtic Sea ecosystem and a rise of the predation pressure exerted on smaller demersal fish, crustaceans, and cephalopods as highlighted by the biomass decline of the latter and the increase in the HTI index.

Climate Change in Ambush

The importance of the fishing driver in the Celtic Sea contributed to mask the impacts of environmental changes on the ecosystem. Indeed, many abundance trends of exploited groups reflected stock depletions and recoveries independently of warming effects. The dominance of the fishing driver in observed time series is consistent with the lack of evidence of any warming effect in the Celtic Sea from studies that analyzed species biomass trends or community size-structure (Genner et al., 2004; Blanchard et al., 2005). However, through the use of GAM predictions and temperature forcing, we were able to account for the cumulative impacts of fishing and environment changes in EwE and to disentangle the relative contributions of these different drivers of change. The mid-1990s were characterized by a net warming of the Atlantic Ocean that was attributed to a shift of the Atlantic Multidecadal Oscillation (AMO) from a negative to a positive phase, which was likely amplified by anthropogenic climate change (Ting et al., 2009). As a response to this large-scale warming events, both sea surface and bottom temperatures in the Celtic Sea increased. The Celtic Sea EwE with Ecospace model suggests that these temperature changes led to a decrease in the productivity of most of Boreal species, including herring, sprat, cod, whiting and haddock, and to an increase in the productivity of functional groups with warm water affinity, particularly species with extreme thermal preferenda such as sardine, sea bass, mixed medium pelagic fish [mainly anchovy (*Engraulis encrasicolus*)] and cephalopods, and to a lesser extent, widely distributed pelagic species such as mackerel, horse mackerel and boarfish. In future years, these trends in species productivity may impair the recovery of some current commercially important species (i.e., gadoids) and oblige fishers to target less exploited warm-water species. Additionally, the species distributions predicted by Ecospace indicated a relative concentration of Boreal species' biomasses in a smaller area around the mid-1990s. This modification of Boreal functional groups' distributions persisted until the end of the study period and resulted from a contraction of these groups' niches induced by warming. If the scale of these changes was limited, it confirmed the response of these species to climate change, which was barely detectable in temporal trends. The niche contraction of demersal Boreal species in the south of the Celtic Sea was associated to an increase in functional groups diversity, related to the largest proportion of biomass represented by species with warmer water affinities. The latter, the trophic diversity declined in response to change in assemblage, being mainly benthivorous and of low trophic level.

These responses of functional groups' productivity and distribution to ocean warming predicted in this study were consistent with the findings of multiple fish community studies that were conducted across Europe for a large proportion of both demersal and pelagic species. In such studies, species were shown to respond to warming in the 1990s (Simpson et al., 2011; Montero-Serra et al., 2015). Changes were mostly correlated to species' preferred temperature and central latitude of their range so that the abundance or recruitment of cold water species decreased while that of warm water, widely distributed species increased (Poulard and Blanchard, 2005; Simpson et al., 2011; Auber et al., 2017, 2015; Bentley et al., 2020). If no homogeneous poleward shifts of the communities were highlighted over the European shelf (Dulvy et al., 2008; Simpson et al., 2011), the spatial distribution of numerous species was affected by warming

(Baudron et al., 2020), some displaying displacements of their center of distribution and others showing migration to deeper waters (Dulvy et al., 2008; Punzón et al., 2016). The potential changes in the distribution of species located south of the Celtic Sea or already present in low abundance in the Celtic Sea are responsible for the increase in species diversity observed by Hiddink and ter Hofstede (2008) and ter Hofstede et al. (2010).

The Relative Stability of the Celtic Sea Ecosystem

When spatializing fish communities' responses to warming over the European shelf, Simpson et al. (2011) pointed out that the Celtic Sea was less impacted than the neighboring areas. This result may be linked to the lower variability of Celtic Sea thermal conditions after the mid-1990s that resulted from the particular hydrographic situation of the Celtic Sea (i.e., Gulf Stream influence, Hughes et al., 2017; Tinker et al., 2020). However, the amplitude of warming in the mid-1990s suggested that local thermal conditions were not the only reason for the weaker response of the Celtic Sea ecosystem to warming compared to neighboring ecosystems. Ecospace results suggest that the greater stability of Celtic Sea communities may be due to the complex spatial structuration and high biodiversity of the Celtic Sea ecosystem. According to various theoretical and modeling studies, the meta-community organization of food webs may act as a stabilizer of trophic dynamics (McCann et al., 2005; Gravel et al., 2011; Mougi and Kondoh, 2016). The spatial arrangement of environmental gradients in the Celtic Sea is complex compared to other ecosystems where gradients are more correlated together (e.g., the Bay of Biscay, the North Sea). Additionally, though they are developed from collated data from multiple origins, harmonized seabed maps at the European scale indicate that substrate patchiness is higher than in neighboring ecosystems (e.g., the North Sea, the Eastern English Channel). The spatial structuration of the Celtic Sea ecosystem may favor a stable meta-community organization and allow for more resistance to the impacts of environmental changes. The complex spatial structure of the Celtic Sea may also reduce the probability of co-occurrence of "autochtonous" and a "allochtonous" species in the ecosystem, hence lowering the risks of competition between these two types of species if they have similar trophic niches. Finally, the substantial contribution of both benthic and pelagic pathways to matter flows in the Celtic Sea ecosystem may also participate in the stability of the ecosystem (Rooney et al., 2006; Blanchard et al., 2011).

We also found that the Celtic Sea is relatively stable in terms of basal productivity. As reflected by biogeochemical models and satellite-derived time-series, the oceanographic conditions favoring phytoplankton and zooplankton abundances over the study period remained overall constant. This may be due to the mechanisms involved in the production of mesoscale structures in the Celtic Sea that favor plankton production. Indeed, a substantial part of total primary production in the Celtic Sea is due to the tidally-induced semi-permanent mixing fronts that occur in the central part of the eastern Celtic shelf, i.e., the Ushant Front and the Celtic Sea Front. Contrary to other ecosystems in which productivity fronts are largely dependent on climatic conditions, tidal mixing fronts in the Celtic Sea can form simply under the mechanical action of wave activity, resulting in a more regular production in the Celtic Sea region, which is consistent with the production of mesozooplankton (Druon et al., 2019).

A Step Further Toward Ecosystem-Based Management?

This new EwE with Ecospace model of the Celtic Sea ecosystem represents a significant step forward in the integration of ecological realism in trophic modeling of the Celtic Sea ecosystem (Guénette and Gascuel, 2009; Bentorcha et al., 2017; Moullec et al., 2017). In the Celtic Sea, highly mixed-species fisheries catch a large diversity of fish assemblages and employ a large diversity of fishing techniques and strategies (Moore et al., 2019) that can result in highly different catch compositions for the same location over time (Martinez et al., 2013; Dolder et al., 2018). In this context, resource mapping and optimization of fishing practices in time and space have been identified as a critical need to reduce the ecosystem impacts of fishing in the Celtic Sea, e.g., by reducing unwanted catch (Dolder et al., 2018; Calderwood et al., 2019; Reid et al., 2019; Robert et al., 2019). The Celtic Sea Ecospace model reproduced the patterns observed during fisheries-independent surveys but also clearly identified the spatial structuration and species assemblages that were identified in some spatial studies of fisheries catch, based on logbooks and vessel monitoring systems (Gerritsen et al., 2012; Mateo et al., 2017).

The EwE with Ecospace model developed in this study represents a valuable tool for the spatial management of fishing activities in the Celtic Sea. In future studies, the Celtic Sea Ecospace model could be employed to produce multiple spatial food-web indicators to describe ecosystem status as part of ecosystem-based management (Tam et al., 2017), or to identify critical areas of the Celtic Sea in terms of diversity and functionalities (Babcock et al., 2005). As other ecosystem models, our EwE with Ecospace model could be also used to inform spatial zoning in the Celtic Sea (e.g., Kaplan et al., 2012; Abdou et al., 2016; Halouani et al., 2016) and other management regulations (e.g., relative to discarding practices, Pennino et al., 2020). Such framework can therefore provide great support to policies such as the Common Fisheries Policy (e.g., spatial fishing capacities) and the Marine Strategy Framework Directive (e.g., descriptor D3 commercially exploited fish, D4 food webs, e.g., Piroddi et al., 2015; Piroddi et al., submitted).

Although fishing appeared to be the main driver of changes in the Celtic Sea ecosystem over the three last decades, this may likely not be the case anymore in the future. While fishing pressure in the Celtic Sea region has been substantially reduced over the recent years and is still currently (slowly) declining, the relative stability of environmental conditions observed over the last two decades may likely not hold; projections of coupled physical and biogeochemical models under various CO_2 emission scenarios predict a global increase in surface and bottom temperatures and a decline in primary production in the Celtic Sea ecosystem (Kay et al., 2018). In this context, similarly to previous temporal or spatio-temporal ecosystem modeling studies (Serpetti et al., 2017; Corrales et al., 2018; Moullec et al., 2019a), the calibrated the Celtic Sea Ecospace model would be a powerful tool to project the potential impacts of climate change on the regional living resources and the fisheries that these resources support.

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. The Celtic Sea Ecopath model at the core of this study can be accessed from EcoBase, the open-access database of Ecopath with Ecosim (EwE) models published worldwide in the scientfic literature. EcoBase is an information repository of EwE models freely accessible online at http://ecobase.ecopath.org/ or via the EwE software.

AUTHOR CONTRIBUTIONS

P-YH designed the study, performed the main statistical analyses, and built and ran the ecosystem model. P-YH, J-ND, MR, DG, and IP provided and gathered the data used in the study. AG, J-ND, CP, and DG helped to and participated in designing and applying the habitat and trophic modeling approaches integrated in the present modeling framework. DG, MR, and DK contributed to the design of the integrated modeling framework. DG, MR, DK, AG, J-ND, CP, and IP contributed to results analysis and interpretation. This work was part of a Ph.D. project designed by DG, MR, and DK. P-YH led the drafting of the manuscript with the contributions and revisions from all the authors. All authors contributed to the article and approved the submitted version.

FUNDING

This work was part of a Ph.D. funded by the Région Bretagne and the French Institute for the Exploitation of the Sea (IFREMER). The temporary stay of the principal investigator at the Joint Research Center of the European Commission as part of this research project was funded by an international mobility grant from IFREMER.

ACKNOWLEDGMENTS

We are particularly grateful to the Joint Research Center of the European Commission who hosted the main investigator during his international mobility. We thank the CPR survey and David Jones for providing access to the plankton data. We also thank Dr. John Pinnegar (CEFAS) and Dr. Verena Trenkel (IFREMER) for access to the UK-WCGFS survey data.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.578717/full#supplementary-material

REFERENCES

Abdou, K., Halouani, G., Hattab, T., Romdhane, M. S., Frida Ben, and Le Loc'h, F. (2016). Exploring the potential effects of marine protected areas on the ecosystem structure of the Gulf of Gabes using the Ecospace model. *Aquat. Living Resour.* 29:202. doi: 10.1051/alr/2016014

Agnetta, D., Badalamenti, F., Colloca, F., D'Anna, G., Di Lorenzo, M., Fiorentino, F., et al. (2019). Benthic-pelagic coupling mediates interactions in Mediterranean mixed fisheries: an ecosystem modeling approach. *PLoS One* 14:e0210659. doi: 10.1371/journal.pone.0210659

Ahrens, R. N. M., Walters, C. J., and Christensen, V. (2012). Foraging arena theory: foraging arena theory. *Fish Fish.* 13, 41–59. doi: 10.1111/j.1467-2979.2011.00432.x

Ainsworth, C., and Pitcher, T. (2006). Modifying Kempton's species diversity index for use with ecosystem simulation models. *Ecol. Indic.* 6, 623–630. doi: 10.1016/j.ecolind.2005.08.024

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Trans. Automatic Control* 19, 716–723. doi: 10.1109/TAC.1974.1100705

Albouy, C., Velez, L., Coll, M., Colloca, F., Le Loc'h, F., Mouillot, D., et al. (2014). From projected species distribution to food-web structure under climate change. *Glob. Change Biol.* 20, 730–741. doi: 10.1111/gcb.12467

Araújo, J., and Bundy, A. (2012). Effects of environmental change, fisheries and trophodynamics on the ecosystem of the western Scotian Shelf, Canada. *Mar. Ecol. Prog. Ser.* 464, 51–67. doi: 10.3354/meps09792

Auber, A., Gohin, F., Goascoz, N., and Schlaich, I. (2017). Decline of cold-water fish species in the Bay of Somme (English Channel, France) in response to ocean warming. *Estuar. Coast. Shelf Sci.* 189, 189–202. doi: 10.1016/j.ecss.2017.03.010

Auber, A., Travers-Trolet, M., Villanueva, M. C., and Ernande, B. (2015). Regime shift in an exploited fish community related to natural climate oscillations. *PLoS One* 10:e0129883. doi: 10.1371/journal.pone.0129883

Audzijonyte, A., Pethybridge, H., Porobic, J., Gorton, R., Kaplan, I., and Fulton, E. A. (2019). Atlantis: a spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules. *Methods Ecol. Evol.* 10, 1814–1819. doi: 10.1111/2041-210X.13272

Babcock, E. A., Pikitch, E. K., McAllister, M. K., Apostolaki, P., and Santora, C. (2005). A perspective on the use of spatialized indicators for ecosystem-based fishery management through spatial zoning. *ICES J. Mar. Sci.* 62, 469–476. doi: 10.1016/j.icesjms.2005.01.010

Baretta, J. W., Ebenhöh, W., and Ruardij, P. (1995). The European regional seas ecosystem model, a complex marine ecosystem model. *Neth. J. Sea Res.* 33, 233–246. doi: 10.1016/0077-7579(95)90047-0

Barnett, A., and Semmens, J. M. (2012). Sequential movement into coastal habitats and high spatial overlap of predator and prey suggest high predation pressure in protected areas. *Oikos* 121, 882–890. doi: 10.1111/j.1600-0706.2011.20000.x

Baudron, A. R., Brunel, T., Blanchet, M., Hidalgo, M., Chust, G., Brown, E. J., et al. (2020). Changing fish distributions challenge the effective management of European fisheries. *Ecography* 43, 494–505. doi: 10.1111/ecog.04864

Beaugrand, G., Ibañez, F., and Reid, P. (2000). Spatial, seasonal and long-term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. *Mar. Ecol. Prog. Ser.* 200, 93–102. doi: 10.3354/meps200093

Behrenfeld, M. J., and Falkowski, P. G. (1997). Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr.* 42, 1–20. doi: 10.4319/lo.1997.42.1.0001

Bentley, J., Serpetti, N., Fox, C. J., Reid, D. G., and Heymans, J. J. (2019). *Modelling the Food Web in the Irish Sea in the Context of a Depleted Commercial Fish Community. Part 2: ICES Ecopath with Ecosim Key Run.*

Oban: Scottish Association for Marine Science. doi: 10.13140/RG.2.2.15136.12809

Bentley, J. W., Serpetti, N., Fox, C. J., Heymans, J. J., and Reid, D. G. (2020). Retrospective analysis of the influence of environmental drivers on commercial stocks and fishing opportunities in the Irish Sea. *Fish. Oceanogr.* 29, 415–435. doi: 10.1111/fog.12486

Bentley, J. W., Serpetti, N., and Heymans, J. J. (2017). Investigating the potential impacts of ocean warming on the Norwegian and Barents Seas ecosystem using a time-dynamic food-web model. *Ecol. Model.* 360, 94–107. doi: 10.1016/j.ecolmodel.2017.07.002

Bentorcha, A., Gascuel, D., and Guénette, S. (2017). Using trophic models to assess the impact of fishing in the Bay of Biscay and the Celtic Sea. *Aquat. Living Resour.* 30:7. doi: 10.1051/alr/2017006

Blanchard, F., and Vandermeirsch, F. (2005). Warming and exponential abundance increase of the subtropical fish Capros aper in the Bay of Biscay (1973–2002). *C. R. Biol.* 328, 505–509. doi: 10.1016/j.crvi.2004.12.006

Blanchard, J. L., Dulvy, N. K., Jennings, S., Ellis, J. R., Pinnegar, J. K., Tidd, A., et al. (2005). Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? *ICES J. Mar. Sci.* 62, 405–411. doi: 10.1016/j.icesjms.2005.01.006

Blanchard, J. L., Law, R., Castle, M. D., and Jennings, S. (2011). Coupled energy pathways and the resilience of size-structured food webs. *Theor. Ecol.* 4, 289–300. doi: 10.1007/s12080-010-0078-9

Bourdaud, P., Gascuel, D., Bentorcha, A., and Brind'Amour, A. (2016). New trophic indicators and target values for an ecosystem-based management of fisheries. *Ecol. Indic.* 61(Part 2), 588–601. doi: 10.1016/j.ecolind.2015.10.010

Brophy, D. (2002). Tracing populations of Atlantic herring (Clupea harengus L.) in the Irish and Celtic Seas using otolith microstructure. *ICES J. Mar. Sci.* 59, 1305–1313. doi: 10.1006/jmsc.2002.1304

Brunel, T., and Boucher, J. (2007). Long-term trends in fish recruitment in the north-east Atlantic related to climate change. *Fish. Oceanogr.* 116: 16, 336–349. doi: 10.1111/j.1365-2419.2007.00435.x

Calderwood, J., Robert, M., Pawlowski, L., Vermard, Y., Radford, Z., Catchpole, T. L., et al. (2019). Hotspot mapping in the Celtic Sea: an interactive tool using multinational data to optimise fishing practices. *Mar. Policy* 116: 103511. doi: 10.1016/j.marpol.2019.103511

Chase, J. M., and Leibold, M. A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches, Interspecific Interactions*. Chicago, IL: University of Chicago Press.

Chassot, E., Bonhommeau, S., Reygondeau, G., Nieto, K., Polovina, J. J., Huret, M., et al. (2011). Satellite remote sensing for an ecosystem approach to fisheries management. *ICES J. Mar. Sci.* 68, 651–666. doi: 10.1093/icesjms/fsq195

Chassot, E., Rouyer, T., Trenkel, V. M., and Gascuel, D. (2008). Investigating trophic-level variability in Celtic Sea fish predators. *J. Fish Biol.* 73, 763–781. doi: 10.1111/j.1095-8649.2008.01938.x

Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., and Walters, C. J. (2014). Representing variable habitat quality in a spatial food web model. *Ecosystems* 17, 1397–1412. doi: 10.1007/s10021-014-9803-3

Christensen, V., and Walters, C. J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model.* 172, 109–139. doi: 10.1016/j.ecolmodel.2003.09.003

Christensen, V., Walters, C. J., Ahrens, R., Alder, J., Buszowski, J., Christensen, L. B., et al. (2009). Database-driven models of the world's large marine ecosystems. *Ecol. Model.* 220, 1984–1996. doi: 10.1016/j.ecolmodel.2009.04.041

Christensen, V., Walters, C. J., and Pauly, D. (2008). *Ecopath with Ecosim version 6 user guide. Lenfest Ocean Futures Project 2008*. Vancouver: University of British Columbia.

Citores, L., Ibaibarriaga, L., Lee, D.-J., Brewer, M. J., Santos, M., and Chust, G. (2020). Modelling species presence–absence in the ecological niche theory framework using shape-constrained generalized additive models. *Ecol. Model.* 418:108926. doi: 10.1016/j.ecolmodel.2019.108926

Coad, J. O. (2012). *Boom in Boarfish Abundance: Insight from Otolith Analysis*. Available online at: http://ices.dk/products/CMdocs/CM-2012/J/J1012.pdf

Coll, M., Pennino, M. G., Steenbeek, J., Sole, J., and Bellido, J. M. (2019). Predicting marine species distributions: complementarity of food-web and Bayesian hierarchical modelling approaches. *Ecol. Model.* 405, 86–101. doi: 10.1016/j.ecolmodel.2019.05.005

Coll, M., and Steenbeek, J. (2017). Standardized ecological indicators to assess aquatic food webs: the ECOIND software plug-in for Ecopath with Ecosim models. *Environ. Model. Softw.* 89, 120–130. doi: 10.1016/j.envsoft.2016.12.004

Coll, M., Steenbeek, J., Sole, J., Palomera, I., and Christensen, V. (2016). Modelling the cumulative spatial–temporal effects of environmental drivers and fishing in a NW Mediterranean marine ecosystem. *Ecol. Model.* 331, 100–114. doi: 10.1016/j.ecolmodel.2016.03.020

Corrales, X., Coll, M., Ofir, E., Heymans, J. J., Steenbeek, J., Goren, M., et al. (2018). Future scenarios of marine resources and ecosystem conditions in the Eastern Mediterranean under the impacts of fishing, alien species and sea warming. *Sci. Rep.* 8:14284. doi: 10.1038/s41598-018-32666-x

Cronne, L. (2016). SISP 15 - manual of the IBTS North Eastern Atlantic surveys. *Ser. ICES Surv. Protoc. SISP* 15:92. doi: 10.17895/ices.pub.3519

Dahood, A., Watters, G. M., and de Mutsert, K. (2019). Using sea-ice to calibrate a dynamic trophic model for the Western Antarctic Peninsula. *PLoS One* 14:e0214814. doi: 10.1371/journal.pone.0214814

Day, L., Kopp, D., Robert, M., and Le Bris, H. (2019). Trophic ecology of large gadiforms in the food web of a continental shelf ecosystem. *Prog. Oceanogr.* 175, 105–114. doi: 10.1016/j.pocean.2019.03.007

Dinter, W. P. (2001). *Biogeography of the OSPAR Maritime Area: A Synopsis and Synthesis of Biogeographical Distribution Patterns Described for the North East Atlantic*. Bonn: Federal Agency for Nature Conservation.

Dolder, P. J., Thorson, J. T., and Minto, C. (2018). Spatial separation of catches in highly mixed fisheries. *Sci. Rep.* 8:13886. doi: 10.1038/s41598-018-31881-w

Druon, J.-N., Hélaouët, P., Beaugrand, G., Fromentin, J.-M., Palialexis, A., and Hoepffner, N. (2019). Satellite-based indicator of zooplankton distribution for global monitoring. *Sci. Rep.* 9:4732. doi: 10.1038/s41598-019-41212-2

Druon, J. N., Langlois, G., and Le Fèvre, J. (2001). Simulating vertical mixing in a shelf-break region: addition of a shear instability model, accounting for the overall effect of internal tides, on top of a one-dimensional turbulence closure mixed layer model. *Cont. Shelf Res.* 21, 423–454. doi: 10.1016/S0278-4343(00)00090-X

Duhamel, E., Pawlowski, L., and Garren, F. (2018). *EVHOE 2018 cruise,Thalassa R/V*. Available online at: https://campagnes.flotteoceanographique.fr/campagnes/18000518/ (accessed July 1, 2020).

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmller, V., Dye, S. R., and Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J. Appl. Ecol.* 45, 1029–1039. doi: 10.1111/j.1365-2664.2008.01488.x

Dunn, M. R., and Pawson, M. G. (2002). The stock structure and migrations of plaice populations on the west coast of England and Wales. *J. Fish Biol.* 61, 360–393. doi: 10.1111/j.1095-8649.2002.tb01571.x

Edwards, K. P., Barciela, R., and Butenschön, M. (2012). Validation of the NEMO-ERSEM operational ecosystem model for the North West European Continental Shelf. *Ocean Sci.* 8, 983–1000. doi: 10.5194/os-8-983-2012

Ellis, J. R., Lancaster, J. E., Cadman, P. S., and Rogers, S. I. (2002). "The marine fauna of the Celtic Sea," in *Marine Biodiversity in Ireland and Adjacent Waters*, ed. J. D. Nuun (Belfasts: Ulster Museum), 45–46.

Ellis, J. R., Martinez, I., Burt, G. J., and Scott, B. E. (2013). Epibenthic assemblages in the Celtic Sea and associated with the Jones Bank. *Prog. Oceanogr.* 117, 76–88. doi: 10.1016/j.pocean.2013.06.012

Ellis, J. R., Rogers, S. I., and Freeman, S. M. (2000). Demersal Assemblages in the Irish Sea, St George's Channel and Bristol Channel. *Estuar. Coast. Shelf Sci.* 51, 299–315. doi: 10.1006/ecss.2000.0677

Farmer, N. A., and Karnauskas, M. (2013). Spatial distribution and conservation of speckled hind and warsaw grouper in the Atlantic Ocean off the southeastern US. *PloS one*, 8:e78682. doi: 10.1371/journal.pone.0078682

Fulton, E. A., Parslow, J. S., Smith, A. D. M., and Johnson, C. R. (2004). Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance. *Ecol. Model.* 173, 371–406. doi: 10.1016/j.ecolmodel.2003.09.024

Gardner, M. B. (1981). Effects of turbidity on feeding rates and selectivity of bluegills. *Trans. Am. Fish. Soc.* 110, 446–450. doi: 10.1577/1548-8659(1981)110<446:eotofr>2.0.co;2

Gascuel, D., Coll, M., Fox, C., Guénette, S., Guitton, J., Kenny, A., et al. (2016). Fishing impact and environmental status in European seas: a diagnosis from stock assessments and ecosystem indicators. *Fish Fish.* 17, 31–55. doi: 10.1111/faf.12090

Genner, M. J., Sims, D. W., Wearmouth, V. J., Southall, E. J., Southward, A. J., Henderson, P. A., et al. (2004). Regional climatic warming drives long–term community changes of British marine fish. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 271, 655–661. doi: 10.1098/rspb.2003.2651

Gerritsen, H. D., Lordan, C., Minto, C., and Kraak, S. B. M. (2012). Spatial patterns in the retained catch composition of Irish demersal otter trawlers: high-resolution fisheries data as a management tool. *Fish. Res.* 129–130, 127–136. doi: 10.1016/j.fishres.2012.06.019

Giering, S. L. C., Wells, S. R., Mayers, K. M. J., Schuster, H., Cornwell, L., Fileman, E. S., et al. (2019). Seasonal variation of zooplankton community structure and trophic position in the Celtic Sea: a stable isotope and biovolume spectrum approach. *Prog. Oceanogr.* 177:101943. doi: 10.1016/j.pocean.2018.03.012

Giraldo, C., Ernande, B., Cresson, P., Kopp, D., Cachera, M., Travers-Trolet, M., et al. (2017). Depth gradient in the resource use of a fish community from a semi-enclosed sea. *Limnol. Oceanogr.* 62, 2213–2226. doi: 10.1002/lno.10561

Gravel, D., Canard, E., Guichard, F., and Mouquet, N. (2011). Persistence increases with diversity and connectance in trophic metacommunities. *PLoS One* 6:e19374. doi: 10.1371/journal.pone.0019374

Grüss, A., Babcock, E. A., Sagarese, S. R., Drexler, M., Chagaris, D. D., Ainsworth, C. H., et al. (2016). Improving the spatial allocation of functional group biomasses in spatially-explicit ecosystem models: insights from three Gulf of Mexico models. *Bull. Mar. Sci.* 92, 473–496. doi: 10.5343/bms.2016.1057

Grüss, A., Chagaris, D. D., Babcock, E. A., and Tarnecki, J. H. (2018). Assisting ecosystem-based fisheries management efforts using a comprehensive survey database, a large environmental database, and generalized additive models. *Trans. Am. Fish. Soc.* 10, 40–70. doi: 10.1002/mcf2.10002

Grüss, A., Rose, K. A., Justiæ, D., and Wang, L. (2020). Making the most of available monitoring data: a grid-summarization method to allow for the combined use of monitoring data collected at random and fixed sampling stations. *Fish. Res.* 229:105623. doi: 10.1016/j.fishres.2020.105623

Guénette, S., and Gascuel, D. (2009). "Considering Both Fishing and Climate in a model of the Celtic Sea and the Bay of Biscay: what do we learn?" in *Proceedings of the International Council for the Exploration of the Sea, Annual Science Conference*, Berlin.

Guénette, S., and Gascuel, D. (2012). Shifting baselines in European fisheries: the case of the Celtic Sea and Bay of Biscay. *Ocean Coast. Manage*. 70, 10–21. doi: 10.1016/j.ocecoaman.2012.06.010

Halouani, G., Ben Rais, Lasram, F., Shin, Y.-J., Velez, L., Verley, P., et al. (2016). Modelling food web structure using an end-to-end approach in the coastal ecosystem of the Gulf of Gabes (Tunisia). *Ecol. Model.* 339, 45–57. doi: 10.1016/j.ecolmodel.2016.08.008

Hansson, S. (1984). Competition as a Factor Regulating the Geographical Distribution of Fish Species in a Baltic Archipelago: a neutral model analysis. *J. Biogeogr.* 11, 367–381. doi: 10.2307/2844802

Hawkins, S. J., Southward, A. J., and Genner, M. J. (2003). Detection of environmental change in a marine ecosystem—evidence from the western English Channel. *Sci. Total Environ. Detect. Environ. Change* 310, 245–256. doi: 10.1016/S0048-9697(02)00645-9

Hernvann, P.-Y., and Gascuel, D. (2020). Exploring the impacts of fishing and environment on the Celtic Sea ecosystem since 1950. *Fish. Res.* 225:105472. doi: 10.1016/j.fishres.2019.105472

Heymans, J. J., Coll, M., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., et al. (2016). Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecol. Model.* 331, 173–184. doi: 10.1016/j.ecolmodel.2015.12.007

Hickman, A., Moore, C., Sharples, J., Lucas, M., Tilstone, G., Krivtsov, V., et al. (2012). Primary production and nitrate uptake within the seasonal thermocline of a stratified shelf sea. *Mar. Ecol. Prog. Ser.* 463, 39–57. doi: 10.3354/meps09836

Hiddink, J. G., and ter Hofstede, R. (2008). Climate induced increases in species richness of marine fishes. *Glob. Change Biol.* 14, 453–460. doi: 10.1111/j.1365-2486.2007.01518.x

Holligan, P. M., and Groom, S. B. (1986). Phytoplankton distributions along the shelf break. *Proc. R. Soc. Edinb. Sect. B Biol. Sci.* 88, 239–263. doi: 10.1017/S0269727000004589

Holling, C. S. (1959). The components of predation as revealed by a study of small-mammal predation of the european pine sawfly. *Can. Entomol.* 91, 293–320. doi: 10.4039/Ent91293-5

Hughes, S. L., Tinker, J., and Dye, S. (2017). Temperature. *MCCIP Science Review 2017. MCCIP Science Review 2017*. 22–41. Available online at: http://www.mccip.org.uk/media/1750/2017arc_sciencereview_003_tem.pdf (accessed July 1, 2020).

Hunsicker, M. E., Ciannelli, L., Bailey, K. M., Buckel, J. A., Wilson White, J., Link, J. S., et al. (2011). Functional responses and scaling in predator-prey interactions of marine fishes: contemporary issues and emerging concepts. *Ecol. Lett.* 14, 1288–1299. doi: 10.1111/j.1461-0248.2011.01696.x

Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harb. Symp. Quant. Biol.* 22, 415–427. doi: 10.1101/SQB.1957.022.01.039

Huxel, G. R., and McCann, K. (1998). Food web stability: the influence of trophic flows across habitats. *Am. Nat.* 152, 460–469. doi: 10.1086/286182

Issac, P., Robert, M., Le Bris, H., Rault, J., Pawlowski, L., and Kopp, D. (2017). Investigating feeding ecology of two anglerfish species, *Lophius piscatorius* and *Lophius budegassa* in the Celtic Sea using gut content and isotopic analyses. *Food Webs* 13, 33–37. doi: 10.1016/j.fooweb.2017.08.001

Johns, D. (2019). Monthly Averaged Data for Diatoms, Dinoflagellates, Small Copepods, Large Copepods, and Various Taxonomic Groups of Zooplankton in the D4 CPR Standard Area 1958–2016 as Recorded by the Continuous Plankton Recorder Survey. Plymouth, MA: CPR survey. doi: 10.7487/2019.150.1.1197

Joint, I., Wollast, R., Chou, L., Batten, S., Elskens, M., Edwards, E., et al. (2001). Pelagic production at the Celtic Sea shelf break. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 48, 3049–3081. doi: 10.1016/S0967-0645(01)00032-7

Joint, I. R., and Williams, R. (1985). Demands of the herbivore community on phytoplankton production in the Celtic Sea in August. *Mar. Biol.* 87, 297–306. doi: 10.1007/BF00397809

Jones, M. C., Dye, S. R., Pinnegar, J. K., Warren, R., and Cheung, W. W. L. (2012). Modelling commercial fish distributions: prediction and assessment using different approaches. *Ecol. Model.* 225, 133–145. doi: 10.1016/j.ecolmodel.2011.11.003

Jordan, M. B., and Joint, I. R. (1984). Studies on phytoplankton distribution and primary production in the western English Channel in 1980 and 1981. *Cont. Shelf Res.* 3, 25–34. doi: 10.1016/0278-4343(84)90041-4

Kaiser, M. J., Armstrong, P. J., Dare, P. J., and Flatt, R. P. (1998). Benthic communities associated with a heavily fished scallop ground in the english channel. *J. Mar. Biol. Assoc. U.K.* 78, 1045–1059. doi: 10.1017/S0025315400044313

Kaiser, M. J., Bergmann, M., Hinz, H., Galanidi, M., Shucksmith, R., Rees, E. I. S., et al. (2004). Demersal fish and epifauna associated with sandbank habitats. *Estuar. Coast. Shelf Sci.* 60, 445–456. doi: 10.1016/j.ecss.2004.02.005

Kaplan, I. C., Horne, P. J., and Levin, P. S. (2012). Screening California Current fishery management scenarios using the Atlantis end-to-end ecosystem model. *Prog. Oceanogr.* 102, 5–18. doi: 10.1016/j.pocean.2012.03.009

Kay, S., Anderson, H., Eilola, K., Wehde, H., Ramirez-Romero, E., Jordà, G., et al. (2018). *Climate Change and European Aquatic RESources - Deliverable D1.3 Projections of Physical and Biogeochemical Parameters and Habitat Indicators for European Seas, Including Synthesis of Sea Level Rise and Storminess*. Plymouth: Plymouth Marine Laboratory (PML).

Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A. V., and Planque, B. (2019). Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. *Ecography* 42, 295–308. doi: 10.1111/ecog.03443

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., and Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proc. R. Soc. B Biol. Sci.* 282:20151546. doi: 10.1098/rspb.2015.1546

Kramer, S. J., Roesler, C. S., and Sosik, H. M. (2018). Bio-optical discrimination of diatoms from other phytoplankton in the surface ocean: evaluation and refinement of a model for the Northwest Atlantic. *Remote Sens. Environ.* 217, 126–143. doi: 10.1016/j.rse.2018.08.010

Le Danois, E. (1948). *Les Profondeurs de la mer; Trente ans de Recherches sur la Faune Sous-Marine au Large des Côtes de France*. Paris: Payot.

Le Fèvre, J. (1987). Aspects of the biology of frontal systems. *Adv. Mar. Biol.* 23, 163–299. doi: 10.1016/S0065-2881(08)60109-1

Libralato, S. (2013). "System Omnivory Index," in *Encyclopedia of Ecology*, ed. B. Fath (Amsterdam: Elsevier), 481–486. doi: 10.1016/B978-0-12-409548-9.00605-9

Libralato, S., Pranovi, F., Stergiou, K., and Link, J. (2014). Trophodynamics in marine ecology: 70 years after Lindeman. *Mar. Ecol. Prog. Ser.* 512, 1–7. doi: 10.3354/meps11033

Libralato, S., and Solidoro, C. (2009). Bridging biogeochemical and food web models for an End-to-End representation of marine ecosystem dynamics: the Venice lagoon case study. *Ecol. Model.* 220, 2960–2971. doi: 10.1016/j.ecolmodel.2009.08.017

Link, J. S. (2010). Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. *Ecol. Model.* 221, 1580–1591. doi: 10.1016/j.ecolmodel.2010.03.012

Logerwell, E. A., and Hargreaves, N. B. (1996). The distribution of sea birds relative to their fish prey off Vancouver Island: opposing results at large and small spatial scales. *Fish. Oceanogr.* 5, 163–175. doi: 10.1111/j.1365-2419.1996.tb00115.x

Lowerre-Barbieri, S. K., Catalán, I. A., Frugård Opdal, A., and Jørgensen, C. (2019). Preparing for the future: integrating spatial ecology into ecosystem-based management. *ICES J. Mar. Sci.* 76, 467–476. doi: 10.1093/icesjms/fsy209

Mackinson, S. (2014). Combined analyses reveal environmentally driven changes in the North Sea ecosystem and raise questions regarding what makes an ecosystem model's performance credible? *Can. J. Fish. Aquat. Sci.* 71, 31–46. doi: 10.1139/cjfas-2013-0173

Mackinson, S., Daskalov, G., Heymans, J. J., Neira, S., Arancibia, H., Zetina-Rejón, M., et al. (2009). Which forcing factors fit? Using ecosystem models to investigate the relative influence of fishing and changes in primary productivity on the dynamics of marine ecosystems. *Ecol. Model.* 220, 2972–2987. doi: 10.1016/j.ecolmodel.2008.10.021

Madec, G. (2008). *NEMO Ocean Engine*. Paris: Institut Pierre-Simon Laplace (IPSL).

Martinez, I., Ellis, J. R., Scott, B., and Tidd, A. (2013). The fish and fisheries of Jones Bank and the wider Celtic Sea. *Prog. Oceanogr.* 117, 89–105. doi: 10.1016/j.pocean.2013.03.004

Mateo, M., Pawlowski, L., and Robert, M. (2017). Highly mixed fisheries: fine-scale spatial patterns in retained catches of French fisheries in the Celtic Sea. *ICES J. Mar. Sci.* 74, 91–101. doi: 10.1093/icesjms/fsw129

Maureaud, A., Hodapp, D., van Denderen, P. D., Hillebrand, H., Gislason, H., Spaanheden Dencker, T., et al. (2019). Biodiversity–ecosystem functioning relationships in fish communities: biomass is related to evenness and the environment, not to species richness. *Proc. R. Soc. B Biol. Sci.* 286:20191189. doi: 10.1098/rspb.2019.1189

McCann, K. S., Rasmussen, J. B., and Umbanhowar, J. (2005). The dynamics of spatially coupled food webs: spatially coupled food webs. *Ecol. Lett.* 8, 513–523. doi: 10.1111/j.1461-0248.2005.00742.x

McCormack, S. A., Trebilco, R., Melbourne-Thomas, J., Blanchard, J. L., Fulton, E. A., and Constable, A. (2019). Using stable isotope data to advance marine food web modelling. *Rev. Fish Biol. Fish.* 29, 277–296. doi: 10.1007/s11160-019-09552-4

McGinty, N., Power, A. M., and Johnson, M. P. (2011). Variation among northeast Atlantic regions in the responses of zooplankton to climate change: not all areas follow the same path. *J. Exp. Mar. Biol. Ecol.* 400, 120–131. doi: 10.1016/j.jembe.2011.02.013

Melian, C. J., and Bascompte, J. (2002). Food web structure and habitat loss. *Ecol. Lett.* 5, 37–46. doi: 10.1046/j.1461-0248.2002.00280.x

Menge, B. A., and Lubchenco, J. (1981). Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol. Monogr.* 51, 429–450. doi: 10.2307/2937323

Mérillet, L., Kopp, D., Robert, M., Mouchet, M., and Pavoine, S. (2020). Environment outweighs the effects of fishing in regulating demersal community structure in an exploited marine ecosystem. *Glob. Change Biol.* 26, 2106–2119. doi: 10.1111/gcb.14969

Montero-Serra, I., Edwards, M., and Genner, M. J. (2015). Warming shelf seas drive the subtropicalization of European pelagic fish communities. *Glob. Change Biol.* 21, 144–153. doi: 10.1111/gcb.12747

Moore, C., Davie, S., Robert, M., Pawlowski, L., Dolder, P., and Lordan, C. (2019). Defining métier for the Celtic Sea mixed fisheries: a multiannual international study of typology. *Fish. Res.* 219:105310. doi: 10.1016/j.fishres.2019.105310

Morel, A., and Berthon, J.-F. (1989). Surface pigments, algal biomass profiles, and potential production of the euphotic layer: relationships reinvestigated in view of remote-sensing applications. *Limnol. Oceanogr.* 34, 1545–1562. doi: 10.4319/lo.1989.34.8.1545

Moriarty, M., Sethi, S. A., Pedreschi, D., Smeltz, T. S., McGonigle, C., Harris, B. P., et al. (2020). Combining fisheries surveys to inform marine species distribution modelling. *ICES J. Mar. Sci.* 77, 539–552. doi: 10.1093/icesjms/fsz254

Mougi, A., and Kondoh, M. (2016). Food-web complexity, meta-community complexity and community stability. *Sci. Rep.* 6:24478. doi: 10.1038/srep24478

Moullec, F., Barrier, N., Drira, S., Guilhaumon, F., Marsaleix, P., Somot, S., et al. (2019a). An end-to-end model reveals losers and winners in a warming mediterranean sea. *Front. Mar. Sci.* 6:345. doi: 10.3389/fmars.2019.00345

Moullec, F., Velez, L., Verley, P., Barrier, N., Ulses, C., Carbonara, P., et al. (2019b). Capturing the big picture of Mediterranean marine biodiversity with an end-to-end model of climate and fishing impacts. *Prog. Oceanogr.* 178, 102179. doi: 10.1016/j.pocean.2019.102179

Moullec, F., Gascuel, D., Bentorcha, K., Guénette, S., and Robert, M. (2017). Trophic models: What do we learn about Celtic Sea and Bay of Biscay ecosystems? *J. Mar. Syst.* 172, 104–117. doi: 10.1016/j.jmarsys.2017.03.008

Murdoch, W. W. (1969). Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39, 335–354. doi: 10.2307/1942352

Neat, F. C., Bendall, V., Berx, B., Wright, P. J., Ó Cuaig, M., Townhill, B., et al. (2014). Movement of Atlantic cod around the British Isles: implications for finer scale stock management. *J. Appl. Ecol.* 51, 1564–1574. doi: 10.1111/1365-2664.12343

Pade, N. G., Queiroz, N., Humphries, N. E., Witt, M. J., Jones, C. S., Noble, L. R., et al. (2009). First results from satellite-linked archival tagging of porbeagle shark, Lamna nasus: area fidelity, wider-scale movements and plasticity in diel depth changes. *J. Exp. Mar. Biol. Ecol.* 370, 64–74. doi: 10.1016/j.jembe.2008.12.002

Parker, R. A. (1991). Eddy diffusion of phytoplankton and nutrients: estimating coefficients from simulated and observed vertical distributions. *J. Plankton Res.* 13, 815–830. doi: 10.1093/plankt/13.4.815

Pauly, D., Christensen, V., and Walters, C. (2000). Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES J. Mar. Sci.* 57, 697–706. doi: 10.1006/jmsc.2000.0726

Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., et al. (2018). Comparing species interaction networks along environmental gradients: Networks along environmental gradients. *Biol. Rev.* 93, 785–800. doi: 10.1111/brv.12366

Pellissier, L., Rohr, R. P., Ndiribe, C., Pradervand, J.-N., Salamin, N., Guisan, A., et al. (2013). Combining food web and species distribution models for improved community projections. *Ecol. Evol.* 3, 4572–4583. doi: 10.1002/ece3.843

Pennino, M. G., Bevilacqua, A. H., Torres, M. A., Bellido, J. M., Sole, J., Steenbeek, J., et al. (2020). Discard ban: a simulation-based approach combining hierarchical Bayesian and food web spatial models. *Mar. Policy* 116:103703. doi: 10.1016/j.marpol.2019.103703

Persohn, C., Lorance, P., and Trenkel, V. M. (2009). Habitat preferences of selected demersal fish species in the Bay of Biscay and Celtic Sea, North-East Atlantic. *Fish. Oceanogr.* 18, 268–285. doi: 10.1111/j.1365-2419.2009.00515.x

Pethybridge, H. R., Choy, C. A., Polovina, J. J., and Fulton, E. A. (2018). Improving marine ecosystem models with biochemical tracers. *Annu. Rev. Mar. Sci.* 10, 199–228. doi: 10.1146/annurev-marine-121916-063256

Pingree, R. D. (1980). "Chapter 13 Physical Oceanography of the Celtic Sea and English Channel," in *Elsevier Oceanography Series*, eds F. T. Banner, M. B. Collins, and K. S. Massie (Amsterdam: Elsevier), 415–465. doi: 10.1016/S0422-9894(08)71358-8

Pingree, R. D., Holligan, P. M., Mardell, G. T., and Head, R. N. (1976). The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. *J. Mar. Biol. Assoc. U.K.* 56, 845–873. doi: 10.1017/S0025315400020919

Pingree, R. D., Mardell, G. T., Holligan, P. M., Griffiths, D. K., and Smithers, J. (1982). Celtic Sea and Armorican current structure and the vertical distributions of temperature and chlorophyll. *Cont. Shelf Res.* 1, 99–116. doi: 10.1016/0278-4343(82)90033-4

Pinnegar, J. K., Jennings, S., O'Brien, C. M., and Polunin, N. V. C. (2002). Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *J. Appl. Ecol.* 39, 377–390. doi: 10.1046/j.1365-2664.2002.00723.x

Piroddi, C., Coll, M., Liquete, C., Macias, D., Greer, K., Buszowski, J., et al. (2017). Historical changes of the Mediterranean Sea ecosystem: modelling the role and impact of primary productivity and fisheries changes over time. *Sci. Rep.* 7:44491. doi: 10.1038/srep44491

Piroddi, C., Teixeira, H., Lynam, C. P., Smith, C., Alvarez, M. C., Mazik, K., et al. (2015). Using ecological models to assess ecosystem status in support of the European Marine Strategy Framework Directive. *Ecol. Indic.* 58, 175–191. doi: 10.1016/j.ecolind.2015.05.037

Pitois, S. G., and Fox, C. J. (2006). Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data. *ICES J. Mar. Sci.* 63, 785–798. doi: 10.1016/j.icesjms.2006.03.009

Polis, G. A., Anderson, W. B., and Holt, R. D. (1997). Toward an integration of landscape and food-web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 28, 289–316. doi: 10.1146/annurev.ecolsys.28.1.289

Polis, G. A., Holt, R. D., Menge, B. A., and Winemiller, K. O. (1996). "Time, space, and life history: influences on food webs," in *Food Webs*, eds G. A. Polis and K. O. Winemiller (Boston, MA: Springer), 435–460. doi: 10.1007/978-1-4615-7007-3_38

Poulard, J.-C., and Blanchard, F. (2005). The impact of climate change on the fish community structure of the eastern continental shelf of the Bay of Biscay. *ICES J. Mar. Sci.* 62, 1436–1443. doi: 10.1016/j.icesjms.2005.04.017

Punzón, A., Serrano, A., Sánchez, F., Velasco, F., Preciado, I., González-Irusta, J. M., et al. (2016). Response of a temperate demersal fish community to global warming. *J. Mar. Syst.* 161, 1–10. doi: 10.1016/j.jmarsys.2016.05.001

Rault, J., Le Bris, H., Robert, M., Pawlowski, L., Denamiel, M., and Kopp, D. (2017). Diets and trophic niches of the main commercial fish species from the Celtic Sea. *J. Fish Biol.* 91, 1449–1474. doi: 10.1111/jfb.13470

Raymont, J. E. G. (1980). *Plankton & Productivity in the Oceans*, Second Edn. Oxford: Pergamon Press Ltd. doi: 10.1016/C2009-0-10951-0

Rees, H. (1999). A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas. *ICES J. Mar. Sci.* 56, 228–246. doi: 10.1006/jmsc.1998.0438

Reid, D. G. (2001). SEFOS-shelf edge fisheries and oceanography studies: an overview. *Fish. Res.* 50, 1–15. doi: 10.1016/S0165-7836(00)00238-1

Reid, D. G., Calderwood, J., Afonso, P., Bourdaud, P., Fauconnet, L., González-Irusta, J. M., et al. (2019). "The Best Way to Reduce Discards Is by Not Catching Them!," in *The European Landing Obligation*, eds S. S. Uhlmann, C. Ulrich, and S. J. Kennelly (Cham: Springer), 257–278. doi: 10.1007/978-3-030-03308-8_13

Robert, M., Calderwood, J., Radford, Z., Catchpole, T., Reid, D. G., and Pawlowski, L. (2019). Spatial distribution of discards in mixed fisheries: species trade-offs, potential spatial avoidance and national contrasts. *Rev. Fish Biol. Fish.* 29, 917–934. doi: 10.1007/s11160-019-09581-z

Romagnoni, G., Mackinson, S., Hong, J., and Eikeset, A. M. (2015). The Ecospace model applied to the North Sea: evaluating spatial predictions with fish biomass and fishing effort data. *Ecol. Model.* 300, 50–60. doi: 10.1016/j.ecolmodel.2014.12.016

Rooney, N., McCann, K., Gellner, G., and Moore, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature* 442, 265–269. doi: 10.1038/nature04887

Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W., and Votier, S. C. (2014). REVIEW: on the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *J. Appl. Ecol.* 51, 1575–1583. doi: 10.1111/1365-2664.12330

Scott, E., Serpetti, N., Steenbeek, J., and Heymans, J. J. (2016). A Stepwise Fitting Procedure for automated fitting of Ecopath with Ecosim models. *SoftwareX* 5, 25–30. doi: 10.1016/j.softx.2016.02.002

Serpetti, N., Baudron, A. R., Burrows, M. T., Payne, B. L., Helaouët, P., Fernandes, P. G., et al. (2017). Impact of ocean warming on sustainable fisheries management informs the Ecosystem Approach to Fisheries. *Sci. Rep.* 7:13438. doi: 10.1038/s41598-017-13220-7

Sharples, J., Ellis, J. R., Nolan, G., and Scott, B. E. (2013). Fishing and the oceanography of a stratified shelf sea. *Prog. Oceanogr.* 117, 130–139. doi: 10.1016/j.pocean.2013.06.014

Sharples, J., Tweddle, J. F., Mattias Green, J. A., Palmer, M. R., Kim, Y.-N., Hickman, A. E., et al. (2007). Spring-neap modulation of internal tide mixing and vertical nitrate fluxes at a shelf edge in summer. *Limnol. Oceanogr.* 52, 1735–1747. doi: 10.4319/lo.2007.52.5.1735

Shephard, S., Fung, T., Houle, J. E., Farnsworth, K. D., Reid, D. G., and Rossberg, A. G. (2012). Size-selective fishing drives species composition in the Celtic Sea. *ICES J. Mar. Sci.* 69, 223–234. doi: 10.1093/icesjms/fsr200

Shephard, S., Reid, D. G., and Greenstreet, S. P. R. (2011). Interpreting the large fish indicator for the Celtic Sea. *ICES J. Mar. Sci.* 68, 1963–1972. doi: 10.1093/icesjms/fsr114

Shin, Y., and Cury, P. (2001). Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. *Aquat. Living Resour.* 14, 65–80. doi: 10.1016/S0990-7440(01)01106-8

Simpson, J. H. (1976). A boundary front in the summer regime of the Celtic Sea. *Estuar. Coast. Mar. Sci.* 4, 71–81. doi: 10.1016/0302-3524(76)90008-6

Simpson, S. D., Jennings, S., Johnson, M. P., Blanchard, J. L., Schön, P.-J., Sims, D. W., et al. (2011). Continental Shelf-Wide Response of a Fish Assemblage to Rapid Warming of the Sea. *Curr. Biol.* 21, 1565–1570. doi: 10.1016/j.cub.2011.08.016

Southward, A. J., Boalch, G. T., and Maddock, L. (1988). Fluctuations in the herring and pilchard fisheries of devon and cornwall linked to change in climate since the 16th century. *J. Mar. Biol. Assoc. U.K.* 68, 423–445. doi: 10.1017/S0025315400043320

Steenbeek, J., Buszowski, J., Christensen, V., Akoglu, E., Aydin, K., Ellis, N., et al. (2016). Ecopath with Ecosim as a model-building toolbox: source code capabilities, extensions, and variations. *Ecol. Model.* 319, 178–189. doi: 10.1016/j.ecolmodel.2015.06.031

Steenbeek, J., Coll, M., Gurney, L., Mélin, F., Hoepffner, N., Buszowski, J., et al. (2013). Bridging the gap between ecosystem modeling tools and geographic information systems: driving a food web model with external spatial–temporal data. *Ecol. Model.* 263, 139–151. doi: 10.1016/j.ecolmodel.2013.04.027

Steenbeek, J., Corrales, X., Platts, M., and Coll, M. (2018). Ecosampler: a new approach to assessing parameter uncertainty in Ecopath with Ecosim. *SoftwareX* 7, 198–204. doi: 10.1016/j.softx.2018.06.004

Tam, J. C., Link, J. S., Rossberg, A. G., Rogers, S. I., Levin, P. S., Rochet, M.-J., et al. (2017). Towards ecosystem-based management: identifying operational food-web indicators for marine ecosystems. *ICES J. Mar. Sci.* 74, 2040–2052. doi: 10.1093/icesjms/fsw230

ter Hofstede, R., Hiddink, J., and Rijnsdorp, A. (2010). Regional warming changes fish species richness in the eastern North Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 414, 1–9. doi: 10.3354/meps08753

Théro, H., Rivot, E., Robert, M., Guitton, J., Kopp, D., Gascuel, D., et al. (2020). *EcoDiet. R package version 1.0.0.0*. doi: 10.5281/zenodo.4081537

Tidd, A. N., and Warnes, S. (2006). *Species Distributions from English Celtic Sea Groundfish Surveys, 1992–2003 (Science Series Technical Report)*. Lowestoft: Cefas.

Ting, M., Kushnir, Y., Seager, R., and Li, C. (2009). Forced and internal twentieth-century SST trends in the North Atlantic. *J. Clim.* 22, 1469–1481. doi: 10.1175/2008JCLI2561.1

Tinker, J. P., Howes, E. L., Wakelin, S., Menary, M., Kent, E., Berry, D., et al. (2020). The impacts of climate change on temperature (air and sea), relevant to the coastal and marine environment around the UK. *MCCIP Sci. Rev.* 2020, 1–30. doi: 10.14465/2020.ARC01.TEM

Tomczak, M. T., Niiranen, S., Hjerne, O., and Blenckner, T. (2012). Ecosystem flow dynamics in the Baltic Proper—Using a multi-trophic dataset as a basis for food–web modelling. *Ecol. Model.* 230, 123–147. doi: 10.1016/j.ecolmodel.2011.12.014

Torres, L. G., Read, A. J., and Halpin, P. (2008). Fine-scale habitat modeling of a top marine predator: Do prey data improve predictive capacity? *Ecol. Appl.* 18, 1702–1717. doi: 10.1890/07-1455.1

Travers, M., Shin, Y.-J., Jennings, S., and Cury, P. (2007). Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. *Prog. Oceanogr.* 75, 751–770. doi: 10.1016/j.pocean.2007.08.001

Travers, M., Shin, Y.-J., Jennings, S., Machu, E., Huggett, J. A., Field, J. G., et al. (2009). Two-way coupling versus one-way forcing of plankton and fish models to predict ecosystem changes in the Benguela. *Ecol. Model.* 220, 3089–3099. doi: 10.1016/j.ecolmodel.2009.08.016

Trenkel, V., Pinnegar, J., Dawson, W., Du Buit, M., and Tidd, A. (2005). Spatial and temporal structure of predator-prey relationships in the Celtic Sea fish community. *Mar. Ecol. Prog. Ser.* 299, 257–268. doi: 10.3354/meps299257

Trenkel, V. M., Huse, G., MacKenzie, B. R., Alvarez, P., Arrizabalaga, H., Castonguay, M., et al. (2014). Comparative ecology of widely distributed pelagic fish species in the North Atlantic: implications for modelling climate and fisheries impacts. *Prog. Oceanogr.* 129, 219–243. doi: 10.1016/j.pocean.2014.04.030

Vallet, C., and Dauvin, J.-C. (1998). Composition and diversity of the benthic boundary layer macrofauna from the english channel. *J. Mar. Biol. Assoc. U.K.* 78, 387–409. doi: 10.1017/S0025315400041527

Walters, C. (1999). Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2, 539–554. doi: 10.1007/s100219900101

Walters, C., Christensen, V., and Pauly, D. (1997). Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fish.* 7, 139–172. doi: 10.1023/A:1018479526149

Ward, T., Hoedt, F., McLeay, L., Dimmlich, W., Jackson, G., Rogers, P., et al. (2001). Have recent mass mortalities of the sardine *Sardinops sagax* facilitated an expansion in the distribution and abundance of the anchovy *Engraulis australis* in South Australia? *Mar. Ecol. Prog. Ser.* 220, 241–251. doi: 10.3354/meps220241

Warnes, S., and Jones, B. W. (1995). *Species Distributions from English Celtic Sea Groundfish Surveys, 1984 to 1991 (Fisheries Research Technical Report)*. Lowestoft: MAFF Directorate of Fisheries Research.

Wood, S. N. (2017). *Generalized Additive Models: An Introduction with R*, 2nd Edn. London: Chapman and Hall. doi: 10.1201/9781315370279

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 18 December 2020
doi: 10.3389/fmars.2020.566686

The Seasonal Distribution of a Highly Commercial Fish Is Related to Ontogenetic Changes in Its Feeding Strategy

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OPEN ACCESS

Edited by:
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Reviewed by:
Davide Agnetta,
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Institute for Biological Resources and Marine Biotechnology (CNR), Italy

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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: 28 May 2020
Accepted: 16 November 2020
Published: 18 December 2020

Citation:
Lloret-Lloret E, Navarro J, Giménez J, López N, Albo-Puigserver M, Pennino MG and Coll M (2020) The Seasonal Distribution of a Highly Commercial Fish Is Related to Ontogenetic Changes in Its Feeding Strategy. Front. Mar. Sci. 7:566686. doi: 10.3389/fmars.2020.566686

Improving the knowledge on the biology, ecology and distribution of marine resources exploited by fisheries is necessary to achieve population recovery and sustainable fisheries management. European hake (*Merluccius merluccius*) is one of the most important target species in the Mediterranean Sea and is largely overexploited by industrial fisheries. Here, we used two methodological approaches to further investigate the seasonal variation in the spatial distribution of European hake considering ontogenetic changes and trophic ecology in the western Mediterranean Sea. Our main aim was to explore if spatial changes in hake distribution were related to trophic behavior, in addition to key environmental factors. We employed a hierarchical Bayesian species distribution modeling approach (B-SDM), using spatial data from two oceanographic surveys conducted during winter and summer. We analyzed how the environmental variables, together with abundance and mean weight distribution of the main preys identified for European hake, affected the seasonal distribution of the species. Results revealed clear differences in the distribution of the European hake between seasons, which were indeed partially correlated to the distribution of their main preys, in addition to the environment. Stable isotope values and Bayesian isotopic mixing models (MixSIAR) revealed substantial seasonal and ontogenetic differences in trophic habits of European hake, partly matching the spatial distribution results. These findings could have implications for a future seasonal-based adaptive fisheries management, as local depletion of prey, or variation in size and condition may affect European hake presence in this area. Moreover, this study illustrates how the sequential application of methodologies provides a more holistic understanding of species seasonality, which is essential to understand the phenological processes of exploited species and their potential shifts due to environmental changes.

Keywords: European hake, fisheries, marine predator, mediterranean sea, *Merluccius merluccius*, spatial distribution, stable isotopes, trophic ecology

INTRODUCTION

Identifying and understanding the main factors that affect the spatial distribution of marine organisms is important to evaluate the current distribution patterns and predict potential impacts of human activity (Lasram et al., 2010; Morfin et al., 2012). Changes in species distributions may be driven by environmental seasonal variation, as well as by prey availability (Carney, 2005; Morfin et al., 2012). Seasonal variations of life cycle events in animals and plants characterize the seasonal phenology and long term dynamics of a species, which is one of the most sensitive indicators to environmental changes (Cormon et al., 2014; Scranton and Amarasekare, 2017).

Seasonality takes place in all marine ecosystems, but their duration and intensity varies according to the geographical area, in general terms being more evident in tropical waters than in temperate waters (Valiela, 1995). Nevertheless, at a more regional scale, the western Mediterranean Sea is characterized by having a high seasonality (Coll et al., 2010); with a marked thermocline in summer and a lack of nutrients on the surface layer *versus* a mixing of the water column and an upraise of nutrients to the photic layer during winter (Margalef, 1985). Variations in environmental factors drive the distribution of nutrients and primary production, in fact phytoplankton blooms in this area peak in winter-spring coinciding with the stabilization of the water column and again in autumn, when the waters start to mix again (Estrada, 1996; Salat et al., 2002). The seasonal changes in environmental and biological variables in the entire Mediterranean basin is a well-studied subject (Psarra et al., 2000; Bosc et al., 2004; Zveryaev, 2015) and some studies have also been done on the effect of seasonality at different levels of biological organization (Gaertner, 2000; De Souza et al., 2011; Puerta et al., 2016). Nevertheless, the analysis of the interplay of seasonality with higher level trophic organisms tends to be scarce and patchy. Environmental factors have shown to affect species distribution (Katsanevakis et al., 2009; Pennino et al., 2013; Navarro et al., 2015; Puerta et al., 2015) and these environmental factors also show strong intra-annual variation in the Mediterranean Sea (Salat et al., 2002), therefore it could be relevant to take seasonality into account when analyzing species spatial patterns in this basin.

Several studies have used species distribution models (SDM) (Guisan and Zimmermann, 2000) to investigate the spatial patterns of marine species and most agreed on biological, environmental and human related variables affecting species distributions in the Mediterranean Sea (Katsanevakis et al., 2009; Navarro et al., 2015). On this context, several Mediterranean commercial marine species, including the European hake (*Merluccius merluccius*), present seasonality on their spatial distribution (Demestre and Sánchez, 1998; Paradinas et al., 2015; Sion et al., 2019; Lloret-Lloret et al., under review). European hake is one of the most important demersal target species for commercial fisheries in the Mediterranean basin (Sánchez et al., 2007), but it is reaching overexploitation levels in numerous areas (Lleonart and Maynou, 2003; Fernandes et al., 2017) to the point that it is currently listed as Vulnerable species by the International Union for the Conservation of the Nature (IUCN)(Di Natale et al., 2011). Therefore, achieving a better understanding of spatial patterns of European hake and how they relate to seasonal processes could be of use to inform ecosystem-based management actions that result on more sustainable fisheries.

Due to the ecological and economic importance of European hake, different published studies had been focused on its spatial distribution (e.g., Demestre et al., 2000; Abella et al., 2005; Druon et al., 2015; Sion et al., 2019). These studies indicated that European hake occupies a wide bathymetric distribution range (from 20 to 1,000 meters), inhabiting the shelf and upper slope in the Mediterranean Sea (Fisher et al., 1987; Demestre et al., 2000; Orsi-Relini et al., 2002). Oceanographically, this species is mainly present in cooler bottom waters (from 9.65 to 19.23°C) (Maravelias et al., 2006). Seasonal variations in the density of European hake have been recorded in some areas of the Mediterranean Sea and the Atlantic Ocean with movements to deeper and cooler waters during summer (Fariña et al., 1997; Maravelias and Papaconstantinou, 2006; Maravelias et al., 2006; Lloret-Lloret et al. under review).

SDMs generally focus on abiotic factors, however species spatial patterns are also related to the availability and preference of prey, hence the importance of considering information on feeding strategies when analyzing the spatial distribution of a species (Navarro et al., 2016). In the case of European hake, many studies have analyzed its feeding ecology (Bozzano et al., 1997; Carpentieri et al., 2005; Cartes et al., 2009) but few have directly studied the relationship between trophic behavior and spatial distribution in the Mediterranean Sea (Johnson et al., 2012, 2013).

European hake has been described as an ambush demersal predator (Pitcher and Alheit, 1995), which also feeds on the water column performing nocturnal diel migrations, important for the juvenile individuals (Bozzano et al., 2005; Aguzzi et al., 2015). Trophic studies of this species have generally focused on immature individuals (Oliver and Massuti, 1995; Bozzano et al., 2005) except for a few number that include a wider range of sizes (Bozzano et al., 1997; Carpentieri et al., 2005; Mellon-Duval et al., 2017). Despite these studies, there is still a lack of information on the ecology of European hake, especially regarding variation of the diet with seasonality.

The study of the diet of marine fish normally relies on stomach content analyses (Hyslop, 1980). Although this technique provides quantitative diet composition, it is limited by degradation and ingestion rates, amongst other constraints (Hyslop, 1980). In addition, high levels of regurgitation have been recorded for European hake (Modica et al., 2011), which difficult the analysis of the diet based on stomach content analysis. As an alternative, the use of stable isotopes analysis and isotopic mixing models are additional techniques to examine the diet of marine predators (Davis and Pineda-Munoz, 2016). Despite the extended use of these methodologies, only a small number of studies have used them to characterize the feeding ecology of European hake in the western Mediterranean Sea [e.g., (Sinopoli et al., 2012; Fanelli et al., 2018)] and more specifically in the northwestern Mediterranean Sea [e.g., (Ferraton et al., 2007; Albo-Puigserver et al., 2016; Mellon-Duval et al., 2017; Rueda et al., 2019)].

In this study, we aimed to investigate the seasonal differences in the spatial distribution and trophic habits of European hake in a highly exploited area of the northwestern Mediterranean Sea, considering ontogenetic variations. To analyze the seasonal spatial distribution, we employed a hierarchical Bayesian species distribution modeling approach (B-SDM) and we used the mean weight values estimated from two oceanographic surveys conveyed in winter and summer 2013, as a proxy of body size (Chih-Lin et al., 2010) and consequently age class. We expected that juvenile (i.e., lower mean weight) and adult individuals (i.e., higher mean weight) will distribute differently within the same season and between seasons and these differences might be explained by feeding preferences on top of environmental variables. We included depth and sea bottom temperature (SBT) as environmental variables, in addition to potential preys' abundance and mean weight distribution as trophic components. Furthermore, we used stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ to determine the ontogenetic and seasonal changes in diet using Bayesian mass-balanced isotopic mixing models (MixSIAR) (Stock and Semmens, 2016) and corrected standard ellipses area (SEA_c) and Bayesian standard ellipses area (SEA_b) using SIBER – Stable Isotope Bayesian Ellipses in R (Jackson et al., 2011) to estimate niche width and overlap. Then, we examined if spatial differences did coincide with seasonal differences in the trophic habits and plasticity. This is to our knowledge one of the first studies to use this multidisciplinary approach to analyze the spatial and seasonal variations of European hake distribution and trophic ecology, accounting for ontogenetic changes. Specifically, we hypothesized that seasonal changes observed in European hake distribution could be partly due to prey availability, in addition to environmental variability, which could change between the juvenile and the adult stages of the population due to dissimilar trophic preferences or feeding capabilities.

MATERIALS AND METHODS

Data Collection

In order to estimate biomass and abundance, European hake individuals were collected from two experimental fishing surveys conducted in winter (22 February-8 March) and summer (2–17 July) 2013 (ECOTRANS Project, Institut de Ciències del Mar - CSIC) on board of the RV Ángeles Alvariño. These surveys were conducted in the northwestern Mediterranean Sea (**Figure 1**) covering an extension of ~8,000 km^2, including the continental shelf and upper slope. Sampling sites were randomly distributed over the continental shelf areas and the upper slopes, with a total of 82 hauls conducted; 37 in winter and 45 in summer (**Figure 1**). Experimental fishing surveys were performed following EU-funded Mediterranean Trawl Survey (MEDITS) trawling protocols (see Bertrand et al., 2002) using a GO73 experimental mesh of 10 mm (stretched mesh). On board, all organisms were identified and classified to the lowest taxonomic level. In addition, the length frequency distribution (TL, in cm) and total number of individuals per haul was recorded. Biological sampling on board was done for 103 European hake's individuals, the body length (TL, in cm) and weight (to the nearest 0.001 g) was measured and a piece of muscle tissue was taken and frozen at −20°C. Sampled individuals ranged from 7.3 to 50.2 cm in total length. We classified individuals into two size ranges (juveniles, $TL < 25$ cm, and mature adults, $TL \geq 25$ cm; **Supplementary Table 1**) based on the first maturity for this area of the Mediterranean Sea (Bozzano et al., 1997; Lleonart, 2002).

Estimates of biomass (kg/km^2) and abundance (n/km^2) were calculated with the standard swept area method for all the species collected.

Bayesian Species Distribution Models

Explanatory and Response Variables

The biomass and abundance data for European hake was used to calculate mean weight data (kg/n) (biomass/abundance in kg/n) (Chih-Lin et al., 2010; Garofalo et al., 2018) per haul and was used as the response variable to develop the B-SDMs. As European hake weight increases with length and age, generally heavier individuals are larger and older (i.e., adults), whereas lighter individuals are smaller and younger (i.e., juveniles) (Recasens et al., 1998; Mellon-Duval et al., 2010; Soykan et al., 2015). According to the length-weight relationship for European hake for the western Mediterranean ($a = 0.048$, $b = 3.055$) (Morey et al., 2003), for an individual of 25 cm (adult), the corresponding mean weight would be around 0.0895 kg. Mean weight is used here as a proxy of body size and consequently age class (**Supplementary Table 6**).

Sea Bottom Temperature (SBT, in °C) and bathymetry (in meters, m) were selected as the main environmental explanatory predictors for the species distribution models. We chose these two environmental predictors based on previous studies conducted with European hake in the Mediterranean Sea (Lleonart, 2002; Maravelias et al., 2006; Katsanevakis et al., 2009; Sion et al., 2019). Bathymetry data was obtained from EMODnet bathymetry (http://portal.emodnet-bathymetry.eu/) and Sea Bottom Temperature (SBT, °C) for each haul was collected through CTDs conducted during the survey cruises (**Supplementary Figure 2**). QGIS software (QGIS-Development-Team, 2012) was used to generate raster maps [Inverse Distance Weighted (IDW) interpolation], at a 0.1° x 0.1°; resolution) with the interpolate SBT data collected *in situ* during the survey to the entire study area for both seasons (**Supplementary Figure 2**).

To create prey distributions variables, we first identified potential prey for European hake in the western Mediterranean Sea based on published studies (Bozzano et al., 1997, 2005; Cartes et al., 2004, 2009; Ferraton et al., 2007; Mellon-Duval et al., 2017) (**Supplementary Table 2**). From the prey species identified in these studies, we selected those that were also collected during our surveys. We ended up with a total of 54 potential preys' species in winter and 38 in summer (**Supplementary Table 3**), aggregated in two functional categories (fish and crustaceans), for each season. For both potential prey groups, total values of biomass (kg/km^2) and abundance (n/km^2), as well as mean weight (biomass/abundance, in kg/n), were calculated per haul. Abundance and mean weight data for each group were plotted and interpolated [Inverse Distance Weighted (IDW)

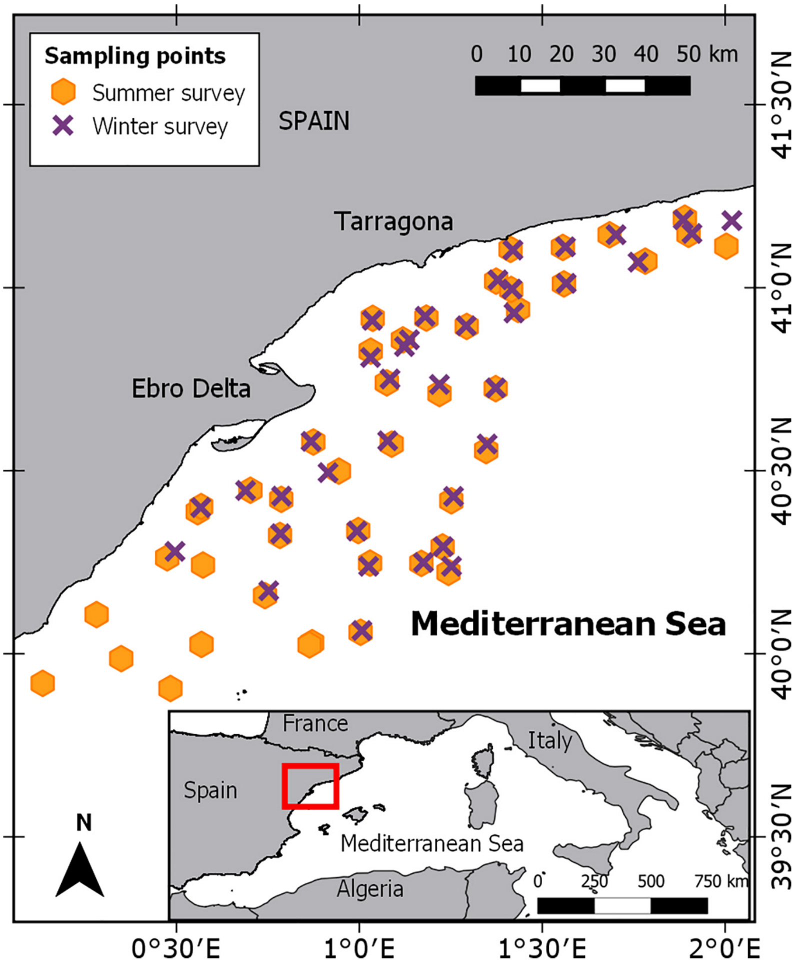

FIGURE 1 | Study area and geographical positions of the sample sites of ECOTRANS survey for winter and summer.

interpolation] at a 0.1 × 0.1 degree spatial resolution, for both seasons, using QGIS software (QGIS-Development-Team, 2012; **Figure 2**).

Response variables were aggregated at the same spatial resolution of 0.1 × 0.1 degrees for each season using the "raster" package (Hijmans, 2018) in the R software (R version 3.5.1.) (R Core Team, 2018). Standardized data exploration techniques were used to identify any outliers and possible correlation and collinearity between the explicative variables (Zuur et al., 2010). In particular, all the variables were checked for linearity with the draftsman's plot, for multi-collinearity using the *corvif* function in R software (R version 3.5.1) (R Core Team, 2018) that assesses the Generalized Variance-Inflation Factors (GVIF) (Fox and Weisberg, 2011), and for correlation using Spearman measure with the *corrplot* function (Wei and Simko, 2017) in R software. A GVIF lower than 3 and a correlation lower than 0.70 were found for all the explanatory variables in winter and summer (**Supplementary Figure 8**) (Zuur et al., 2010; Dormann et al., 2013). Moreover, to better interpret both the direction (positive or negative) and magnitudes (effect sizes) of the parameter estimates in relation to the others, the explanatory variables were standardized, *i.e.,* difference from the mean divided by the corresponding standard deviation (Gelman et al., 2008).

Spatial Model Fitting, Estimation, Validation and Prediction

Hierarchical Bayesian species distribution models (B-SDMs) were implemented to identify the relationships of the explanatory variables with the European hake's mean weight and to map posterior predicted probabilities of this species in both seasons. In particular, we developed and compared four different models, two for each season, using the environmental characteristics corresponding to the season (bathymetry and SBT), and alternating the corresponding seasonal abundance and mean weight of the preys (fish and crustaceans, see **Table 1**).

Despite mean weight data could take any positive value, in this specific case the European hake's mean weight data ranged between 0 and 1. Therefore, for each model, we used a beta distribution $Y_i \sim Be\ (\mu_i,\Phi_i)$ for the response variable Y_i at the location i. This type of beta distribution fulfils the required characteristics of this dataset while being very flexible

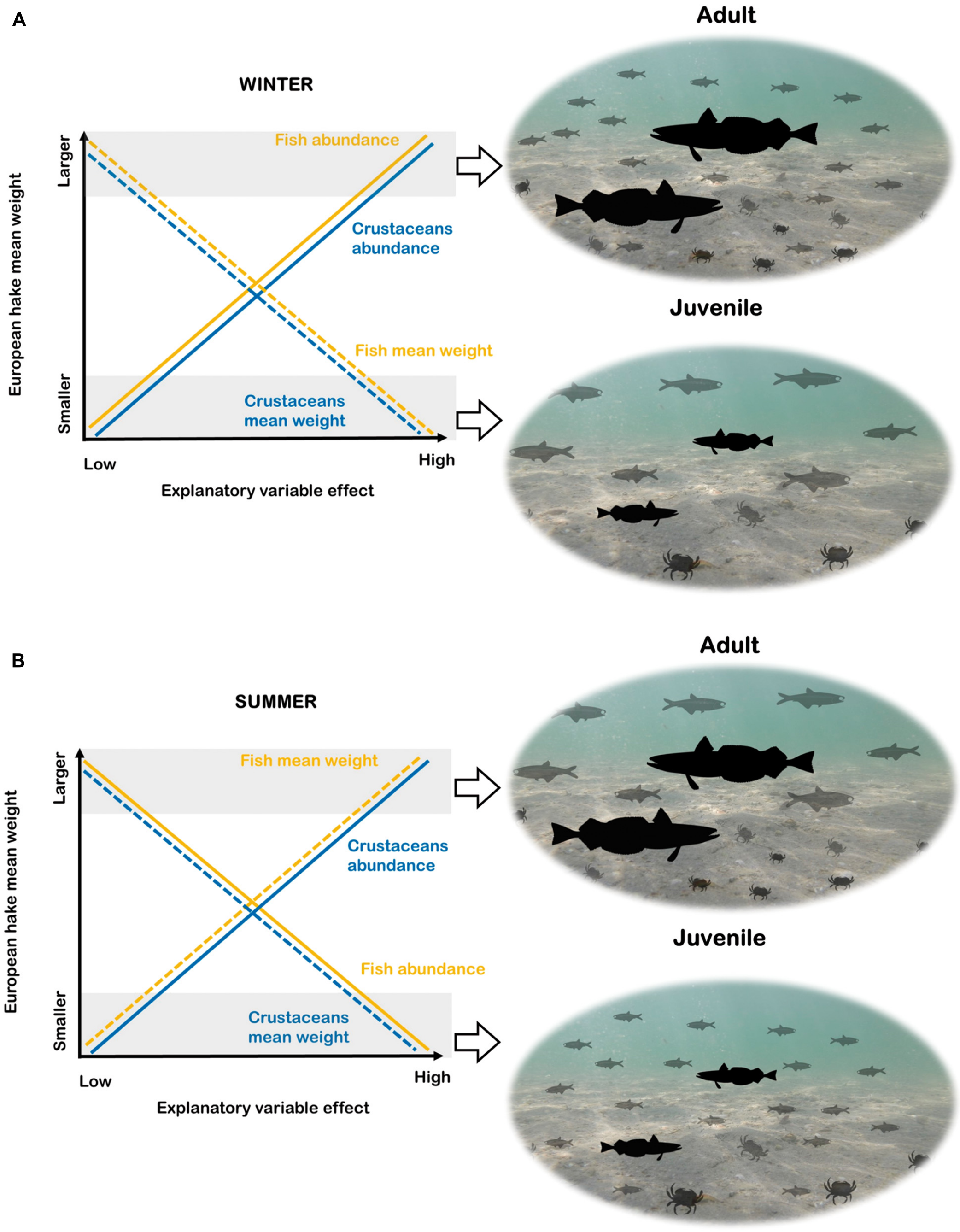

FIGURE 2 | Graphical interpretation of the results for the species distribution models (B-SDM) in winter **(A)** and summer **(B)**. The y-axis of the graphs show the response variable (European hake mean weight) and the x-axis the intensity (from lower to higher) of the explanatory variables of "Fish" and "Crustaceans." The yellow lines represent "Fish" and the blue lines "Crustaceans". In both cases, the straight line is used to represent the response variables related to abundance and the dotted line the response variables related to mean weight. Images from PhyloPic: European hake ("http://phylopic.org/image/8d92b454-3131-4bbd-ac9c-e1df14c2fc5a/") this image available for reuse under the Public Domain Mark 1.0, Engraulidae ("http://phylopic.org/image/6bd3702d-3ef1-44d0-83bf-93377875017c/") by M. Kolmann this image available for reuse under the Public Domain Mark 1.0 and *Liocarcinus depurator* "http://phylopic.org/image/01dd976b-f6e9-4204-bae1-c15a32234f73/") by Hans Hillewaert (vectorized by T. Michael Keesey) this image available for reuse under the Creative commons attribution-share Alike 3.0 Unported. "license."

in terms of shapes (Gupta and Nadarajah, 2004; Paradinas et al., 2016). Nevertheless, in the event that these kind of models are repeated and the mean weight values exceed 1, a beta distribution would not be suitable. In addition to the explanatory variables a spatial unstructured random effect was added to each model to account for the spatial correlation. For this spatial

TABLE 1 | Summary table of the four Bayesian species distribution models performed (*Model 1, Model 2, Model 3, and Model 4*).

		Explanatory variables							
		Bat	SBT	Prey Abundance (kg/km^2)		Prey Mean weight data (kg/n)			
Models	**Season**			**Fish**	**Crustacean**	**Fish**	**Crustacean**	**ρ**	**Failures**
Model 1	Winter	▨	▨	▨	▨			0.77*	0
Model 2	Winter	▨	▨			▨	▨	0.75*	0
Model 3	Summer	▨	▨	▨	▨			0.24	0
Model 4	Summer	▨	▨			▨	▨	0.44*	0

*Spearman's spatial correlations (ρ), between observed and predicted values indicate the goodness of the predictions. The * symbols marks the significance (p-value < 0.01) of this correlation. The column "Failures," indicates the sum of the failure vector calculated by the internal leave-one-out cross-validation of R-INLA. Gray cells indicate the included variables in each model. Variables acronyms are: Bat (Bathymetry, m), and SBT (Sea Bottom Temperature, °C). All models include the spatial effect.*

component, a multivariate Gaussian distribution with mean zero and a Matérn correlation matrix was assumed (Muñoz et al., 2013). For the fixed effects, we assigned a non-informative zero-mean Gaussian prior distribution with a variance of 100, as no prior information was available. B-SDMs were performed using the Integrated Nested Laplace Approximation (INLA) methodology and software[1] (Rue et al., 2009). To evaluate the goodness-of-fit of each model, we used the R-INLA (Rue et al., 2009) internal cross validation procedure, which consists on a leave-one-out cross-validations that generate a failure vector ranging from 0 to 1 (values equal to 0 mean that the predictive measure is reliable while values equal to 1 indicate that the predictive measure for that particular observation is not reliable) (Blangiardo and Cameletti, 2015).

Seasonal European hake's mean weight predictions were then generated predicting the response variable for the entire study area using linear interpolation via a Bayesian kriging (Pennino et al., 2013). To assess the fit of the predicted model, predicted and observed values were compared using using the *corLocal* function (Hijmans, 2018) of the R software that compute the Spearman's spatial correlations *r*. As usual, values of Spearman's correlation range from −1 to 1, being 1 equal to a perfect positive correlation between the two datasets (Spearman, 1904).

Stable Isotopes Analysis

All collected muscle hake samples were freeze-dried and powdered, and 0.28-0.33 mg of each sample was packed into tin capsules. Stable isotope analyses were performed at the Laboratorio de Isótopos Estables Estación Biológica de Doñana[2]. Samples, were combusted at 1020°C using a continuous flow isotope-ratio mass spectrometry system by means of a Flash HT Plus elemental analyzer coupled to a Delta-V Advantage isotope ratio mass spectrometer via a CONFLO IV interface (Thermo Fisher Scientific, Bremen, Germany). The isotopic composition was reported in the conventional delta (δ) per mil notation (‰), relative to atmospheric N_2 ($\delta^{15}N$) and Vienna Pee Dee Belemnite ($\delta^{13}C$). Replicate assays of standards routinely inserted within the sampling sequence indicated analytical measurement errors of ± 0.2 and ± 0.1 for $\delta^{15}N$ and $\delta^{13}C$, respectively. The standards used were: EBD-23 (cow horn, internal standard), LIE-BB (whale baleen, internal standard) and LIE-PA (razorbill feathers, internal standard). These laboratory standards were previously calibrated with international standards supplied by the International Atomic Energy Agency (IAEA, Vienna). Because all samples showed a C:N ratio lower than 3.5‰ we did not correct the $\delta^{13}C$ values to account for the presence of lipids in muscle samples (Logan and Lutcavage, 2008).

The values of $\delta^{15}N$ and $\delta^{13}C$ were used to calculate corrected standard ellipses area (SEA_c, area containing 40% of the data) and Bayesian standard ellipses area (SEA_b) as a measure of trophic width, using "SIBER" – Stable Isotope Bayesian Ellipses in R (Jackson et al., 2011). These metrics allowed comparing the degree of niche width and overlap between seasons (winter vs. summer) and between life stages (adults *vs* juveniles) (**Table 3**). Differences on $\delta^{15}N$ and $\delta^{13}C$ values between hake ontogenetic groups (adults *vs* juveniles) and seasons (winter *vs* summer) were tested using a 2-way semiparametric permutation multivariate analyses (PERMANOVA tests) and pairwise tests on the Euclidian distance matrix with the software PRIMER-E 6 with PERMANOVA (Anderson et al., 2008); the latter only performed in the case of significance results ($p < 0.05$) for the interaction of both factors (season*stage).

To assess the relative contribution of different preys in the diet of juveniles and adults of European hake in winter and summer, we used the mass-balanced Bayesian stable isotope mixing model MixSIAR (Stock et al., 2018). Bayesian isotopic mixing models incorporate uncertainty in the consumers, sources and diet-to-tissue discrimination factors and are capable of producing robust estimates on complex dietary systems (Parnell et al., 2010), as it is the case of this generalist predator. Prey items included in the MixSIAR models were selected based on the diet published information from stomach content analysis (**Supplementary Tables 2**, **4**). Only those species/groups representing > 5% of the stomach content in percentage of weight (%W) or index of relative importance (%IRI) were included in the MixSIAR models. Potential prey species were 21 (**Supplementary Table 4**). Stable isotope values from these identified prey species were taken from an isotopic database containing demersal and pelagic species collected during the same oceanographic survey as

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[1] http://www.r-inla.org/

[2] www.ebd.csic.es/lie/index.html

hake (ECOTRANS Project Isolibrary) and published literature (Madurell et al., 2008; Fanelli et al., 2009; Valls et al., 2014; Barría et al., 2015, 2018; **Table 6**). In order to reduce the end-members of the mixing model *a priori* cluster analysis was performed. Potential preys were grouped in 5 different clusters based in their isotopic similarities after applied Ward's hierarchical cluster analysis. Some clusters are exclusively formed of crustaceans' species; as it is the case of cluster 2, 3, and 4, whereas cluster 1 is exclusively formed of fish species. On the other hand, cluster 5 consists on a mixture of fish and crustaceans' species. (Cluster 1: *Cepola macrophthalma, Boops boops, Spicara maena, Spicara smaris, Argentina sphyraena, Trisopterus minutus, Lepidopus caudatus, Sardina pilchardus, Maurolicus muelleri, Gadiculus argenteus,* and *Micromesistius poutassou;* Cluster 2: *Chlorotocus crassicornis*, *Nematoscelis megalops,* and *Phronima sedentaria*; Cluster 3: *Vibilia armata*; in violet, Cluster 4: *Anchialina agilis* and *Meganyctiphanes norvegica* and Cluster 5: *Engraulis encrasicolus, Plesionika heterocarpus, Sardinella aurita,* and *Solenocera membranacea*, **Figure 5** and **Supplementary Figure 3**). These five prey groups were likely to explain the isotopic signature of all the consumers as they all fell within the 95% probabilities of the mixing region (see **Supplementary Figure 4**), verifying that the fitted model could correctly calculate the source contribution for all the consumers (Smith et al., 2013).

Five MixSIAR models were constructed (**Supplementary Table 5**) using season and stage as categorical variables, as well as total length as continuous variable. The continuous variable was included as the linear regression between the isotopic values of $\delta^{15}N$ and $\delta^{13}C$ and individual's total length (TL, in cm) was found to be significant (**Supplementary Figure 5**). Model selection was based on the deviance information criterion (DIC) and on the relative support for each model (Leave-one-out cross validation (LOO) and Akaike weights) using *compare_models* function of the "MixSIAR" packages in R software (**Supplementary Table 5**). When running the models, a diet-to-tissue discrimination factors (DTDF) of $\Delta^{13}C = -0.25\ \delta^{13}C - 3.48$ and $\Delta^{15}N = -0.28\ \delta^{15}N + 5.88$ was used (Caut et al., 2009). Convergence was assessed using the Geweke-test and Gelman-Rubin diagnostics. MixSIAR models were run on the "extreme" setting (with 3 Markov chains Monte Carlo (MCMC), 3,000,000 iterations, a burn-in-phase of 1,500,000 and a thinning of 100). Residual and process error were included in the models, except for when total length is a covariate, in which cases, following recommendations (Stock et al., 2018), process error was not included.

RESULTS

Spatial Explanatory Variables

According to the winter models (*Model 1* and *Model 2*) there was a positive relationship of fish and crustaceans' abundance with European hake mean weight and negative relationship with fish and crustaceans' mean weight (**Tables 1**, **2**, **Figure 2**). This means that adults of European hake (areas with higher mean weight) were related to higher abundances of small-size (low mean weight) fish and crustaceans (**Figure 2**). The opposite occurred for low values of the response variable (areas with lower mean weight, thus more presence of juveniles)

TABLE 2 | Summary of the posterior distribution for the four models (*Model 1, Model 2, Model 3, and Model 4*).

Models	Season	Predictor	Mean	SD	$Q_{0.025}$	$Q_{0.50}$	$Q_{0.975}$
Model 1	Winter	Intercept	−3.309	1.15	−5.59	−3.31	−1.05
		Bathymetry	−0.939	1.30	−3.54	−0.92	1.58
		Sea Bottom Temperature	0.001	0.16	−0.32	0.00	0.32
		Fish (abundance)	0.098	0.08	−0.07	0.10	0.23
		Crustacean (abundance)	0.066	0.07	−0.07	0.07	0.20
Model 2	Winter	Intercept	−2.356	0.85	−4.07	−2.34	−0.72
		Bathymetry	0.185	0.92	−1.70	0.21	1.93
		Sea Bottom Temperature	−0.088	0.16	−0.41	−0.09	0.23
		Fish (mean weight)	−0.070	0.08	−0.22	−0.07	0.09
		Crustacean (mean weight)	−0.070	0.09	−0.27	−0.07	0.10
Model 3	Summer	Intercept	−1.192	0.51	−2.24	−1.18	−0.23
		Bathymetry	2.357	0.64	1.06	2.37	3.57
		Sea Bottom Temperature	−0.048	0.07	−0.20	−0.04	0.08
		Fish (abundance)	−0.204	0.07	−0.37	−0.20	−0.08
		Crustacean (abundance)	0.016	0.04	−0.06	0.02	0.08
Model 4	Summer	Intercept	−2.522	0.56	−3.66	−2.51	−1.46
		Bathymetry	0.622	0.68	−0.74	0.64	1.91
		Sea Bottom Temperature	−0.094	0.09	−0.28	−0.09	0.07
		Fish (mean weight)	0.019	0.05	−0.08	0.02	0.11
		Crustacean (mean weight)	−0.007	0.06	−0.12	−0.01	0.11

It includes the mean, the standard deviation (SD), the median ($Q_{0.50}$) and a 95% credible interval ($Q_{0.025}$ - $Q_{0.975}$), which is a central interval containing 95% of the probability under the posterior distribution. All models include the spatial effect.

that were related to lower abundances of large-size (high mean weight) fish and crustaceans (**Figure 2**). On the other hand, in summer (***Model 3*** and ***Model 4***), high values of the response variables (high mean weight, more presence of adults) were related to higher abundances of small-size (low mean weight) crustaceans and with lower abundance of large-size (high mean weight) fish. Again, the opposite occurred for low values of the response variable (areas with more presence of juveniles) that were related to higher abundances of small-size (low mean weight) fish and lower abundances of large-size (high mean weight) crustaceans (**Figure 2**). Related to the environmental variables, overall SBT had a negative relationship with the response variable, meaning that the larger mean weight individuals (adults) prefer lower SBT and thus, colder temperatures (**Table 2** and **Supplementary Figure 6**). According to previous results, overall bathymetry has a positive relationship with the European hake's mean weight on the continental shelf, meaning that larger mean weight individuals (adults) tend to prefer deeper waters (**Table 2** and **Supplementary Figure 6**).

European Hake's Spatial Distributions

The "failure vector" showed extremely low values in all cases (<0.1), proving a good goodness of fit of the models (**Table 1**). Furthermore, Spearman's correlation between the predicted and observed mean weight also showed significant correlations in three of the four models (**Table 1**). The predicted posterior mean weight distribution of European hake showed spatial differences between winter and summer (**Figure 3**). In winter, higher mean weight areas were predicted on the southern of the Ebro Delta, close to the coast; whereas in summer, higher mean weight were predicted in all the northern part of the study area, showing respectively clustering areas southern to the Ebro Delta and northern of Tarragona (**Figures 1, 3**). Both winter models (***Model 1*** and ***Model 2***) predict very similar posterior spatial distribution patterns and same occurred for both summer models (***Model 3***

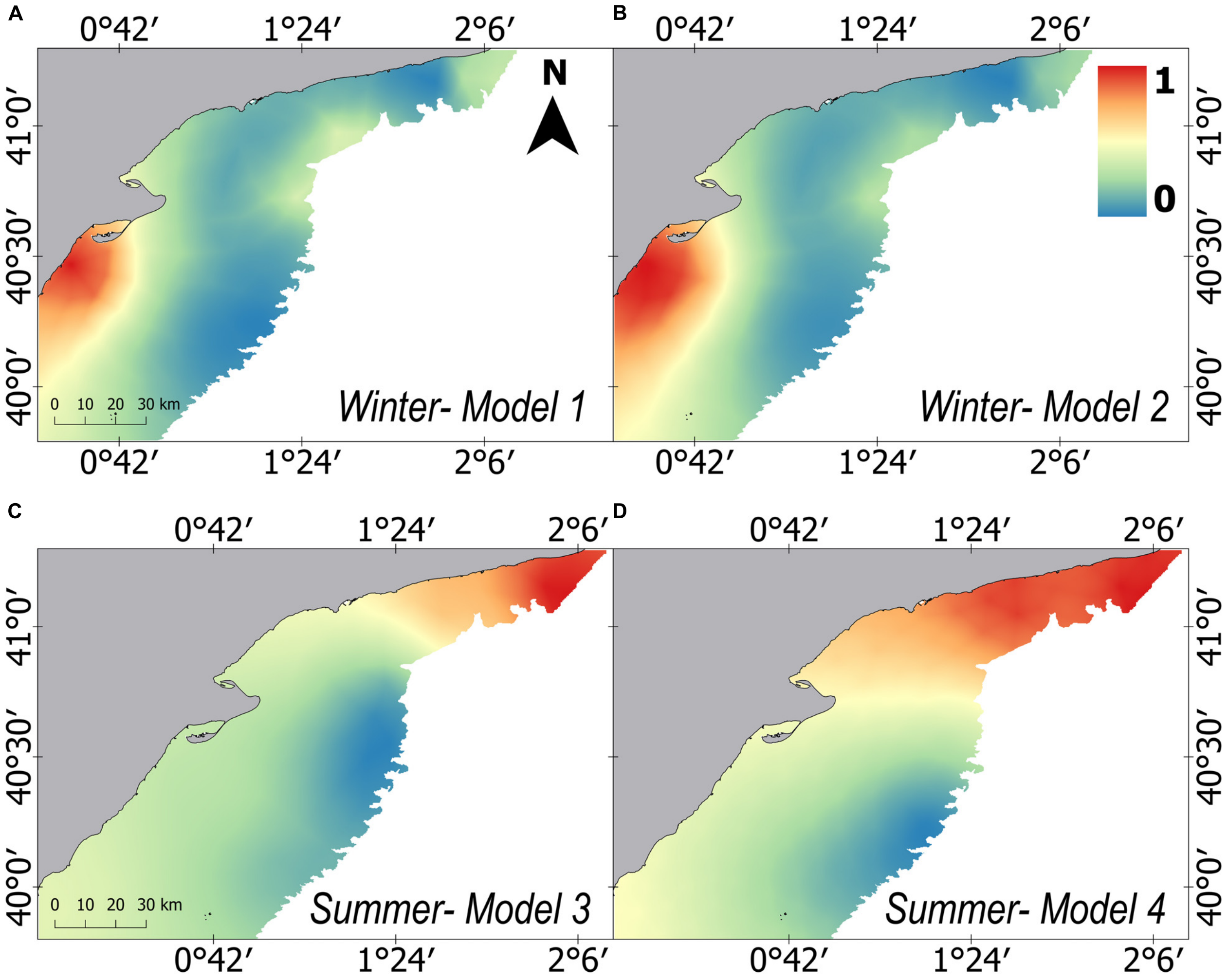

FIGURE 3 | Predicted distribution of the posterior mean of the relative mean weight (kg/n) for European hake in winter **(A,B)** and summer **(C,D)** for each one of the four models developed. Model 1 and Model 3 consider prey explanatory variables on abundance measure, whereas Model 2 and Model 4 include prey explanatory variables on mean weight measure. All results have been standardized and share a common scale ranging from 0 to 1.

and ***Model 4***). The only distinguishable difference for models using fish and crustacean's abundance (***Model 2*** and ***Model 4***) being that the predicted areas of high mean weight are subtly more confined and concentrated (**Figures 3B–D**).

Stable Isotopes Results

δ^{13}C values of European hake ranged from −20.29 ‰ to −17.94 ‰, and from 7.44 ‰ to 11.81 ‰ in the case of δ^{15}N values (**Table 3**). Significant differences were found for δ^{13}C between life stages (pseudo-F = 119.82, $p < 0.001$) and season (pseudo-F = 22.72, $p < 0.001$) but not for the interaction between season and stage (pseudo-F = 3.01, $p = 0.08$). For δ^{15}N values, we only found differences between stages (pseudo-F = 129.21, p-value < 0.001) and for the interaction between season and stage (pseudo-F = 12.32, p-value < 0.001). Pairwise analysis showed differences between juveniles and adults for summer (p-value < 0.001) and winter (p-value < 0.001). Differences were also observed in the case of juveniles and adults between winter and summer (p-values < 0.05) (**Tables 4**, **5** and **Figure 4**). Regarding the isotopic niche, the group of juveniles-summer presented the smallest standard ellipses area (SEA$_B$), followed by adults-winter, juveniles-winter and finally, adults-summer (**Figure 4** and **Table 4**).

The best MixSIAR model was the one that included fish length as a continuous variable and season as a factor (**Supplementary Table 5**). Outputs indicated that the relative importance of the different prey groups in the diet of European hake changed with season and fish length (cm) (**Figure 6**). In winter, the smallest European hakes consumed mainly the prey included in Cluster 3, followed by Cluster 4 and Cluster 5. As we moved to larger sizes, there was a sharp decrease in Cluster 3 and an increase in Cluster 2. Moreover, Cluster 4 also decreased with size, representing almost 0% of the diet proportion for the largest individuals. The opposite occurred for Cluster 2, which was absent in the diet of small individuals and its proportion increased with fish length. Noteworthy, the highest proportion of Cluster 5 occurred for intermediate fish lengths. On the other hand, in summer, Cluster 4 dominated the diet of the smallest individuals followed by Cluster 3, the latter at a lower proportion than in winter. The proportion of Cluster 4 decreased with fish length at the same time that Cluster 2 increased. During summer, Cluster 5 represented lower proportion for all fish length, but maintained maximum values at intermediate fish length. Cluster 1 appeared similar to winter results.

TABLE 3 | Summary table of δ^{13}C and δ^{15}N stable isotopes values of European hake for each age and season.

		δ^{13}C (‰)				δ^{15}N (‰)			
Group	**n**	**mean**	**SD**	**min**	**max**	**mean**	**SD**	**min**	**max**
Adults-winter	27	−18.49	0.30	−18.98	−17.94	10.23	0.75	9.11	11.81
Adults-summer	13	−19.00	0.41	−19.55	−18.17	9.55	1.00	7.77	11.19
Juveniles-winter	28	−19.48	0.45	−20.11	−18.62	7.98	0.75	7.02	9.93
Juveniles-summer	35	−19.71	0.32	−20.29	−19.03	8.36	0.52	7.44	9.79

n: number of samples, SD: standard deviation, min: minimum values and max: maximum values.

TABLE 4 | Bayesian Standard Ellipses Area (SEA$_B$) values for each life stage (Adult-Juvenile) and each season (winter-summer).

	Adults-winter	**Adults-summer**	**Juveniles-winter**	**Juveniles-summer**
Min	0.3109	0.3905	0.3412	0.2205
Median	0.5769	0.9245	0.5801	0.3864
Mean	0.5927	0.9773	0.5942	0.3934
Max	1.3676	2.8402	1.2206	0.7895

Min: minimum values and Max: maximum values.

DISCUSSION

The spatial distribution of marine species is known to be affected by interannual and seasonal environmental factors and habitat parameters, but also by species interactions factors (Gilinsky, 1984; Hixon and Carr, 1997; Carney, 2005; Morfin et al., 2012). In the present study, we applied a multidisciplinary approach that analyses the spatial distribution of European hake, using its main environmental and feeding related drivers explaining European hake distribution. For this, we applied Hierarchical Bayesian species distribution models (B-SDMs) and stable isotope analysis, considering a seasonal and ontogenetic perspective. Overall, our results showed seasonal and ontogenetic differences in the spatial distribution of European hake in the northwestern Mediterranean Sea. In addition to the effect of particular environmental factors, these spatial changes were partially explained by the distribution of the main prey consumed by European hake. We also gathered information about the ontogenetic and seasonal variation in European hake diet to provide further insight into how feeding preferences may affect species spatial occurrence.

Our species distribution models showed that adult individuals had a tendency to be present in deeper areas, with lower bottom temperatures. These environmental preferences have already been described for this species in the Mediterranean Sea (Demestre and Sánchez, 1998; Maravelias et al., 2006; Katsanevakis et al., 2009; Sion et al., 2019). Particularly, bathymetry has repeatedly been reported as a main driver in hake spatial distribution (Recasens et al., 1998; Orsi-Relini et al., 2002; Maynou et al., 2003; Paradinas et al., 2015). The importance of temperature and depth as key factors on SDMs has also been reported to vary intra-annually. For example, in the Aegean Sea (Central Mediterranean Sea) in 2016, the effect of temperature in the distribution of European hake was more pronounced during months of thermal stratification (Yalçln and Gurbet, 2016). Indeed the influence of environmental factors on determining abundance of demersal fish in general are reported to be intensified during summer and autumn in the Aegean Sea (Katsanevakis et al., 2009). Furthermore, a seasonal and ontogenetic migration along the bathymetric gradient was

TABLE 5 | Percentage of Bayesian Standard Ellipses Area (SEA_B) overlap between European hake adults and juveniles for summer and winter.

	Adults-winter	Adults-summer	Juveniles-winter	Juveniles-summer
Adults-winter	-	46.1 (35.63- 56.02)	22.51 (14.35-29.96)	12.57 (3.96-23.94)
Adults-summer	76.67 (59.38-90.68)	-	10.25 (2.51-19.91)	12.96 (1.80-22.48)
Juveniles-winter	21.53 (16.21-31.12)	7.26 (1.33-13.40)	-	14.48 (6.16-23.30)
Juveniles-summer	8.15 (2.06-15.77)	8.26 (1.13-16.07)	8.57 (4.21-15.07)	-

The 25% and 75% credible intervals of the overlap are given between parentheses.

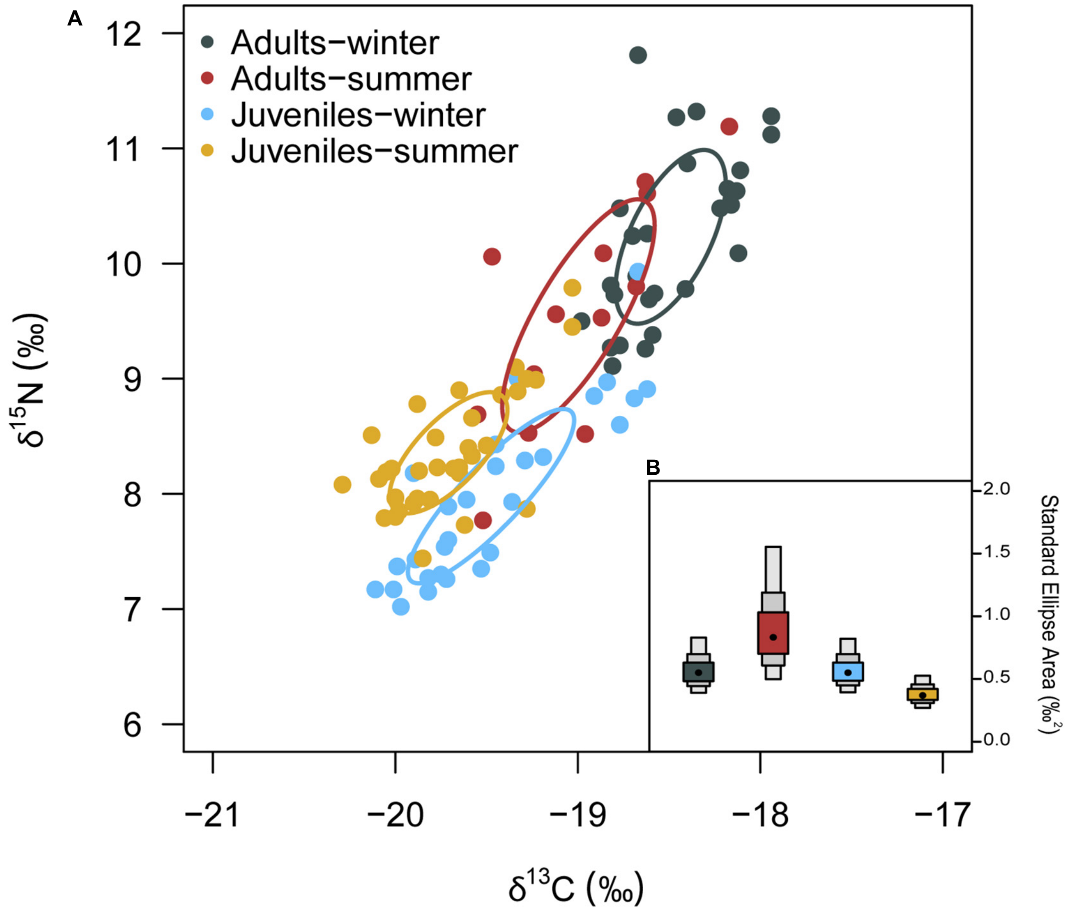

FIGURE 4 | (A) $\delta^{13}C$ and $\delta^{15}N$ values and corrected Standard Ellipses Area (SEAc) for European hake by season and stage. **(B)** Bayesian standard ellipses area (SEA_B) for each groups. Density plots represent the 95, 75 and 50% credibility intervals of SEA_B.

also observed for European hake outside the Mediterranean Sea, for example in the Galician waters (Atlantic Ocean) (Fariña et al., 1997).

Our results showed a spatial segregation between adult and juvenile European hakes, with adults mainly present in the southern area during winter and in the northern area during summer. Ontogenetic spatial differentiation and areas of aggregation for this species have previously been related to life cycle events (Demestre and Sánchez, 1998), nursery areas (Druon et al., 2015), areas with high food availability (Sion et al., 2019) or changes in diet (Carpentieri et al., 2005; Garofalo et al., 2018). In general, it seems that adult females choose deeper areas whereas juveniles prefer the shallower continental shelf (Demestre and Sánchez, 1998). For instance, a study from late spring of 2015 using the same modeling approach than us detected three main hotspots area for European hake nurseries in the northwestern Mediterranean Sea, one of the three located northern of the Ebro Delta, similar to the distribution found here for adults' hake in winter (Paradinas et al., 2015). In this context, European hake in the western Mediterranean Sea presents a spawning peak during autumn and winter (Maynou et al., 2003), hence the aggregation found close to the Ebro Delta during winter in our study might also correspond to a reproduction/nursery area. Furthermore, changes in the spatial distribution between seasons have also previously been detected in our study area, with individuals

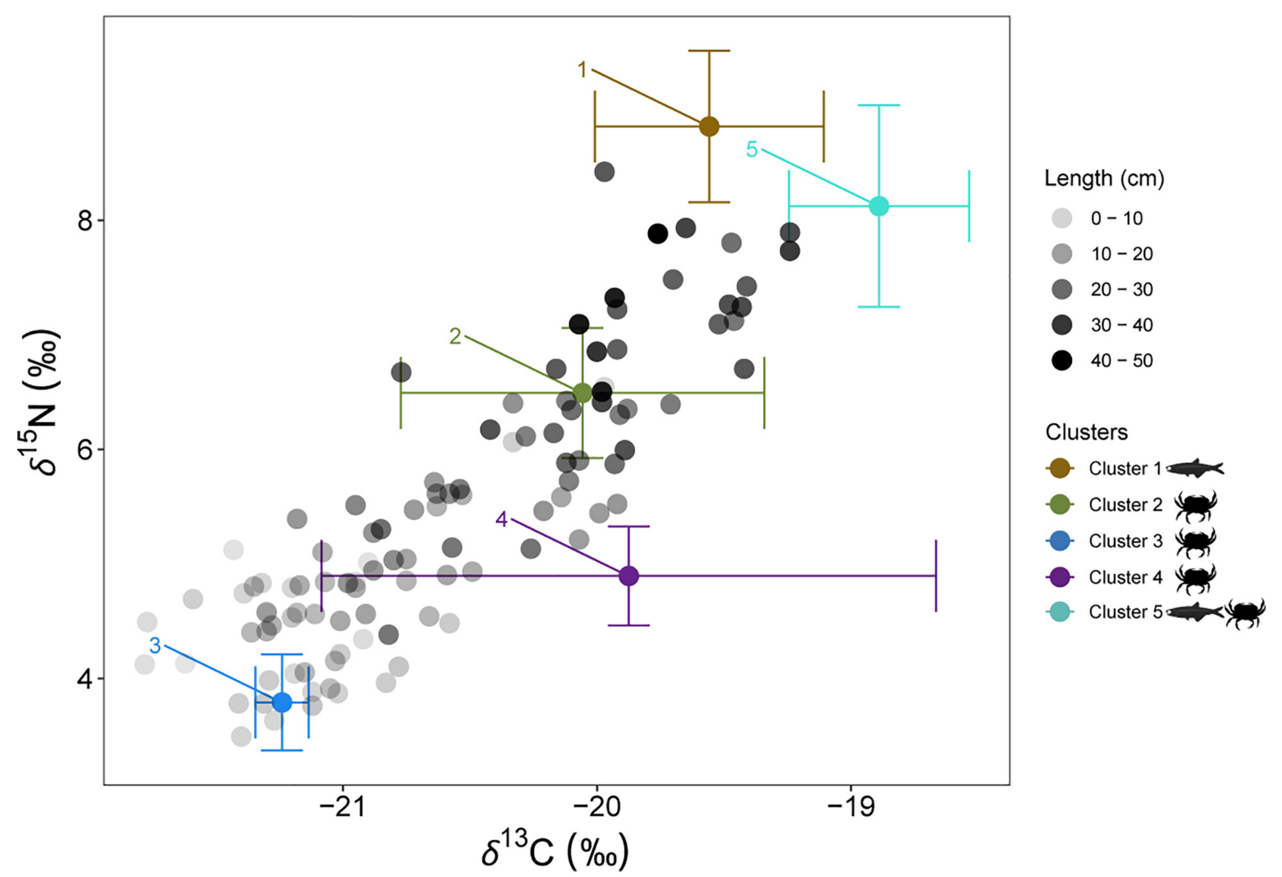

FIGURE 5 | Individual European hake $\delta^{13}C$ and $\delta^{15}N$ values and mean and standard deviation $\delta^{13}C$ and $\delta^{15}N$ values of the potential prey sources. Black shaded scale of European hake represents the body length of the individuals. In brown, **Cluster 1**: *Cepola macrophthalma, Boops boops, Spicara maena, Spicara smaris, Argentina sphyraena, Trisopterus minutus, Lepidopus caudatus, Sardina pilchardus, Maurolicus muelleri, Gadiculus argenteus* and *Micromesistius poutassou;* in green, **Cluster 2**: *Chlorotocus crassicornis*, *Nematoscelis megalops* and *Phronima sedentaria*; in blue, **Cluster 3**: *Vibilia armata*; in violet, **Cluster 4**: *Anchialina agilis* and *Meganyctiphanes norvegica* and in aquamarine, **Cluster 5**: *Engraulis encrasicolus, Plesionika heterocarpus, Sardinella aurita* and *Solenocera membranacea.*

intensifying their spatial differentiation during summer and spring (Demestre and Sánchez, 1998).

In addition to the importance of the environmental variables on the distribution of European hake and although bathymetry showed the highest impact in all four models, the distribution of European hake main prey, both fish and crustaceans, also provided valuable information explaining the distribution of hake in the northwestern Mediterranean Sea. Specifically, the spatial distributions and abundance of potential preys were used as indirect proxies of trophic behavior in species spatial occurrence (Navarro et al., 2016). However, just including prey distribution was not enough in this case, as European hake is an ambush predator and its mouth gape is a limiting factor for prey selection and ingestion (this being especially true for juvenile individuals) (Johnson et al., 2012). This is why we also considered the information about potential preys' size as an explanatory variable. In this regard, our results indicated that European hake's juveniles in winter were associated with low abundance of relatively large fish preys. The size of these individuals could potentially outbound the mouth gape limitations of the predators, and thus juvenile's European hake would mostly be feeding on small crustaceans as has been described in previous feeding studies (Mellon-Duval et al., 2017). However, in summer, juveniles are correlated with smaller and more abundant fish prey implying a potential capacity of also ingesting available small fish, in addition to crustaceans. Nevertheless, these results on their own were not sufficient to drawn a robust conclusion and the use of stable isotope analyses complemented the SDMs results providing additional information of European hake seasonal and ontogenetic trophic metrics.

In this context, differences in $\delta^{13}C$ and $\delta^{15}N$ values pointed out to potential differences in trophic habits of adults and juveniles between winter and summer. Furthermore, the low overlap between the different isotopic niches showed a strong degree of niche differentiation between seasons and stages, also confirmed by the mixing model. More specifically, the wide isotopic niche observed for adults suggests a more diversified feeding behavior, contrasting with the narrow isotopic niche breadth recorded for juveniles. This is in contrast with previous studies, in the same area and in the Tyrrhenian Sea (central Mediterranean Sea), that have described juveniles as being more opportunistic than adults (Modica et al., 2013). Our

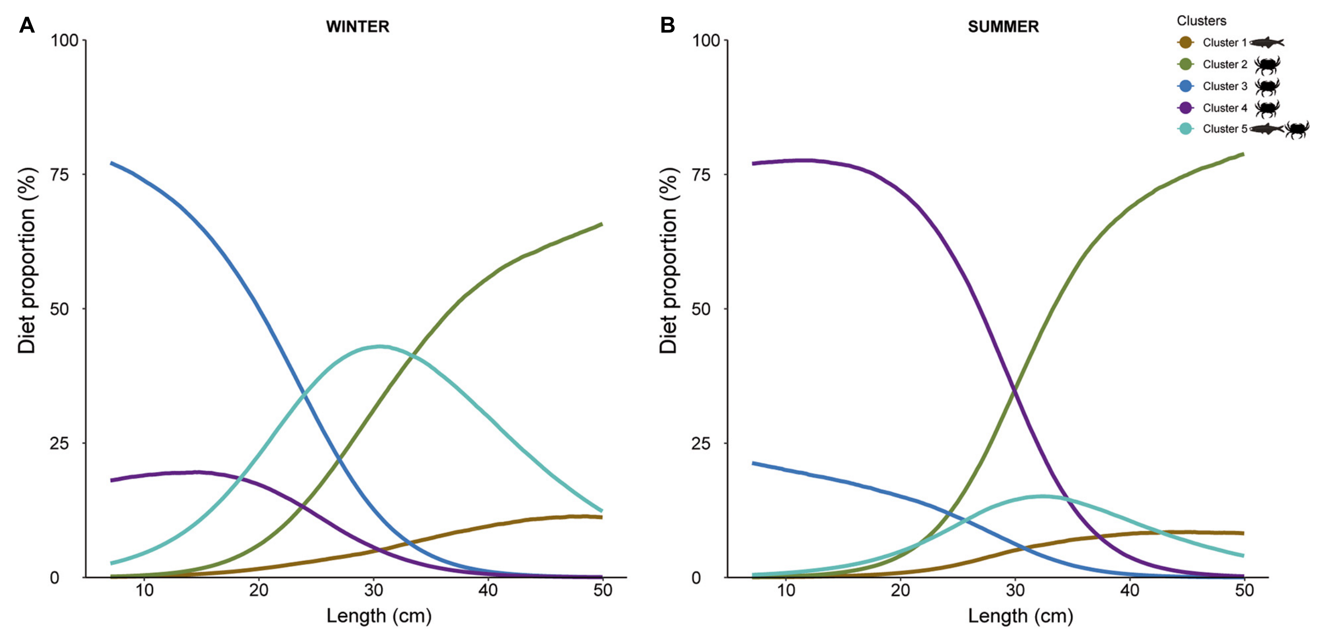

FIGURE 6 | MixSIAR model results showing estimated diet proportions of each potential prey clusters (1, 2, 3, 4, and 5) contributing to European hake diet, as a function of length (in cm) for each season (**(A):** winter and **(B):** summer). **Cluster 1**: *Cepola macrophthalma, Boops boops, Spicara maena, Spicara smaris, Argentina sphyraena, Trisopterus minutus, Lepidopus caudatus, Sardina pilchardus, Maurolicus muelleri, Gadiculus argenteus,* and *Micromesistius poutassou*, **Cluster 2**: *Chlorotocus crassicornis*, *Nematoscelis megalops,* and *Phronima sedentaria*, **Cluster 3**: *Vibilia armata*, **Cluster 4**: *Anchialina agilis* and *Meganyctiphanes norvegica,* and **Cluster 5**: *Engraulis encrasicolus, Plesionika heterocarpus, Sardinella aurita,* and *Solenocera membranacea.*

isotopic results also suggest a seasonal differentiation in adults' diet, with higher consumption of crustaceans during summer compared to winter. To a certain extent, this relates to our observations of the SDMs, as adults' hake during summer were correlated with small-size crustaceans. Related to juveniles, the differences in δ^{15}N values when compared to adults, and the positive trend with body size (**Supplementary Figure 5**) indicated ontogenetic variations in diet; with the lower values recorded for juveniles suggesting a consumption of lower trophic level organisms. In addition, MixSIAR outputs showed that cluster 3 (formed uniquely of the amphipod *Vibilia armata*) represented the highest diet proportion for juveniles in winter, followed by cluster 4 (formed exclusively of crustaceans) and the same clusters but in the opposite level of importance dominated for summer. This concurred with previous findings that reported a diet based on crustaceans for juveniles of European hake (Bozzano et al., 1997; Cartes et al., 2004, 2009; Ferraton et al., 2007).

However, partly contrasting the results of the B-SDM, juveniles larger than 20 cm in winter showed a higher proportion of cluster 5 (formed by several crustaceans and small fish, *i.e.*, *Sardinella aurita* and *Engraulis encrasicolus*) when compared to juveniles from summer. Consumption of small pelagic fish has also been recorded for this species for individuals as small as 7 cm in nearby areas (Gulf of Lions) (Mellon-Duval et al., 2017). Within this context, the SIA results suggested that summer juveniles may have been feeding on higher trophic levels prey sources, as they showed higher δ^{15}N values (Navarro et al., 2011) compared to juveniles in winter. However, rather than an increase of piscivorous diet during summer, it could be due to the fact that at this time of the year, juveniles feed more on cluster 4 than cluster 3, which occupied a slightly higher isotopic position. Nevertheless, it is important to consider that changes in δ^{15}N values can also reflect variations in the baseline rather than in diet, especially when comparing values from different seasons (Costalago et al., 2012; Mellon-Duval et al., 2017). Thus, further and more extensive analysis that include this aspect should be done to verify this seasonal variation in the diet.

Overall, our trophic analysis results were partly consistent with published data (Bozzano et al., 1997; Cartes et al., 2004, 2009; Ferraton et al., 2007), where juveniles showed a crustaceans dominated diet and switch to a more piscivorous diet as they reached larger body size. Here we observed an evident ontogenetic variation in diet, with increased consumption of fish preys as individuals reach intermediate and large body size. We also observed that the species of crustaceans consumed varied with ontogenetic stage and season. However, not all the studies concur on the body length and the reason why this switch occurs. It has been suggested that the diet's switch corresponds to an increase in individual's mobility in the water column (Mellon-Duval et al., 2017) along a proportional increase in mouth dimensions (Karpouzi and Stergiou, 2003) that facilitates ingestion of larger preys (Modica et al., 2013). Piscivorous diet has also been associated with the retinal changes and the improvement in vision acuity (Bozzano and Catalán, 2002) that permit European hake detects prey from higher distances and even in more turbid waters. These physiological

TABLE 6 | Number of samples, mean, standard deviation (SD) of $\delta^{13}C$ and $\delta^{15}N$ values of the prey used in the Bayesian mixing models to estimate the diet of European hake.

		$\delta^{13}C$		$\delta^{15}N$	
Species	**n**	**mean**	**SD**	**mean**	**SD**
Cluster 1: Fish	49	−19.56	0.45	8.82	0.66
Argentina sphyraena	3	−19.19	0.44	9.30	1.05
Boops boops	3	−19.73	0.39	9.29	0.60
Cepola macrophthalma	2	−20.40	0.05	8.16	0.04
Gadiculus argenteus	3	−19.43	0.13	8.85	0.69
Lepidopus caudatus	3	−19.71	0.10	8.43	0.24
Maurolicus muelleri	5	−19.39	0.10	9.02	0.02
Micromesistius poutassou	2	−19.43	0.12	8.83	0.25
Sardina pilchardus	19	−19.66	0.51	8.43	0.48
Spicara maena	3	−19.72	0.17	9.51	0.67
Spicara smaris	3	−19.15	0.57	9.58	1.04
Trisopterus minutus	3	−19.14	0.12	9.30	0.13
Cluster 2: Crustaceans	13	−20.06	0.72	6.49	0.57
Chlorotocus crassicornis	3	−19.71	0.63	6.99	0.47
Nematoscelis megalops	5	−20.33	0.61	6.57	0.25
Phronima sedentaria	5	−19.99	0.88	6.12	0.66
Cluster 3: Crustaceans					
Vibilia armata	5	−21.24	0.10	3.79	0.42
Cluster 4: Crustaceans	8	−19.88	1.21	4.90	0.43
Anchialina agilis	5	−19.47	1.39	4.82	0.51
Meganyctiphanes norvegica	3	−20.55	0.40	5.01	0.32
Cluster 5: Mixed (Fish & Crustaceans)	36	−18.89	0.35	8.12	0.88
Boops boops	3	−19.73	0.39	9.29	0.60
Engraulis encrasicolus	20	−18.87	0.25	7.62	0.73
Plesionika heterocarpus	3	−18.57	0.14	8.09	0.38
Sardinella aurita	10	−18.77	0.18	8.78	0.55

Summary statistics are provided for Cluster 1, 2, 3, 4, and 5. n: number of samples.

changes altogether will ease prey selectivity and an intake preference for higher energy preys (Stagioni et al., 2011; Modica et al., 2013).

Overall, our results show that seasonality plays a role when looking at the distribution and feeding behavior of European hake. Seasonality can affect prey availability and thus predators' diet. In our study, despite diet variations were more distinct between stages, differences between seasons should not be disregarded. Previous studies have also recorded diet variation with seasonality in the Western Mediterranean Sea (Mellon-Duval et al., 2017) and non-Mediterranean areas (Velasco and Olaso, 1998), with mixed conclusions. A study from the north-eastern Mediterranean Sea showed an increase in fish ingestion in winter and dominance of crustaceans during summer (Stagioni et al., 2011). This is partly in line with our results, as despite high proportions of cluster 2, 3, and 4 (formed exclusively of crustaceans) were observed during both seasons, consumption of cluster 5 (formed of fish and crustaceans) was overall higher during winter. Some studies have also recorded an increase on juveniles feeding on euphausiids in spring, coinciding with the aggregating reproductive behavior of this species (Ferraton et al., 2007), as well as an increase of gobiids consumption during autumn. Furthermore, a study from the Gulf of Lyon (northwestern Mediterranean Sea) found lower proportion of pelagic fish ingestion in adults' diet in spring when compared to autumn (Mellon-Duval et al., 2017).

Despite valuable information, and the novelty and benefits of using a continuous covariate in the MixSIAR analyses, which is a relatively novel technique (Francis et al., 2011; Stock and Semmens, 2016; Gagne et al., 2018; Stock et al., 2018; Gorman et al., 2019), this study is subjected to some limitations. Unfortunately, this study only covers one year and it is not possible to prove repeatability of the seasonal pattern observed in the analysis. Moreover, the use of the mean weight as a proxy of European hake size and life stages in the B-SDM is appropriate to identify areas mostly occupied by juveniles and large adults in winter and summer. This type of variable can be of interest when wanting to account for changes related to life stages but where data of individuals' body length is scarce, not available or not feasible. For example, oceanographic surveys where total biomass and abundance per haul is usually recorded but the individual sampling of all specimens for biological analysis is unrealistic. However, this kind of proxy also presents some limitations, not directly informing of the less extreme phases of the life cycle, as intermediate values of mean weight cannot be categorized into adults other juveniles and are likely composed of mixed life stages. Furthermore, according to the length-weight relationship for European hake in the western Mediterranean Sea (Morey et al., 2003), for an individual of 25 cm, which is the length above which we classified individuals as "adults" (Bozzano et al., 1997; Lleonart, 2002), the corresponding mean weight is around 0.0895 kg. This means that for our data, only a reduced number of hauls had mean weight values over this threshold (**Supplementary Table 6**). This translates into an under-representation of adult individuals, especially during summer. This is partly related to the fact that all the data for this study was collected through bottom trawling, whereas generally larger individuals of European hake are caught trough long net gears. This means that adults were not very abundant and that our maximum individuals' size is 50.2 cm, but European hake in these waters can reach body lengths of more than 80 cm. Therefore, the diet and spatial distribution described here is not representing the entire population, omitting the largest individuals.

Our findings could have clear implications for a future seasonal-based adaptive fisheries management, as local depletion of prey, or variation in prey size and/or condition may affect hake presence in an area. This is of particular interest for this study as overfishing has led to a general decrease on demersal species (FAO-MED, 2018), some of which are prey to European hake, as well as a decline in small pelagic fish (e.g., *Sardina pilchardus* and *Engraulis encrasicolus*) (Coll and Bellido, 2019). Indeed, previous studies have already expressed their concerns about the underlying effect of these alterations for hake's population stock and distribution (Sion et al., 2019). Combining this information with future climate-change scenarios could result on major variations of the potential distribution of European hake in this area. Therefore, this study presents important information in the context of phenological processes of exploited species and their potential changes due to climate change. It does also emphasize, the need for additional monitoring efforts that consider a seasonal sampling of the marine ecosystems. Further information about spatial trophic analysis with season and ontogenetic stages is necessary if we want to fully understand species ecological roles, spatial-temporal population and food-web dynamics within marine ecosystems.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The authors declare that all fieldwork was approved by the Ethics Committee of CSIC, in accordance with the Spanish and EU legislation on the protection of animals used for scientific purposes.

AUTHOR CONTRIBUTIONS

EL-L, MC, JN, and MA-P: conceptualization and design of the experiment. MC, JN, NL and MA-P: samples collection. NL and MA-P: samples preparations. EL-L, MA-P, and JG: formal analysis. EL-L: writing – original draft preparation. MP, JN, MC, JG, MA-P, NL, and EL-L: writing – reviewing and editing. All authors contributed to the article and approved the submitted version.

FUNDING

This study took advantage of data collected under the ECOTRANS projects (CTM2011-26333, 2012–2014, Spanish Ministry of Economy and Competiveness, Spain). EL-L was supported by a FPU grant (FPU1704395, Spanish Ministry of Education). JN was supported by the Spanish National Program Ramón y Cajal (RYC-2015-17809, Spanish Ministry of Economy and Competiveness, Spain). Also funded by Project IMPRESS (RTI2018-099868-B-I00) project, ERDF, Ministry of Science, Innovation and Universities – State Research Agency.

ACKNOWLEDGMENTS

The authors would like to acknowledge all participants of the ECOTRANS project that helped in the sampling and laboratory work. We also would like to acknowledge Brian Stock for his assistance and support on developing the continuous MixSIAR models. This study is a contribution of the projects PELWEB (CTM2017-88939-R) and RESNEP (CTM2017-82991-C2-1-R) of the Spanish Ministry of Economy and Competiveness of Spain). The authors declare that all experimental procedures were conducted in strict accordance with good animal practice as defined by the current Spanish, Catalonian and European legislation.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.566686/full#supplementary-material

REFERENCES

Abella, A., Serena, F., and Ria, M. (2005). Distributional response to variations in abundance over spatial and temporal scales for juveniles of European hake (*Merluccius merluccius*) in the Western Mediterranean Sea. *Fish. Res.*71, 295–310. doi: 10.1016/j.fishres.2004.08.036

Aguzzi, J., Sbragaglia, V., Tecchio, S., Navarro, J., and Company, J. B. (2015). Rhythmic behaviour of marine benthopelagic species and the synchronous dynamics of benthic communities. *Deep Res. Part I* 95, 1–11. doi: 10.1016/j.dsr.2014.10.003

Albo-Puigserver, M., Navarro, J., Coll, M., Layman, C. A., and Palomera, I. (2016). Trophic structure of pelagic species in the northwestern Mediterranean Sea. *J. Sea Res.* 117, 27–35. doi: 10.1016/j.seares.2016.09.003

Anderson, M. J., Gorley, R. N., and Clarke, K. R. (2008). *PERMANOVA+ for PRIMER*. Plymouth: Guid. to Softw. Stat. methods. Prim. Ltd.

Barría, C., Coll, M., and Navarro, J. (2015). Unravelling the ecological role and trophic relationships of uncommon and threatened elasmobranchs in the western Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 539, 225–240. doi: 10.3354/meps11494

Barría, C., Navarro, J., and Coll, M. (2018). Feeding habits of four sympatric sharks in two deep-water fishery areas of the western Mediterranean Sea. *Deep Res. Part I* 142, 34–43. doi: 10.1016/j.dsr.2018.09.010

Bertrand, J. A., de Sola, L. G., Papaconstantinou, C., Relini, G., and Souplet, A. (2002). The general specifications of the MEDITS surveys. *Sci. Mar.* 66, 169–182. doi: 10.3989/scimar.2002.66s2169

Blangiardo, M., and Cameletti, M. (2015). *Spatial and Spatio-temporal Bayesian Models with R-INLA*. Hoboken, NJ: John Wiley.

Bosc, E., Bricaud, A., and Antoine, D. (2004). Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. *Glob. Biogeochem. Cycles* 18, 1–17. doi: 10.1029/2003GB002034

Bozzano, A., and Catalán, A. (2002). Ontogenetic changes in the retinal topography of the European hake, *Merluccius merluccius*: implications for feeding and depth distribution. *Mar. Biol.* 141, 549–559. doi: 10.1007/s00227-002-0840-7

Bozzano, A., Recasens, L., and Sartor, P. (1997). Diet of the european hake *Merluccius merluccius* (Pisces: Merluciidae) in the Western Mediterranean (Gulf of Lions). *Sci. Mar.* 61, 1–8.

Bozzano, A., Sardà, F., and Ríos, J. (2005). Vertical distribution and feeding patterns of the juvenile European hake, *Merluccius merluccius* in the NW Mediterranean. *Fish. Res.* 73, 29–36. doi: 10.1016/j.fishres.2005.01.006

Carney, R. (2005). Zonation of deep biota on continental margins. *Oceanogr. Mar. Biol. Annu. Rev.* 43, 211–278. doi: 10.1201/9781420037449.ch6

Carpentieri, P., Colloca, F., Cardinale, M., Belluscio, A., and Ardizzone, G. D. (2005). Feeding habits of European hake (*Merluccius merluccius*) in the central Mediterranean Sea. *Fish. Bull.* 103, 411–416.

Cartes, J. E., Hidalgo, M., Papiol, V., Massutí, E., and Moranta, J. (2009). Changes in the diet and feeding of the hake *Merluccius merluccius* at the shelf-break of the Balearic Islands: influence of the mesopelagic-boundary community. *Deep. Res. Part I Oceanogr. Res. Pap.* 56, 344–365. doi: 10.1016/j.dsr.2008.09.009

Cartes, J. E., Rey, J., Lloris, D., and Gil De Sola, L. (2004). Influence of environmental variables on the feeding and diet of European hake (*Merluccius merluccius*) on the Mediterranean Iberian coasts. *J. Mar. Biol. Assoc. U.K.* 84, 831–835. doi: 10.1017/S0025315404010021h

Caut, S., Angulo, E., and Courchamp, F. (2009). Variation in discrimination factors (Δ 15 N and Δ 13 C): the effect of diet isotopic values and applications for diet reconstruction. *J. Appl. Ecol.* 46, 443–453. doi: 10.1111/j.1365-2664.2009.01620.x

Chih-Lin, W., Rowe, G. T., Escobar-Briones, E., Boetius, A., Soltwedel, T., Julian, C. M., et al. (2010). Global patterns and predictions of seafloor biomass using random forests. *PLoS One* 5:e0015323. doi: 10.1371/journal.pone.0015323

Coll, M., and Bellido, J. M. (2019). *Evaluation of The Population Status and Specific Management Alternatives for the Small Pelagic Fish Stocks in the Northwestern Mediterranean Sea (SPELMED)*. Final Report SC NR 02 - TENDER EASME/EMFF/2016/32 – SPELMED:85. Brussels: EU.

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F. B. R., Aguzzi, J., et al. (2010). The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS One* 5:e0011842. doi: 10.1371/journal.pone.0011842

Cormon, X., Loots, C., Vaz, S., Vermard, V., and Marchal, P. (2014). Spatial interactions between saithe (*Pollachius virens*) and hake (*Merluccius merluccius*) in the North Sea. *ICES J. Mar. Sci.* 71, 1342–1355. doi: 10.1038/278097a0

Costalago, D., Navarro, J., Álvarez-Calleja, I., and Palomera, I. (2012). Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. *Mar. Ecol. Prog. Ser.* 460, 169–181. doi: 10.3354/meps09751

Davis, M., and Pineda-Munoz, S. (2016). The temporal scale of diet and dietary proxies. *Ecol. Evol.* 6, 1883–1897. doi: 10.1002/ece3.2054

De Souza, C. S., Mafalda, P., Sallés, S., Ramirez, T., Cortés, D., Garcia, A., et al. (2011). Seasonal changes in the distribution and abundance of marine cladocerans of the Northwest Alboran Sea (Western Mediterranean), Spain. *Braz. Arch. Biol. Technol.* 54, 543–550.

Demestre, M., and Sánchez, P. (1998). Spatio-temporal distribution of the European hake *Merluccius merluccius* off Catalan coast (Northwestern Mediterranean). *Rapp. Comm. Int. Mer. Médit.* 35, 420–421.

Demestre, M., Sánchez, P., and Abelló, P. (2000). Demersal fish assemblages and habitat characteristics on the continental shelf and upper slope of the north-western Mediterranean. *J. Mar. Biol. Assoc. U.K.* 80, 981–988. doi: 10.1017/S0025315400003040

Di Natale, A., Molinari, A., Öztürk, B., Srour, A., and Pollard, D. (2011). *Merluccius Merluccius*. The IUCN Red List of Threatened Species 2011: e.T198562A9031395. Gland: IUCN.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. doi: 10.1111/j.1600-0587.2012.07348.x

Druon, J. N., Fiorentino, F., Murenu, M., Knittweis, L., Colloca, F., Osio, C., et al. (2015). Modelling of European hake nurseries in the Mediterranean Sea: an ecological niche approach. *Prog. Oceanogr.* 130, 188–204. doi: 10.1016/j.pocean.2014.11.005

Estrada, M. (1996). Primary production in the northwestern Mediterranean. *Sci. Mar.* 60, 55–64.

Fanelli, E., Cartes, J. E., Rumolo, P., and Sprovieri, M. (2009). Food-web structure and trophodynamics of mesopelagic – suprabenthic bathyal macrofauna of the Algerian Basin based on stable isotopes of carbon and nitrogen. *Deep Res. Part I* 56, 1504–1520. doi: 10.1016/j.dsr.2009.04.004

Fanelli, E., Rumolo, P., Barra, M., Basilone, G., Genovese, S., and Bonanno, A. (2018). Mesoscale variability in the trophic ecology of the European hake *Merluccius merluccius* in the Strait of Sicily. *Hydrobiologia* 821, 57–72. doi: 10.1007/s10750-017-3268-2

FAO-MED (2018). *The State of Mediterranean and Black Sea Fisheries 2018*. Rome: FAO.

Fariña, A. C., Freire, J., and González-Gurriaran, E. (1997). Demersal fish assemblages in the Galician continental shelf and upper slope (NW Spain): spatial structure and long-term changes. *Estuar. Coast. Shelf Sci.* 44, 435–454. doi: 10.1006/ecss.1996.0148

Fernandes, P. G., Ralph, G. M., Nieto, A., Criado, M. G., Vasilakopoulos, P., Maravelias, C. D., et al. (2017). Coherent assessments of Europe's marine fishes show regional divergence and megafauna loss. *Nat. Ecol. Evol.* 1:0170. doi: 10.1038/s41559-017-0200

Ferraton, F., Harmelin-Vivien, M., Mellon-Duval, C., and Souplet, A. (2007). Spatio-temporal variation in diet may affect condition and abundance of juvenile European hake in the Gulf of Lions (NW Mediterranean). *Mar. Ecol. Prog. Ser.* 337, 197–208. doi: 10.3354/meps337197

Fisher, W., Bauchot, W. M., and Schneider, M. (1987). *Fiches FAO d'indetification des espèces pour les besoins de la pêche. Zone de Pêche 37*. Rome: FAO.

Fox, J., and Weisberg, S. (2011). "Multivariate linear models in R*," in *An R Companion to Applied Regression*, 2nd Edn, Thousand Oaks: Sage, 1–31.

Francis, T. B., Schindler, D. E., Holtgrieve, G. H., Larson, E. R., Scheuerell, M. D., Semmens, B. X., et al. (2011). Habitat structure determines resource use by zooplankton in temperate lakes. *Ecol. Lett.* 14, 364–372. doi: 10.1111/j.1461-0248.2011.01597.x

Gaertner, J. C. (2000). Seasonal organization patterns of demersal assemblages in the Gulf of Lions (north-western Mediterranean Sea). *J. Mar. Biol. Assoc. U.K.* 80, 777–783. doi: 10.1017/S0025315400002745

Gagne, T. O., Hyrenbach, K. D., Hagemann, M. E., and Van Houtan, K. S. (2018). Trophic signatures of seabirds suggest shifts in oceanic ecosystems. *Sci. Adv.* 4:eaao3946.

Garofalo, G., Fezzani, S., Gargano, F., Milisenda, G., Ben Abdallah, O., Ben Hadj Hamida, N., et al. (2018). Predictive distribution models of European hake in the south-central Mediterranean Sea. *Hydrobiologia* 821, 153–172. doi: 10.1007/s10750-017-3338-5

Gelman, A., Jakulin, A., Pittau, M. G., and Su, Y. S. (2008). A weakly informative default prior distribution for logistic and other regression models. *Ann. Appl. Stat.* 2, 1360–1383. doi: 10.1214/08-AOAS191

Gilinsky, E. (1984). The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* 65, 455–468. doi: 10.2307/1941408

Gorman, D., Pucci, M., Soares, L. S. H., Turra, A., and Schlacher, T. A. (2019). Land – ocean connectivity through subsidies of terrestrially derived organic matter to a nearshore marine consumer. *Ecosystems* 22, 796–804. doi: 10.1007/s10021-018-0303-8

Guisan, A., and Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecol. Modell.* 135, 147–186. doi: 10.1016/S0304-3800(00)00354-9

Gupta, A. K., and Nadarajah, S. (2004). *Handbook of Beta Distribution and Its Applications*. New York: Chapman and Hall.

Hijmans, R. J. (2018). *Package Raster: Geographic Data Analysis and Modeling. R package version 2.8-4*.

Hixon, M. A., and Carr, M. H. (1997). Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277, 946–949. doi: 10.1126/science.277.5328.946

Hyslop, E. J. (1980). Stomach contents analysis-a review of methods and their application. *J. Fish Biol.* 17, 411–429. doi: 10.1111/j.1095-8649.1980.tb02775.x

Jackson, A. L., Inger, R., Parnell, A. C., and Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER - stable isotope bayesian ellipses in R. *J. Anim. Ecol.* 80, 595–602. doi: 10.1111/j.1365-2656.2011.01806.x

Johnson, A. F., Jenkins, S. R., Hiddink, J. G., and Hinz, H. (2013). Linking temperate demersal fish species to habitat: scales, patterns and future directions. *Fish Fish.* 14, 256–280. doi: 10.1111/j.1467-2979.2012.00466.x

Johnson, A. F., Valls, M., Moranta, J., Jenkins, S. R., and Hiddink, J. G. (2012). Effect of prey abundance and size on the distribution of demersal fishes. *Can. J. Fish. Aquat. Sci.* 69, 191–200. doi: 10.1139/f2011-138

Karpouzi, V. S., and Stergiou, K. I. (2003). The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *J. Fish Biol.* 62, 1353–1365. doi: 10.1046/j.1095-8649.2003.00118.x

Katsanevakis, S., Maravelias, C. D., Damalas, D., Karageorgis, A. P., Tsitsika, E. V., Anagnostou, C., et al. (2009). Spatiotemporal distribution and habitat use of commercial demersal species in the eastern Mediterranean Sea. *Fish. Oceanogr.* 18, 439–457. doi: 10.1111/j.1365-2419.2009.00523.x

Lasram, F. B. R., Guilhaumin, G., Albouy, C., Somot, S., Thuillers, W., and Mouillot, D. (2010). The Mediterranean Sea as a 'cul-de-sac' for endemic fishes facing climate change. *Glob. Chang. Biol.* 16, 3233–3245. doi: 10.1111/j.1365-2486.2010.02224.x

Lleonart, J. (2002). *Impact of Fishery and Environment on Hake Recruitment in Northwestern Mediterranean*. Final Report European Commission Conract FAIR CT-97-3522. Alicante: Editorial Club Universitario.

Lleonart, J., and Maynou, F. (2003). Fish stock assessments in the Mediterranean: state of the art Fish stock assessments in the Mediterranean: state of the art. *Sci. Mar.* 67, 37–49. doi: 10.3989/scimar.2003.67s137

Logan, J. M., and Lutcavage, M. E. (2008). A comparison of carbon and nitrogen stable isotope ratios of fish tissues following lipid extractions with non-polar and traditional chloroform/methanol solvent systems. *Rapid. Commun. Mass Spectrom.* 22, 1081–1086. doi: 10.1002/rcm.3471

Madurell, T., Fanelli, E., and Cartes, J. E. (2008). Isotopic composition of carbon and nitrogen of suprabenthic fauna in the NW Balearic Islands (western Medterranean). *J. Mar. Syst.* 71, 336–345. doi: 10.1016/j.jmarsys.2007.03.006

Maravelias, C. D., and Papaconstantinou, C. (2006). Geographic, seasonal and bathymetric distribution of demersal fish species in the eastern mediterranean. *J. Appl. Ichthyol.* 22, 35–42. doi: 10.1111/j.1439-0426.2006.00695.x

Maravelias, C. D., Tsitsika, E. V., and Papaconstantinou, C. (2006). Environmental influences on the spatial distribution of European hake (*Merluccius merluccius*) and red mullet (*Mullus barbatus*) in the Mediterranean. *Ecol. Res.* 22, 678–685. doi: 10.1007/s11284-006-0309-0

Margalef, R. (1985). *Key environments: Western Mediterranean*. Oxford: Pergamon.

Maynou, F., Lleonart, J., and Cartes, J. E. (2003). Seasonal and spatial variability of hake (*Merluccius merluccius* L.) recruitment in the NW mediterranean. *Fish. Res.* 60, 65–78. doi: 10.1016/S0165-7836(02)00062-0

Mellon-Duval, C., Harmelin-Vivien, M., Métral, L., Loizeau, V., Mortreux, S., Roos, D., et al. (2017). Trophic ecology of the European hake in the Gulf of Lions, northwestern Mediterranean Sea. *Sci. Mar.* 81:7. doi: 10.3989/scimar.04356.01a

Mellon-Duval, C., Pontual, H., Métral, L., and Quemener, L. (2010). Growth of European hake (*Merluccius merluccius*) in the Gulf of Lions based on conventional tagging. *ICES J. Mar. Sci.* 67, 62–70.

Modica, L., Bozzano, A., and Velasco, F. (2013). The influence of body size on the foraging behaviour of European hake after settlement to the bottom. *J. Exp. Mar. Bio. Ecol.* 444, 46–54. doi: 10.1016/j.jembe.2013.03.001

Modica, L., Bozzano, A., Velasco, F., Albertelli, G., and Olaso, I. (2011). Predation, feeding strategy and food daily ration in juvenile European hake. *Mar. Ecol. Prog. Ser.* 440, 177–189. doi: 10.3354/meps09341

Morey, G., Moranta, J., Massutí, E., Grau, A., Linde, M., Riera, F., et al. (2003). Weight–length relationships of littoral to lower slope fishes from the western Mediterranean. *Fish. Res.* 63, 89–96. doi: 10.1016/S0165-7836(02)00250-3

Morfin, M., Fromentin, J. M., Jadaud, A., and Bez, N. (2012). Spatio-temporal patterns of key exploited marine species in the Northwestern Mediterranean sea. *PLoS One* 7:e0037907. doi: 10.1371/journal.pone.0037907

Muñoz, F., Pennino, M. G., Conesa, D., López-Quílez, A., and Bellido, J. M. (2013). Estimation and prediction of the spatial occurrence of fish species using Bayesian latent Gaussian models. *Stoch. Environ. Res. Risk Assess.* 27, 1171–1180. doi: 10.1007/s00477-012-0652-3

Navarro, J., Cardador, L., Fernández, ÁM., Bellido, J. M., and Coll, M. (2016). Differences in the relative roles of environment, prey availability and human activity in the spatial distribution of two marine mesopredators living in highly exploited ecosystems. *J. Biogeogr.* 43, 440–450. doi: 10.1111/jbi.12648

Navarro, J., Coll, M., Cardador, L., Fernández, ÁM., and Bellido, J. M. (2015). The relative roles of the environment, human activities and spatial factors in the spatial distribution of marine biodiversity in the Western Mediterranean Sea. *Prog. Oceanogr.* 131, 126–137. doi: 10.1016/j.pocean.2014.12.004

Navarro, J., Coll, M., Louzao, M., Palomera, I., Delgado, A., and Forero, M. G. (2011). Comparison of ecosystem modelling and isotopic approach as ecological tools to investigate food webs in the NW Mediterranean Sea. *J. Exp. Mar. Bio. Ecol.* 401, 97–104. doi: 10.1016/j.jembe.2011.02.040

Oliver, P., and Massuti, E. (1995). "Biology and fisheries of western Mediterranean hake (*M. merluccius*)," in *Hake-Fisheries, Ecology And Markets*, eds J. Alheit and T.J. Pitcher (Dordrecht: Springer), 181–202.

Orsi-Relini, L., Papaconstantinou, C., Jukic-peladic, S., Souplet, A., De Sola, L. G., Piccinetti, C., et al. (2002). Distribution of the Mediterranean hake populations (*Merluccius merluccius smiridus* Rafinesque, 1810) (Osteichthyes : Gadiformes) based on six years monitoring by trawl-surveys : some implications for management . *Sci. Mar.* 66, 21–38. doi: 10.3989/scimar.2002.66s221

Paradinas, I., Conesa, D., Pennino, M. G., Muñoz, F., Fernández, A. M., López-Quílez, A., et al. (2015). Bayesian spatio-temporal approach to identifying fish nurseries by validating persistence areas. *Mar. Ecol. Prog. Ser.* 528, 245–255. doi: 10.3354/meps11281

Paradinas, I., Mar, M., Pennino, M. G., Antonio, L., Conesa, D., Barreda, D., et al. (2016). Identifying the best fishing-suitable areas under the new European discard ban. *ICES J. Mar. Sci.* 73, 2479–2487. doi: 10.1093/icesjms/fsw114

Parnell, A. C., Inger, R., Bearhop, S., and Jackson, A. L. (2010). Source partitioning using stable isotopes: coping with too much variation. *PLoS One* 5, 1–5. doi: 10.1371/journal.pone.0009672

Pennino, M. G., Muñoz, F., Conesa, D., López-Qúlez, A., and Bellido, J. M. (2013). Modeling sensitive elasmobranch habitats. *J. Sea Res.* 83, 209–218. doi: 10.1016/j.seares.2013.03.005

Pitcher, T. J., and Alheit, J. (1995). "What makes a hake? A review of the critical biological features that sustain global hake fisheries," in *Hake*, eds J. Alheit and T.J. Pitcher (Dordrecht: Springer), 1–14.

Psarra, S., Tselepides, A., and Ignatiades, L. (2000). Primary productivity in the oligotrophic Cretan Sea (NE Mediterranean): seasonal and interannual variability. *Prog. Oceanogr.* 46, 187–204. doi: 10.1016/S0079-6611(00)00018-5

Puerta, P., Hunsicker, M. E., Quetglas, A., Álvarez-Berastegui, D., Esteban, A., González, M., et al. (2015). Spatially explicit modeling reveals cephalopod distributions match contrasting trophic pathways in the western mediterranean sea. *PLoS One* 10:e0133439. doi: 10.1371/journal.pone.0133439

Puerta, P., Quetglas, A., and Hidalgo, M. (2016). Seasonal variability of cephalopod populations: a spatio-temporal approach in the Western Mediterranean Sea. *Fish. Oceanogr.* 25, 373–389. doi: 10.1111/fog.12159

QGIS-Development-Team (2012). *QGIS Geographic Information System*. Anchorage: QGIS.

R Core Team (2018). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available online at: https://www.r-project.org

Recasens, L., Lombarte, A., Morales-Nin, B., and Torres, G. J. (1998). Spatiotemporal variation in the population structure of the European hake in the NW Mediterranean. *J. Fish Biol.* 53, 387–401. doi: 10.1006/jfbi.1998.0709

Rue, H., Martino, S., and Chopin, N. (2009). Approximate Bayesian inference for latent Gaussian models using integrated nested Laplace approximations. *J. R. Stat. Soc. Ser. b, Stat. Methodol.* 71, 319–392. doi: 10.1111/j.1467-9868.2008.00700.x

Rueda, L., Valls, M., Hidalgo, M., Guijarro, B., Esteban, A., and Massutí, E. (2019). From trophic ecology to fish condition: contrasting pathways for European hake in the western Mediterranean. *Mar. Ecol. Prog. Ser.* 623, 131–143. doi: 10.3354/meps13025

Salat, J., Garcia, M. A., Cruzado, A., Palanques, A., Arín, L., Gomis, D., et al. (2002). Seasonal changes of water mass structure and shelf slope exchanges at the Ebro shelf (NW Mediterranean). *Cont. Shelf Res.* 22, 327–348. doi: 10.1016/S0278-4343(01)00031-0

Sánchez, P., Sartor, P., Recasens, L., Ligas, A., Martin, J., and De Ranieri, S. (2007). Trawl catch composition during different fishing intensity periods in two Mediterranean demersal fishing grounds. *Sci. Mar.* 71, 765–773. doi: 10.3989/scimar.2007.71n4765

Scranton, K., and Amarasekare, P. (2017). Predicting phenological shifts in a changing climate. *PNAS* 114, 13212–13217. doi: 10.1073/pnas.1711221114

Sinopoli, M., Fanelli, E., Anna, G. D., Badalamenti, F., and Pipitone, C. (2012). Assessing the effects of a trawling ban on diet and trophic level of hake, *Merluccius merluccius*, in the southern Tyrrhenian Sea. *Sci. Mar.* 76, 677–690. doi: 10.3989/scimar.03564.29A

Sion, L., Zupa, W., Calculli, C., Garofalo, G., and Hidalgo, M. (2019). Spatial distribution pattern of European hake, *Merluccius merluccius* (Pisces : Merlucciidae), in the Mediterranean Sea Spatial distribution pattern of European hake, *Merluccius merluccius* (Pisces: Merlucciidae), in the Mediterranean Sea. *Sci. Mar.* 83, 21–32. doi: 10.3989/scimar.04988.12A

Smith, J. A., Mazumder, D., Suthers, I. M., and Taylor, M. D. (2013). To fit or not to fit : evaluating stable isotope mixing models using simulated mixing polygons. *Methods Ecol. Evol.* 4, 612–618. doi: 10.1111/2041-210X.12048

Soykan, O., Ilkyaz, A. T., Metrin, G., and Tuncay Kinacigil, H. (2015). Age, growth and reproduction of European hake (*Merluccius merluccius* (Linn ., 1758)) in the Central Aegean Sea, Turkey. *Mar. Biol. Assoc. U.K.* 95, 829–937. doi: 10.1017/S002531541400201X

Spearman, C. (1904). The proof and measurement of association between two things. *Am. J. Psychol.* 15, 72–101. doi: 10.1037/h0065390

Stagioni, M., Montanini, S., and Vallisneri, M. (2011). Feeding habits of European hake, *Merluccius merluccius* (Actinopterygii: Gadiformes: Merlucciidae), from the northeastern Mediterranean sea. *Acta Ichthyol. Piscat.* 41, 277–284. doi: 10.3750/AIP2011.41.4.03

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., and Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *Peer* 6, 1–27. doi: 10.7717/peerj.5096

Stock, B. C., and Semmens, B. X. (2016). *MixSIAR GUI User Manual. Version 3.1.*

Valiela, I. (1995). *Marine Ecological Processes*. Cham: Springer.

Valls, M., Sweeting, C. J., Olivar, M. P., Puelles, M. L. F., De Pasqual, C., Polunin, N. V. C., et al. (2014). Structure and dynamics of food webs in the water column on shelf and slope grounds of the western Mediterranean. *J. Mar. Syst.* 138, 171–181. doi: 10.1016/j.jmarsys.2014.04.002

Velasco, F., and Olaso, I. (1998). European hake *Merluccius merluccius* (L., 1758) feeding in the Cantabrian Sea: seasonal, bathymetric and length variations. *Fish. Res.* 38, 33–44. doi: 10.1016/S0165-7836(98)00111-8

Wei, T., and Simko, V. (2017). *R Package "Corrplot": Visualization of a Correlation Matrix (Version 0.84)*. Available online at: https://github.com/taiyun/corrplot

Yalçln, E., and Gurbet, R. (2016). Environmental influences on the spatio-temporal distribution of european hake (*Merluccius merluccius*) in izmir Bay, Aegean Sea. *Turk. J. Fish. Aquat. Sci.* 14, 1–14. doi: 10.4194/1303-2712-v16

Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. doi: 10.1111/j.2041-210X.2009.00001.x

Zveryaev, I. (2015). Seasonal differences in intraseasonal and interannual variability of Mediterranean Sea surface temperature. *J. Geophys. Res. Ocean* 120, 2813–2825. doi: 10.1002/2014JC010387.Received

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.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 23 February 2021
doi: 10.3389/fmars.2021.578144

Disentangling the Influence of Three Major Threats on the Demography of an Albatross Community

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Climate change, fisheries and invasive species represent three pervasive threats to seabirds, globally. Understanding the relative influence and compounding nature of marine and terrestrial threats on the demography of seabird communities is vital for evidence-based conservation. Using 20 years of capture-mark-recapture data from four sympatric species of albatross (black-browed *Thalassarche melanophris*, gray-headed *T. chrysostoma*, light-mantled *Phoebetria palpebrata* and wandering *Diomedea exulans*) at subantarctic Macquarie Island, we quantified the temporal variability in survival, breeding probability and success. In three species (excluding the wandering albatross because of their small population), we also assessed the influence of fisheries, oceanographic and terrestrial change on these rates. The Southern Annular Mode (SAM) explained 20.87–29.38% of the temporal variability in survival in all three species and 22.72–28.60% in breeding success for black-browed and gray-headed albatross, with positive SAM events related to higher success. The El Niño Southern Oscillation (ENSO) Index explained 21.14–44.04% of the variability in survival, with higher survival rates following La Niña events. For black-browed albatrosses, effort in south-west Atlantic longline fisheries had a negative relationship with survival and explained 22.75–32.21% of the variability. Whereas increased effort in New Zealand trawl fisheries were related to increases in survival, explaining 21.26–28.29 % of variability. The inclusion of terrestrial covariates, reflecting extreme rainfall events and rabbit-driven habitat degradation, explained greater variability in trends breeding probability than oceanographic or fisheries covariates for all three species. These results indicate managing drivers of demographic trends that are most easily controlled, such as fisheries and habitat degradation, will be a viable option for some species (e.g., black-browed albatross) but less effective for others (e.g., light-mantled albatross). Our results illustrate the need to integrate fisheries, oceanographic and terrestrial processes when assessing demographic variability and formulating the appropriate management response.

Keywords: climate change, fisheries, invasive species, multi-event models, reproductive success, seabirds, Southern Ocean, survival

OPEN ACCESS

Edited by:
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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: *30 June 2020*
Accepted: *03 February 2021*
Published: *23 February 2021*

Citation:
Cleeland JB, Pardo D, Raymond B, Tuck GN, McMahon CR, Phillips RA, Alderman R, Lea M-A and Hindell MA (2021) Disentangling the Influence of Three Major Threats on the Demography of an Albatross Community. Front. Mar. Sci. 8:578144. doi: 10.3389/fmars.2021.578144

INTRODUCTION

Climate-driven changes in the marine ecosystem affect animal populations in complex ways (Constable et al., 2014), yet understanding how populations respond to environmental change is vital for predicting their viability (Vargas et al., 2007). In the Southern Ocean, climate change is driving regional trends in sea ice extent and seasonality (Stammerjohn et al., 2012), causing major oceanic fronts to move southwards (Sokolov and Rintoul, 2009), increasing wind intensity (Turner et al., 2009) and enhancing eddy activity (Meredith and Hogg, 2006). Furthermore, large-scale climate cycles such as the Southern Annular Mode (SAM) and the El Niño Southern Oscillation (SOI) are also influenced by climate change, with demographic consequences predicted for multiple species (Forcada and Trathan, 2009).

For marine predators, changes in physical oceanographic and atmospheric conditions may influence individual foraging efficiency by affecting the accessibility and predictability of prey (Lea et al., 2006), or the energetic cost of reaching foraging areas (Weimerskirch et al., 2012). However, these changes are occurring simultaneously with fisheries that overlap with the foraging habitat of numerous seabird species (Tuck et al., 2003). Through incidental mortality (bycatch) (Anderson et al., 2011), discarding of non-target catch and offal (Bartumeus et al., 2010) and increased competition for resources (Cury et al., 2011), fisheries can influence survival or induce changes in foraging behavior that affects breeding frequency or success. For small populations, simultaneous negative effects on both survival and reproductive output can drive rapid declines and lead to extirpation (Weller et al., 2014).

Information about the processes that influence demographic variability is fundamental to evidence-based conservation. However, for species such as albatross that are highly philopatric, long-ranging, pelagic foragers, it can be difficult to quantify these processes. Albatrosses have a delayed onset of maturity (typically > 10 years), after which breeding occurs annually or biennially (Jouventin and Dobson, 2002). Adult survival is high, with individuals of some species living up to 50 years (Weimerskirch et al., 1987). This means any increase in mortality or decrease in reproductive output has considerable consequences for population viability, even if these take some time to become visible in the population (Phillips et al., 2016).

Decreases in adult survival due to fisheries bycatch are the greatest contributor to the rapid, widespread declines of several albatross populations (Tuck et al., 2001; Phillips et al., 2016). Implementation of technological solutions that mitigate bycatch, such as the use of exclusion devices (Maree et al., 2014), integrated-weight lines (Robertson et al., 2010) or underwater line-setters (Gilman et al., 2003) have slowed or stopped declines, with minor increases at some colonies (Inchausti and Weimerskirch, 2001; Robertson et al., 2014). However, as their distributions often span multiple fisheries management boundaries, there is wide variation in the implementation of mitigation measures (Phillips et al., 2016).

Albatrosses also face terrestrial pressures including habitat degradation and effects of invasive species. Introduced mammals are particularly problematic for seabirds through predation (Cuthbert and Hilton, 2004), competition for habitat (Brothers and Bone, 2008) or habitat degradation (Cleeland et al., 2020).

With different life-history traits, each albatross species within a community will respond differently to environmental variation, be it marine or terrestrial. Integrated studies addressing the effects of both at-sea (e.g., oceanographic and fisheries) and terrestrial factors (e.g., habitat quality, weather and invasive species) on the demographic rates of multiple species allow rates to be compared and contrasted, providing a comprehensive understanding of albatross demography. Quantification of marine and terrestrial influences provides the evidence base to support conservation action by reducing uncertainty. Specifically, it allows the identification of drivers that are more easily managed (e.g., invasive species, fisheries), and which buffer against those that are not (e.g., climate change).

Four species of Southern Ocean albatross breed at Macquarie Island; black-browed *Thalassarche melanophris*, gray-headed *Thalassarche chrysostoma*, light-mantled *Phoebetria palpebrata*, and wandering albatrosses *Diomedea exulans*. With the exception of light-mantled albatrosses, these populations are small (< 80 breeding pairs), and therefore at risk of local extinction. At Macquarie Island, declines in adult survival of wandering albatrosses have been linked to bycatch in tuna longline fisheries (de la Mare and Kerry, 1994; Terauds et al., 2006), although no such links have been established for black-browed or gray-headed albatrosses (Terauds et al., 2005). More recently, declines in the breeding probability of black-browed, gray-headed and light-mantled albatrosses have been attributed to wide-scale habitat degradation caused by invasive rabbits *Oryctolagus cuniculus*; for black-browed albatrosses, the combination of heavy rainfall events and rabbit density also caused substantial reductions in breeding success (Cleeland et al., 2020).

To understand the influence of at-sea and terrestrial factors on demography of the Macquarie Island albatross community, we aimed to: (1) determine annual trends in survival, breeding probability and breeding success of each species; (2) compare and contrast demographic variability across species, and; (3) assess the relative influence of various environmental processes on demography.

MATERIALS AND METHODS

Field Methods

We analyzed 20 years (1995–2014) of capture-mark-recapture data from four albatross species breeding at subantarctic Macquarie Island (54.6° S, 158.9° E). There are approximately 40, 80 and five breeding pairs of black-browed, gray-headed and wandering albatrosses, respectively, at Macquarie Island (DPIPWE, 2014). In contrast, there are approximately 2150 breeding pairs of light-mantled albatross (DPIPWE, 2014). All accessible albatross chicks of each species were banded with stainless steel leg bands between 1995 and 2014 (seasons 1994/95 and 2013/14), except for light-mantled albatross, where this applied only to chicks within seven study areas (∼10% of total island breeding population). From 1994 to 2003, any unbanded adults that could be captured safely were also banded. Checks in early incubation allowed breeding adults to be identified, and at the end of chick-rearing to band chicks and quantify fledging rates. Any banded nonbreeding adults were also recorded. All field procedures were approved by the Tasmanian Government Department of Primary Industries, Parks, Water and Environment's Animal Ethics Committee and were carried out in accordance with the approved guidelines (permit number TFA9195).

Demographic Analysis

Demographic parameters – survival (Φ), return (r), breeding probability (β), breeding success (γ), and detection probability (p) – were estimated using a hidden Markov model framework, in which it was assumed individuals transition between different states (e.g., breeder, nonbreeder, etc.; see **Supplementary Figure 1a**) over time, with transitions between states described by a Markov chain. The state of an individual was assumed to be observed indirectly by means of an event (hereafter referred to as an encounter). Encounters were assumed to be dependent on the true, but unobserved, state of the individual. Encounter histories for each individual were used to fit a population-level model, with model parameters related to environmental parameters as described below. Models were fitted in the E-Surge 1.9.0 software (Choquet et al., 2009b) using maximum likelihood estimation.

Individual encounter histories (total birds: black-browed, n = 225; gray-headed, n = 513; light-mantled, n = 1215; and wandering albatross, n = 78) consisted of four observable adult states (successful breeder, failed breeder, nonbreeder and breeder with uncertain breeding outcome) and three unobservable states (post-successful breeder, post-failed breeder, post non-breeder) (**Supplementary Figure 1a**). The unobservable post-breeding states were included to account for differences in year-to-year transitional breeding probability (ψ) generated by biennial breeding behavior (Barbraud and Weimerskirch, 2012). A small proportion of breeding outcomes were unknown, as the nest was not revisited late in the breeding season (1.5%, 1.1%, 1.3%, and 2.3% of observations for black-browed, gray-headed, light-mantled and wandering albatrosses). State uncertainty was incorporated in an event matrix, allowing the likelihood of being a successful breeder to be assessed (Gimenez et al., 2012).

To remain tractable but functional due to the small population sizes, the analysis was restricted to adult demographic parameters by suppressing all chick, juvenile and pre-breeding states before the first breeding attempt. It was also assumed demographic parameters were not affected by age, experience, sex or quality. Further, we expected similar survival, regardless of state. For gray-headed, light-mantled and wandering albatrosses (biennial breeders) the probabilities of return and breeding for successful breeders were estimated separately from those of failed and nonbreeders for the time-dependent models (**Supplementary Table 1**). In contrast, estimates for black-browed albatrosses (annual breeders) were derived using a time-dependent (t) model for all demographic parameters. For all species, time-dependent parameters were retained when modeling the demographic parameter of interest.

Nest accessibility for gray-headed and light-mantled albatrosses was affected by severe habitat degradation due to heavy rabbit grazing during the 2000s, influencing detection probability (p), and so rabbit density was included as a covariate, accordingly (**Supplementary Table 1**). Detection probabilities were also estimated separately for breeders and nonbreeders because bands are easier to read on the former (**Supplementary Figure 2**). Complete model input notation, probability estimation and transition matrix structures are provided in **Supplementary Figure 1**, **Supplementary Table 1**, and **Supplementary Appendix 1**.

To test for goodness-of-fit, encounter histories were transformed to a single-state and assessed using U-Care 2.3.2 software, including tests for transience (Choquet et al., 2009a). Tests for trap-dependence (Test 2: 2.CT + 2.Cl) were excluded since the model structure accounted for differences in breeding probability based on previous breeding states; characteristic of species that defer breeding in some years (Barbraud and Weimerskirch, 2012). Correction for lack of fit within the populations was applied using an over-dispersion factor ($\hat{c}$; Lebreton et al., 1992).

A sequence of models was fitted for each species to disentangle the various influences on demography. First, models were fit using each predictor variable in turn. Significant covariates were then grouped into models that included fisheries, oceanographic or terrestrial covariates, to provide an integrated overview of their effects on demographic rates. Finally, all significant covariates were integrated into a global model to determine the total demographic variability that could be explained by the covariates. Prior to their inclusion in the models environmental covariates were tested for collinearity using a Pearson's correlation matrix in R (R Core Team, 2016). Variables with a correlation coefficient of $>$ 0.8 were excluded from the demographic models.

The significance of environmental covariates for each demographic parameter was evaluated using analysis of deviance tests (ANODEV), and the strength of the effect ascertained by considering the total variation explained by the covariates (Grosbois et al., 2008). This analysis quantifies how much of the annual variation in a demographic parameter can be explained by annual environmental covariates and therefore does not express a direct link between environmental drivers and population level outcomes.

Wandering albatrosses were excluded from the environmental analysis due to their small population size. Base models described the total variation explained by the covariates (%R^2). In addition, because long-term temporal trends in the covariate and demographic rate can obscure their relationship, detrended models that provide a measure of short-term variation were implemented, which described the total variation explained by the covariates when temporal trends were removed (detrended %R^2). The base and detrended models are regarded as explaining long-term and short-term variability, respectively. Model selection was based on Akaike's information criterion (AIC), whereby the model with the lowest AIC (where ΔQAIC > 2) was preferred (Burnham and Anderson, 2002).

Covariates

Fisheries and oceanographic covariates were taken from the foraging distribution of each species determined by previous tracking studies (**Figure 1**; Cleeland et al., 2019). Fisheries covariates represent monthly totals, whereas each oceanographic covariate consisted of a time series of values averaged from daily and monthly data to give an annual mean. The temporal range of each environmental covariate was aligned to the appropriate stage of the breeding cycle for each species (**Supplementary Table 2**).

Oceanographic covariates were obtained as monthly sea ice extent (*ice*), sea surface temperature (*sst*), sea surface height anomaly (*ssha*), wind speed (*wind*), meridional wind (*wind_v*) and zonal wind (*wind_u*). For albatrosses, these oceanographic parameters may directly affect the energetic costs of flight to foraging grounds, or indirectly by influencing prey availability. Sea ice conditions around Antarctica are tightly coupled with primary productivity and the abundance of salps and krill (Loeb et al., 1997). Furthermore, the influence of sea surface temperature on foraging conditions is known demographic parameters and population growth rate in albatrosses (Jenouvrier et al., 2018). Similarly, sea surface height anomalies provide a measure of eddy activity, particularly at frontal regions between cold and warm eddies, and are known to aggregate prey and influence foraging conditions for seabirds (Bost et al., 2009).

Large-scale climate indices – the Southern Annular Mode (SAM) and Southern Oscillation Index (SOI) – were also included in the models. Both the SAM and SOI influence seabird demography by modifying ocean circulation patterns, which in turn influences primary production (Trathan et al., 2007). Furthermore, changes in the Southern Ocean wind regime, associated with the SAM, can have a direct effect on the energetic cost of flight and therefore foraging (Weimerskirch et al., 2012). As temporal lags are likely to exist between changes in SAM and SOI and the responses of prey populations and the vital rates of seabirds, biannual lags from 2 to 3 years were tested for SAM (Barbraud and Weimerskirch, 2003) and half to one and a half years for SOI (Lovenduski and Gruber, 2005).

Fisheries effort within the breeding and nonbreeding distributions was included in models of black-browed and gray-headed albatross survival. These species commonly associate with vessels and are killed incidentally by fishing gear (Phillips et al., 2016). Fisheries effort was a proxy for elevated mortality risk, although discards provide a food resource, from which the benefit may outweigh the negative effects of bycatch (Granadeiro et al., 2014). Fisheries covariates were excluded from models for light-mantled albatrosses because they are not regularly caught as bycatch and are thought to be competitively excluded from attending fisheries vessels (Phillips et al., 2005). Fisheries covariates comprised monthly trawl and longline effort at 5 × 5 degree resolution obtained from regional fisheries management organizations in the form of the number of hooks set, or of hours trawled. Effort data included in the modeling was limited to national and international fisheries with reported evidence of albatross attendance at or interactions with vessels within each fleet.

Terrestrial covariates from Cleeland et al. (2020) were included in the global breeding probability and breeding success models to evaluate the relative importance of conditions at the breeding colony. These comprised rabbit density (a proxy for nesting habitat degradation), and extreme rainfall events during early chick-rearing. The latter represents the number of days in January of rainfall in the 80th percentile of the long-term average and is tested on breeding success to capture the potential these events have on reducing survival of young chicks at the nest.

RESULTS

Comparative Demographic Rates

The Macquarie Island albatross species have differing long-term population trends: black-browed and light-mantled albatrosses are increasing, wandering albatrosses are decreasing, and gray-headed albatrosses are stable (**Figure 2**). Of these, black-browed albatrosses had the lowest adult survival ($\Phi = 0.914 \pm 0.007$) and breeding success ($\gamma = 0.516 \pm 0.015$) (**Table 1**), and wandering albatrosses had the lowest breeding probability ($\beta = 0.738 \pm 0.039$). A negative trend in adult survival, seen in the slope of the linear model, was only evident for wandering albatrosses ($\Phi = -0.56 \pm 0.29$) (**Supplementary Table 3**). Black-browed, gray-headed and wandering albatross breeding probability decreased during the study period ($\beta = -0.89 \pm 0.15$, $\beta = -1.17 \pm 0.18$ and $\beta = -0.62 \pm 0.22$). Modeled breeding success of the four species showed no trend between 1995 and 2014.

Influence of Fisheries on Survival

Longline fishing effort in the south-west and south Atlantic Ocean explained some of the variability in declines in adult survival of black-browed albatrosses. Specifically, higher effort in Chilean (1995–2009), Falklands and ICCAT longline fisheries were associated with a decrease in survival, explaining 22.75–32.21% of the short- and long-term variability (**Figure 3**). Whereas trawl fishing effort in New Zealand waters was linked to higher survival of black-browed and gray-headed albatrosses and explained 21.26–28.29% of variability. For black-browed albatrosses, combined fisheries covariates explained 19.66% of short-term, and 45.34% of the long-term variability in survival (**Table 2**).

Effect of Oceanographic Factors

Effects of oceanographic covariates and large-scale climate indices on albatross demographic rates differed among the species. Sea ice extent explained 29.60% of the short -term variability in light-mantled albatross survival, with greater sea ice extent corresponding to increased survival (**Figure 3**). Increased meridional (southerly) winds were associated with higher survival of black-browed and gray-headed albatrosses. Sea surface height anomaly explained 67.10% and 32.19% of the long-term variability in black-browed and gray-headed albatross breeding probability. This correlation is not particularly

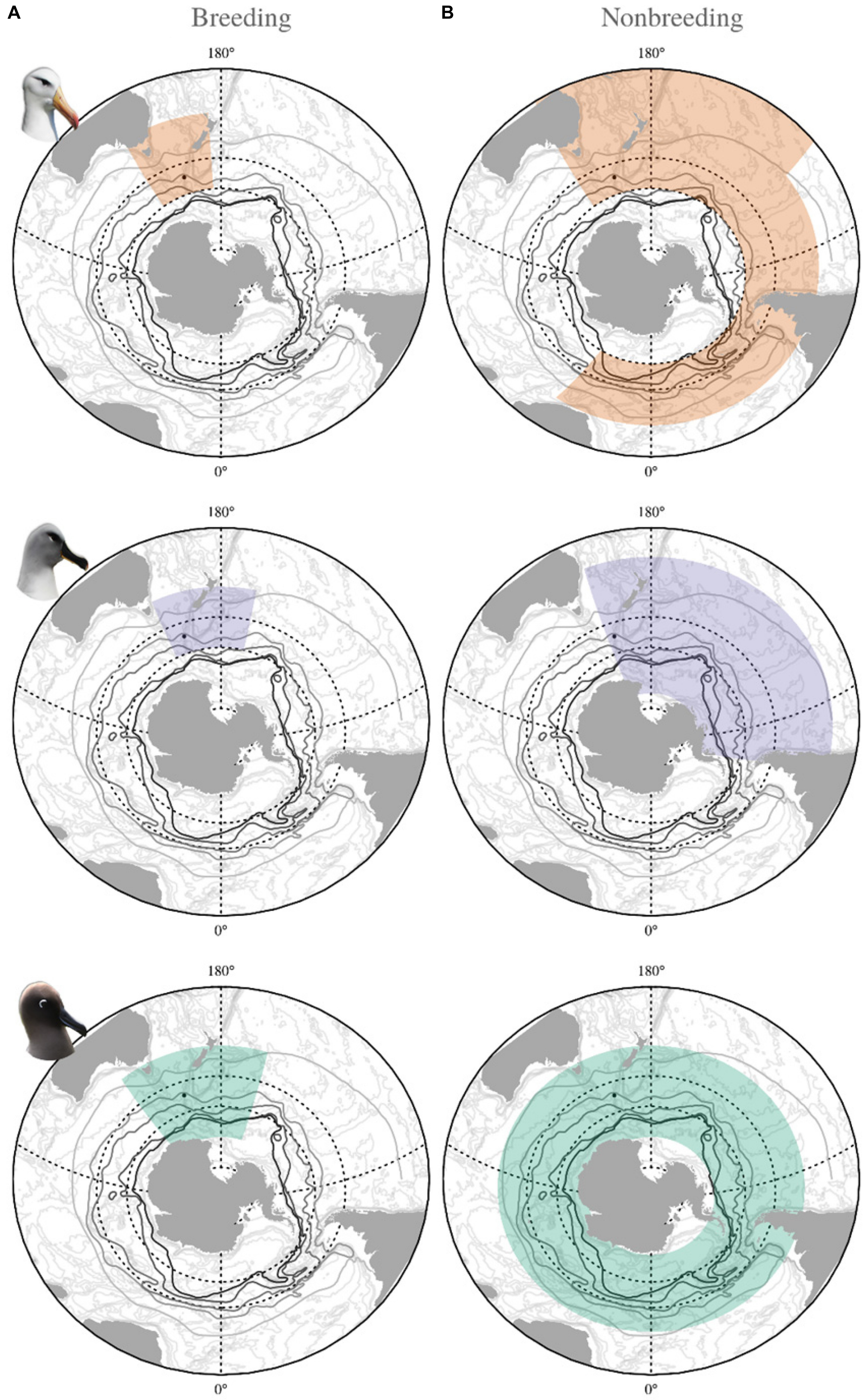

FIGURE 1 | Spatial extent of oceanographic covariates incorporated in the demographic modeling of black-browed (orange), gray-headed (purple) and light-mantled (green) albatross from Macquarie Island during **(A)** breeding, and **(B)** nonbreeding periods.

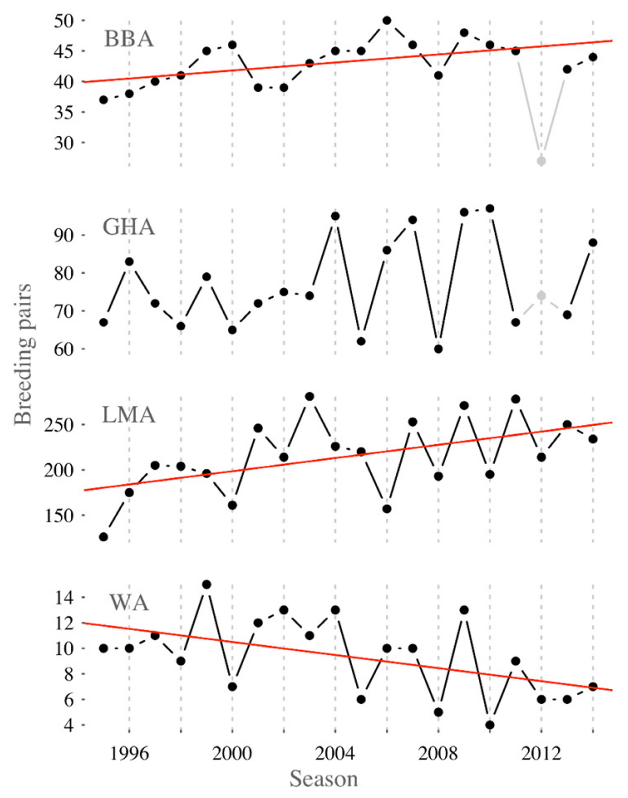

FIGURE 2 | Trends in breeding pairs of black-browed (BBA, $F_{1,17} = 6.88$, $p = 0.018$, $R^2 = 0.25$), gray-headed (GHA, $F_{1,17} = 1.55$, $p = 0.229$, $R^2 = 0.03$), light-mantled (LMA, $F_{1,18} = 6.62$, $p = 0.019$, $R^2 = 0.23$) and wandering albatross (WA, $F_{1,18} = 5.84$, $p = 0.027$, $R^2 = 0.20$) at Macquarie Island in 1995 to 2014. Note that 1) detection probability of black-browed and gray-headed albatross was considerably lower in 2012 than other years and so this point was not included in the linear fit, and 2) the number of light-mantled albatross breeding pairs, represent those within seven study areas and approximately ~10% of the total population.

TABLE 1 | Modeled constant demographic estimates for Macquarie Island albatross from 1995 to 2014.

	Survival (ϕ)	Breeding probability (β)	Breeding success(γ)
Black-browed albatross	0.914 ± 0.007	0.748 ± 0.016	0.516 ± 0.015
Gray-headed albatross	0.933 ± 0.004	0.951 ± 0.008	0.577 ± 0.013
Light-mantled albatross	0.924 ± 0.003	0.989 ± 0.009	0.571 ± 0.024
Wandering albatross	0.939 ± 0.014	0.738 ± 0.039	0.617 ± 0.041

informative and appears to be a result of strong linear trends in both breeding probability and sea surface height anomaly.

The SOI was positively associated with survival for all three species, whereas SAM was positively associated with survival of black-browed and light-mantled albatrosses. With a two-and-a-half-year lag, the SAM explained 29.38 and 26.81% of the short-term and long-term in black-browed albatross survival. With a longer lag time of 3 years, the SAM explained 28.35 and 20.87% of the short and long-term variability, respectively, in light-mantled albatross survival. Breeding success of black-browed and gray-headed albatrosses showed a positive association with SAM with two and two-and-a-half year lags.

A positive association between SOI and adult survival was detected for all species. For black-browed and light-mantled albatrosses, higher survival correlated with higher SOI values with a 1-year lag and explained 44.04 and 40.39% of the short-term variability and 25.36 and 36.84% of the long-term variability, respectively. Survival in gray-headed albatrosses responded more quickly, with a 6-month lag explaining 21.14% of long-term variability. Black-browed albatross breeding probability was negatively related to SOI with a 6-month lag, describing 30.48% of variability.

The most influential oceanographic covariates were combined in models for each species and described 42.61 and 51.74% of the short and long-term variation in light-mantled albatross survival (**Table 2**). Oceanographic factors were not strongly correlated with survival in black-browed albatrosses (short-term variability: $R^2 = 22.15\%$, long-term variability: $R^2 = 10.23\%$) or gray-headed albatrosses (long-term variability: $R^2 = 27.84\%$). Combined sea surface height anomaly and SOI (6-month lag) explained 75.20% of the long-term variability in breeding probability of black-browed albatrosses.

Global Models and Terrestrial Effects

Global models integrated all influential fisheries, oceanographic and terrestrial covariates (**Figure 4**). As shown by Cleeland et al. (2020), habitat degradation caused by heavy rabbit grazing is strongly correlated with the breeding probability of all three species. In this study, we see terrestrial covariates from Cleeland et al. (2020) best explain variability in breeding probability over time when compared to fisheries and oceanographic covariates (**Table 2**). For black-browed albatrosses, fisheries variables best explained the variability in survival (short-term variability: $R^2 = 19.66\%$, long-term variability: $R^2 = 45.34\%$), whereas terrestrial variables best explained breeding success (short-term variability: $R^2 = 50.29\%$, long-term variability: $R^2 = 33.10\%$). The remaining global models included oceanographic and terrestrial factors as correlates of breeding success. All model parameters are described in Appendix S2.

DISCUSSION

Understanding the extrinsic drivers of demographic variability is critical to assess population viability, particularly in small populations where small decreases in vital rates can have a considerable impact on the population. However, the natural demographic stochasticity of small populations makes it challenging to identify the key factors contributing to demographic variability.

Species-Specific Demographic Estimates

Notwithstanding the overall similarity in survival patterns, there were important species-specific differences in survival patterns. Adult survival of black-browed albatrosses was constant

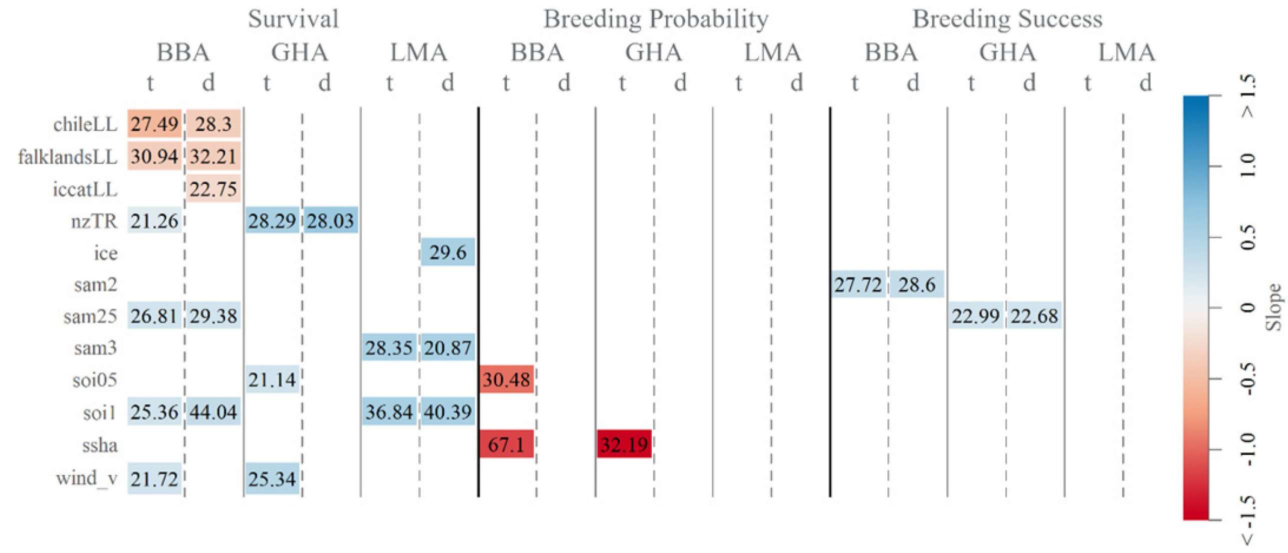

FIGURE 3 | Deviance explained (%R^2) and direction of slope of individual significant fisheries and oceanographic covariates (from **Supplementary Table 2**) included in survival, breeding probability and breeding success time-dependent base (*t*) and linear detrended (*d*) models of black-browed (BBA), gray-headed (GHA) and light-mantled (LMA) albatross at Macquarie Island.

throughout the study period, continuing the pattern reported between 1975 and 2000 (Terauds et al., 2005). Furthermore, the mean was within the range of values for this species at Îles Kerguelen (90.6 ± 0.5% to 94.3 ± 1.4%; Weimerskirch and Jouventin, 1998; Pardo et al., 2013), higher than survival at South Georgia during a similar period (89.3 ± 1.2% and 90.9%; Arnold et al., 2006; Pardo et al., 2017), but lower than that at Falklands (94.2%; Catry et al., 2011). Similarly, breeding success was higher than at South Georgia (Croxall et al., 1998) and lower than at the Falkland Islands (Catry et al., 2011).

Survival in gray-headed albatrosses at Macquarie Island declined by 3.4% from the first assessment between 1975 and 2000 (96.7 ± 1.1%; Terauds et al., 2005), and was lower than the long-term average at South Georgia of 95.2 ± 2.9% (Pardo et al., 2017), where the population is in rapid decline (Poncet et al., 2017), and at Campbell Island (95.3 ± 0.9%; Waugh et al., 1999). In contrast, breeding success for the Macquarie Island population (57.7 ± 1.3%) was considerably higher than Campbell Island (39.7%; Waugh et al., 1999), and that at South Georgia 30.0 ± 17.4%; Pardo et al., 2017). Estimates of gray-headed albatross survival and breeding success are highly variable in the Southern Ocean, suggesting factors that influence survival may originate from local or regional sources such as density-dependent processes and individual fisheries.

The cryptic colouration of light-mantled albatrosses, dispersed distribution of nests, and difficulty in accessing sites on cliffs and steep slopes result in few capture-mark-recapture studies of this species (Schoombie et al., 2016). Survival of light-mantled albatrosses at Macquarie Island (92.4%, 1995–2014) was considerably lower than at the Îles Crozet (97.3%, 1967–1995), whereas breeding success was higher at Macquarie (57.1% in 1995–2014 vs 40.9% in 1980–2005 at Îles Crozet; Delord et al., 2008).

The wandering albatross population at Macquarie Island has declined to an average of only five breeding pairs each year (DPIPWE, 2014). Its long-term persistence seems unlikely given the negative trend in adult survival and breeding probability, and the lack of immigrants from elsewhere (Terauds et al., 2006). The decline in breeding probability may be amplified by reduced survival, as it will be more difficult for widowed birds to find a new mate, particularly given the strong male-biased sex ratio (**Supplementary Figure 3**, Mills and Ryan, 2005). Due to the small population size we could not test for relationships between vital rates and fisheries effort or oceanographic change, but the decline of wandering albatrosses at Macquarie Island has previously been linked to tuna longline fisheries (de la Mare and Kerry, 1994). Nonetheless, this population has recovered from critically low numbers in the past. Harvesting by humans in the 18th century reduced the population to one or two breeding pairs in 1911 (Cumpston, 1968). Subsequently the number of breeding pairs fluctuated from 28 in 1968 to two in 1985, before reaching 15 in 1999 (Terauds et al., 2006). Similarly, the Amsterdam albatross *Diomedea amsterdamensis* increased from five to 31 breeding pairs between 1983 and 2001 (Rivalan et al., 2010). Thus, recovery capacity may not be constrained by genetic bottlenecks, as albatrosses in general show surprisingly low genetic variation (Milot et al., 2007).

Influence of Fisheries on Survival

Bycatch in longline and trawl fisheries is the greatest contributor to declines in albatross populations in the Southern Ocean (Phillips et al., 2016). Our study found a relationship between fishing effort and survival in black-browed albatrosses, with higher mortality rates associated with greater longline effort in the south-west Atlantic, a known wintering region for this population (Cleeland et al., 2019). Bycatch rates in longline

TABLE 2 | Time-dependent (*t*) base and detrended (*d*) models with combined significant oceanographic, fisheries and terrestrial covariates explaining (%R^2) Macquarie Island albatross demographic rates.

			Fisheries	Oceanographic	Terrestrial**	Global model
Survival (ϕ)	***Black-browed albatross***	*t*	45.34	10.23		**64.59**
		d	19.66	22.15		**39.59**
	Gray-headed albatross	*t*	28.29	27.84		**56.40**
		d	28.03			**28.03**
	Light-mantled albatross	*t*		51.74		**51.74**
		d		42.61		**42.61**
Breeding probability (β)	***Black-browed albatross***	*t*		75.20*	75.82	**82.94**
		d			33.82	**33.82**
	Gray-headed albatross	*t*		32.19*	39.19	**37.60**
		d				
	Light-mantled albatross	*t*			33.05	**33.05**
		d			32.45	**32.45**
Breeding success (γ)	***Black-browed albatross***	*t*		27.72	33.10	**50.11**
		d		28.60	50.29	**59.22**
	Gray-headed albatross	*t*		22.99		**22.99**
		d		22.68		**22.68**
	Light-mantled albatross	*t*				**0**
		d				**0**

*Shaded areas represent covariates not considered for each demographic parameter. *Confounded by corresponding linear trends in breeding probability and sea surface height anomaly across black-browed and gray-headed albatross distribution. **Terrestrial covariates including rabbit density and extreme rainfall events from Cleeland et al. (2020).*

fisheries that operate without mitigation measures in the southwest Atlantic ranged from as high as 0.276 black-browed albatrosses/1000 hooks in the Uruguayan tuna fishery (2004–2007) to 0.03 to 0.05 birds/1000 hooks in the Chilean artisanal hake *Merluccius australis* and Patagonian toothfish *Dissostichus eleginoides* fisheries between 1998 and 2002 (Moreno et al., 2006; ICCAT, 2010; Jiménez et al., 2010). From 2006, Chilean industrial longliners converted fishing methods to eliminate seabird bycatch in the Patagonian toothfish fishery (Robertson et al., 2014). Effort data in some fisheries, including those within the Argentinean EEZ, were not publicly available and so could not be included in our models. However, high levels of black-browed albatross bycatch occur in Argentinean longline fisheries, with estimates of 0.010 ± 0.001 birds/1000 hooks caught in 2001–2010 (Favero et al., 2013). Similarly, high mortality of black-browed albatross (0.237 birds/haul, 2008–2010) is recorded in the Argentinean demersal trawl hake *M. hubbsi* fishery (Tamini et al., 2015). The negative relationship between black-browed albatross survival and southwest Atlantic fisheries indicates a direct link, with high bycatch rates of black-browed albatrosses reported there previously (Favero et al., 2013; Yeh et al., 2013).

Survival of black-browed and gray-headed albatrosses at Macquarie Island was related to effort in New Zealand trawl fisheries, but with higher effort associated with increased survival. Attendance of both species at vessels is common within these fisheries, particularly over the Campbell Plateau (Richard et al., 2011), a known foraging area for these populations (Cleeland et al., 2019). Furthermore, they are known scavengers of discards from squid trawlers in this region, with black-browed albatrosses attending in high numbers during the pre-laying and early incubation periods (Petyt, 1995). High attendance, bycatch in New Zealand trawl fisheries is low (0.05 captures per 100 tows per year) (Abraham and Thompson, 2015). Previous findings from Îles Kerguelen have shown discarding practices can influence demographic rates with higher breeding success of black-browed albatrosses attributed to the availability of discards during periods of high fishing effort (Rolland et al., 2008). Furthermore, breeding success is higher at colonies where fisheries discards are detected in the diet of black-browed albatrosses (McInnes et al., 2017). For black-browed albatrosses breeding at Macquarie Island, fish species found in their diet (including *Coryphaenoides* spp., *Cubiceps caeruleus*, *Halargyreus johnsonii*, *Lampris immaculatus, Microstoma* spp., Muraenolepididae and *Paranotothenia magellanica*) are bycatch species in New Zealand deep-water trawl fisheries and are subject to discarding (Anderson, 2017; McInnes et al., 2017). The results from this study represent the first indication that discarding practices may directly influence albatross survival by providing an abundant and predictable supplement to natural food resources.

Effect of Oceanographic Factors

The demographic rates of albatrosses at Macquarie Island were correlated with both the SAM and SOI. The SAM has complex and lagged effects on physical oceanography and biological productivity (Marshall, 2003; Lefebvre and Goosse, 2005). Higher values for the SAM index are associated with fluctuations in penguin populations in the east Antarctic (Ainley et al., 2005), reduced krill densities at South Georgia (Fielding et al., 2014) and improved maternal condition of southern elephant seals *Mirounga leonina* at Macquarie Island (McMahon et al., 2017). However, the underlying mechanisms and ecological

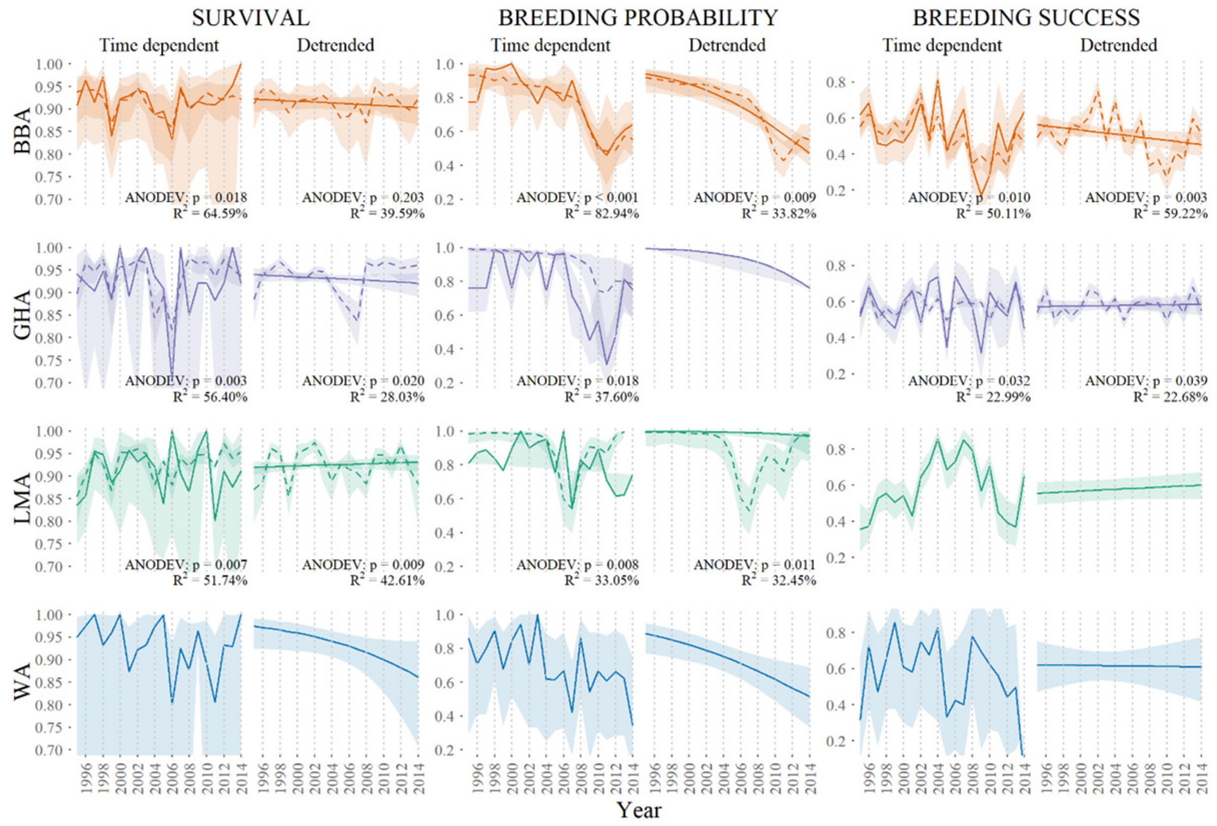

FIGURE 4 | Global integrated models showing annual variation in demographic rates of adult black-browed (BBA, orange), gray-headed (GHA, purple) and light-mantled (LMA, green) albatross at Macquarie Island, modeled as time-dependent and linear detrended (solid colored lines) and as a function of combined significant covariates (broken colored lines) including 0.95 confidence intervals.

consequences are not clear, especially for wide-ranging species such as albatrosses.

High SAM indices correspond to stronger winds closer to the pole and were associated with increased survival of black-browed and light-mantled albatrosses and increased breeding success of black-browed and gray-headed albatrosses at Macquarie Island following a lag of 2 to 3 years. During positive phases of the SAM, surface waters within the Antarctic Zone are colder, have increased upwelling, iron transport, and surface chlorophyll. In contrast, in the Subantarctic Zone, a deeper mixed layer results in reduced surface productivity (Lovenduski and Gruber, 2005). Surface productivity in the Antarctic Zone is transported to lower latitudes through Ekman processes (Lovenduski and Gruber, 2005) and may provide better foraging for albatrosses breeding at Macquarie Island after a 2 to 3 year lag. Positive SAM indices also lead to increased eddy kinetic energy following a 2 to 3 year lag, due to the time taken for stronger wind forcing to influence the Antarctic Circumpolar Current (Meredith and Hogg, 2006). Nonbreeding black-browed and gray-headed and breeding light-mantled albatrosses utilize regions of higher eddy kinetic energy (Cleeland et al., 2019), which tend to aggregate prey (Bost et al., 2009; Scales et al., 2014). Nutrient retention and enrichment of surface waters through upwelling and mixing at mesoscale cyclonic eddy features support higher phytoplankton and prey concentrations relative to surrounding waters (Sokolov and Rintoul, 2007).

A positive relationship between SOI and survival was detected in all three species tested. Positive SOI (La Niña) periods are related to higher productivity in the eastern Pacific boundary currents (Barber and Chavez, 1983; Behrenfeld et al., 2001) and improved hatching success of Indian yellow-nosed albatrosses *Thalassarche carteri* at Amsterdam Island, and breeding success of black-browed albatrosses at Îles Kerguelen (Rolland et al., 2008, 2009). A positive SOI may enhance biological productivity and increase recruitment of mid-trophic prey species (Waluda et al., 1999). El Niño conditions in the Pacific sector covaried positively with a negative SAM during our study period, making it difficult to disentangle the influence of these two large-scale climate cycles (Stammerjohn et al., 2008).

Breeding light-mantled albatrosses forage along the Subantarctic Front near Macquarie Island, and to the south in Antarctic waters (∼65°S) at the southern boundary of the Antarctic Circumpolar Current (Cleeland et al., 2019). They have the most southerly foraging distribution of all Macquarie Island species, which may increase their responsiveness to variability in sea ice concentration and primary productivity on shorter timescales, although the proximal mechanisms are unclear. Survival of this species was positively related to sea ice extent, which may represent improved foraging conditions in more southerly waters (Loeb et al., 1997). In their known foraging habitat off east Antarctica, the abundance of Antarctic krill *Euphasia superba* is found in greater densities in areas of greatest annual sea-ice cover (Nicol et al., 2000). Furthermore, snow petrels *Pagodroma nivea* have also been found to show improved demographic responses to more extensive sea cover, including increased breeding success and fledgling body condition (Barbraud and Weimerskirch, 2001). For light-mantled albatross, an ice independent species, the relationship between sea ice conditions and survival is interesting given the potential for population level consequences due to recent and rapid sea ice loss around Antarctica (Parkinson, 2019).

The positive response of black-browed and gray-headed albatross survival to stronger southerly winds, may be due to the influence of wind on the energetics of flight. The relatively high wing loading of gray-headed albatrosses means stronger winds improve flight efficiency by increasing glide ratios and reducing the cost of reaching foraging areas (Pennycuick, 1982). For black-browed albatrosses, more southerly winds would act similarly, supporting efficient northward flight to foraging areas. In the Indian Ocean, body condition and breeding success of wandering albatrosses improved with increasing wind speed, related to the SAM (Weimerskirch et al., 2012). Furthermore, Pardo et al. (2017) showed a strong positive effect of wind patterns on adult and juvenile survival of wandering albatrosses at South Georgia. Predictions of increasingly positive SAM and subsequent strengthening of circumpolar winds may be beneficial for most albatross species at Macquarie Island, except for the light-mantled albatross.

Global Models and Terrestrial Effects

In this study we found the threat of fisheries to survival was generally more influential than changes in oceanographic factors for black-browed and gray-headed albatrosses. This is supported by the historical evidence of fisheries-related incidental mortality and new evidence of dietary linkages with discarding practices for these species (Tuck et al., 2003; McInnes et al., 2017). It is expected that albatrosses, as long-lived, wide-ranging pelagic foragers, can buffer against oceanographic variability that may influence the accessibility and predictability of prey resources. Therefore, it is noteworthy we detected significant relationships between survival and oceanographic change, suggesting its influence on individual fitness has population level consequences. This is particularly the case for black-browed albatross, where short-term variability in survival is slightly better described by oceanographic variability. Oceanographic factors explained greater variability in survival for light-mantled albatrosses than any other species. The foraging behavior of light-mantled albatrosses shows some degree of plasticity, with individuals showing 'flexible faithfulness' with year-to-year differences in foraging sites, but consistent use of oceanographic features including anticyclonic eddies and frontal regions (Carpenter-Kling et al., 2020). This suggests the magnitude and predictability of dynamic oceanographic features is likely have a pronounced influence on foraging outcomes, and thus has repercussions on the survival of light-mantled albatrosses.

Nesting habitat quality (indicated by rabbit density) was the most influential determinant of the breeding probability of all three species tested, due to overgrazing and widescale slope erosion. With terrestrial factors accounting for most of the variability in breeding probability other environmental drivers are potentially masked from detection. However, this result indicates that habitat restoration at the colony is likely to lead to positive demographic and population-level responses.

The global models show terrestrial covariates are the most influential for breeding success of black-browed albatrosses, whereas for gray-headed albatrosses only oceanographic factors are identified as important. Where over 50% of demographic variability in breeding success could be described for black-browed albatrosses, no factors were detected for light-mantled albatrosses. Despite accounting for biennial breeding in the models, it is possible that this strategy influences our ability to detect significant relationships as the factors that influence breeding success may be more complex and operate over larger spatial and temporal scales.

Our study quantifies the links (e.g., demographic models) between ongoing environmental drivers and adult survival and reproductive success thereby providing information central to developing evidence-based conservation strategies and management plans. Of the three species examined in this study, the gray-headed albatross is the most threatened making it a high priority for management action. Furthermore, our results identify species for which there is no single dominant environmental driver and where multiple, targeted conservation efforts may be required to achieve long-term improvements in demographic outcomes. For black-browed albatrosses on Macquarie Island, changes in fisheries and breeding habitat quality had the greatest influence on survival, breeding probability and breeding success; factors for which mitigation strategies already exist (Croxall et al., 2012; Phillips et al., 2016). The removal of rabbits from Macquarie Island (Springer, 2016) and current bycatch mitigation in the south-west Atlantic (Otley et al., 2007; Moreno et al., 2008) may account for the increasing population of black-browed albatrosses.

By identifying common demographic drivers amongst species this study supports the development of management actions that potentially benefit all three species. Specifically, for all three species, processes on land affected breeding probability, and consequently the recent removal of rabbits from Macquarie Island is likely to ameliorate their negative effects on vegetation stability and improve reproductive output.

Understanding the demographic drivers of wild populations is difficult due to the multitude of interacting factors that can affect survival and reproductive performance. However, a full and complete understanding is not necessarily a prerequisite for management action. In some cases, a particular management intervention might buffer the influence of one driver on the population by addressing the impact of another (Pascoe et al., 2011). This is helpful when management solutions that address a single threat are more logistically practical, economically feasible or effective over more appropriate time and spatial scales than for other threats. Furthermore, intermediary management action may provide reprieve for vulnerable populations until advances in conservation technology or policy can be made. Such options are becoming exceedingly important in the face of rapid and pervasive impacts of climate change. For gray-headed and light-mantled albatrosses, there are currently few options to directly mitigate the effects of climate on their survival and breeding success. The buffer due to the eradication is therefore likely to provide important benefits, at least in the short term. For globally threatened species such as albatross that cross multiple international boundaries and are widely distributed throughout the high seas, such action may be vital.

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: The long-term albatross mark-recapture dataset used in this study is housed by the Marine Conservation Branch within the Department of Primary Industries, Parks Water and Environment, Tasmania, and by the Australian Antarctic Data Centre under the Australian Antarctic program data policy (https://data.aad.gov.au/aadc/about/data_policy.cfm).

ETHICS STATEMENT

The animal study was reviewed and approved by the Tasmanian Government Department of Primary Industries, Parks, Water and Environment's Animal Ethics Committee (permit number TFA9195).

AUTHOR CONTRIBUTIONS

JC, DP, and MH conceived and designed the study. CM and M-AL developed research concepts. RA, GT, and BR provided access to the data. JC and BR performed data management and data quality assurance tasks. JC conducted the statistical analysis and modeling work with support from DP and RP. JC took the lead in writing the manuscript. All authors performed ecological interpretation of results and contributed substantially to manuscript revisions.

FUNDING

The Australian Antarctic Division through the Australian Antarctic Science Program (Project numbers: 751, 2569, 4112) has supported this research at Macquarie Island. JC was supported by a Scientific Committee for Antarctic Research Fellowship and an Antarctic Science Bursary.

ACKNOWLEDGMENTS

We would like to thank Rosemary Gales for her commitment to albatross monitoring at Macquarie Island over the last two decades and Aleks Terauds for valuable guidance. We also thank Sally McCarthy and John Garvey (AFMA); Marco Favero and Wieslawa Misiak (ACAP); Barbara Wienecke, Jonathan Barrington and Juan Carlos Quiroz Espinosa and Dirk Welsford (AAD); Joost Pompert (FIFD); David Ramm (CCAMLR); Nick Vogel (IATTC); Carlos Palma (ICCAT); Christopher Dick (NZ-MPI); and Craig Loveridge (SPRFMO) for contribution of fisheries data. The content of this manuscript has been published in part as part of the thesis of Cleeland (2017).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.578144/full#supplementary-material

REFERENCES

Abraham, E. R., and Thompson, F. N. (2015). *Captures of All Birds in Trawl Fisheries, in the New Zealand Exclusive Economic Zone, from 2002–03 to 2013–14* [Online]. Available online at: https://data.dragonfly.co.nz/psc/v20150002/birds/trawl/all-vessels/eez/all/ (accessed April 31, 2017).

Ainley, D. G., Clarke, E. D., Arrigo, K., Fraser, W. R., Kato, A., Barton, K. J., et al. (2005). Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. *Antarct. Sci.* 17, 171–182. doi: 10.1017/s0954102005002567

Anderson, O. F. (2017). *Fish and Invertebrate Bycatch in New Zealand Deepwater Fisheries from 1990–91 until 2013–14. New Zealand Aquatic Environment and Biodiversity* Report No. 181. Wellington, NZ: Ministry for Primary Industries New Zealand Government.

Anderson, O. R. J., Small, C. J., Croxall, J. P., Dunn, E. K., Sullivan, B. J., Yates, O., et al. (2011). Global seabird bycatch in longline fisheries. *Endanger. Species Res.* 14, 91–106. doi: 10.3354/esr00347

Arnold, J. M., Brault, S., and Croxall, J. P. (2006). Albatross populations in peril: a population trajectory for Black-browed Albatrosses at South Georgia. *Ecol. Appl.* 16, 419–432. doi: 10.1890/03-5340

Barber, R. T., and Chavez, F. P. (1983). Biological consequences of El Niño. *Science* 222, 1203–1210.

Barbraud, C., and Weimerskirch, H. (2001). Contrasting effects of the extent of sea-ice on the breeding performance of an antarctic top predator, the snow petrel pagodroma nivea. *J. Avian Biol.* 32, 297–302. doi: 10.1111/j.0908-8857.2001.320402.x

Barbraud, C., and Weimerskirch, H. (2003). Climate and density shape population dynamics of a marine top predator. *Proc. R. Soc. B Biol. Sci.* 270, 2111–2116. doi: 10.1098/rspb.2003.2488

Barbraud, C., and Weimerskirch, H. (2012). Estimating survival and reproduction in a quasi-biennially breeding seabird with uncertain and unobservable states. *J. Ornithol.* 152, 605–615. doi: 10.1007/s10336-011-0686-1

Bartumeus, F., Giuggioli, L., Louzao, M., Bretagnolle, V., Oro, D., and Levin, S. A. (2010). Fishery discards impact on seabird movement patterns at regional scales. *Curr. Biol.* 20, 215–222. doi: 10.1016/j.cub.2009.11.073

Behrenfeld, M. J., Randerson, J. T., McClain, C. R., Feldman, G. C., Los, S. O., Tucker, C. J., et al. (2001). Biospheric primary production during an ENSO transition. *Science* 291, 2594–2597. doi: 10.1126/science.1055071

Bost, C. A., Cotte, C., Bailleul, F., Cherel, Y., Charrassin, J. B., Guinet, C., et al. (2009). The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J. Mar. Syst.* 78, 363–376. doi: 10.1016/j.jmarsys.2008.11.022

Brothers, N., and Bone, C. (2008). The response of burrow-nesting petrels and other vulnerable bird species to vertebrate pest management and climate change on sub-Antarctic Macquarie Island. *Pap. Proc. R. Soc. Tasman.* 142, 123–148. doi: 10.26749/rstpp.142.1.123

Burnham, K. P., and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York, NY: Springer-Verlag.

Carpenter-Kling, T., Reisinger, R. R., Orgeret, F., Connan, M., Stevens, K. L., Ryan, P. G., et al. (2020). Foraging in a dynamic environment: response of four sympatric sub-Antarctic albatross species to interannual environmental variability. *Ecol. Evol.* 10, 11277–11295. doi: 10.1002/ece3.6766

Catry, P., Forcada, J., and Almeida, A. (2011). Demographic parameters of black-browed albatrosses *Thalassarche melanophris* from the Falkland Islands. *Polar Biol.* 34, 1221–1229. doi: 10.1007/s00300-011-0984-3

Choquet, R., Lebreton, J. D., Gimenez, O., Reboulet, A. M., and Pradel, R. (2009a). U-CARE: utilities for performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography* 32, 1071–1074. doi: 10.1111/j.1600-0587.2009.05968.x

Choquet, R., Rouan, L., and Pradel, R. (2009b). "Program E-SURGE: a software application for fitting multievent models," in *Modeling Demographic Processes in Marked Populations*, eds D. L. Thomson, E. G. Cooch, and M. J. Conroy (Boston, MA: Springer US), 845–865. doi: 10.1007/978-0-387-78151-8_39

Cleeland, J. B. (2017). *Factors that Drive Demographic Change in a Community of Albatrosses*. Ph.D. Thesis, University of Tasmania, Hobart, TAS.

Cleeland, J. B., Alderman, R., Bindoff, A., Lea, M. A., McMahon, C. R., Phillips, R. A., et al. (2019). Factors influencing the habitat use of sympatric albatrosses from Macquarie Island, Australia. *Mar. Ecol. Prog. Ser.* 609, 221–237. doi: 10.3354/meps12811

Cleeland, J. B., Pardo, D., Raymond, B., Terauds, A., Alderman, R., McMahon, C. R., et al. (2020). Introduced species and extreme weather as key drivers of reproductive output in three sympatric albatrosses. *Sci. Rep.* 10:8199.

Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes, D. K. A., et al. (2014). Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Glob. Chang. Biol.* 20, 3004–3025.

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., et al. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv. Int.* 22, 1–34. doi: 10.1017/s0959270912000020

Croxall, J., Prince, P., Rothery, P., and Wood, A. (1998). "Population changes in albatrosses at South Georgia," in *Albatross Biology and Conservation*, eds G. Robertson and R. Gales (Chipping Norton, NSW: Surrey Beattie), 69–83.

Cumpston, J. S. (1968). "Macquarie Island," in *Australian National Antarctic Research Expeditions Reports*, ed. M. R. O Millett (Melbourne, VIC: Australian Antarctic Division, Department of External Affairs).

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., et al. (2011). Global seabird response to forage fish depletion – one-third for the birds. *Science* 334, 1703–1706. doi: 10.1126/science.1212928

Cuthbert, R., and Hilton, G. (2004). Introduced house mice Mus musculus: a significant predator of threatened and endemic birds on Gough Island, South Atlantic Ocean? *Biol. Conserv.* 117, 483–489. doi: 10.1016/j.biocon.2003.08.007

de la Mare, W. K., and Kerry, K. R. (1994). Population dynamics of the wandering albatross (*Diomedea exulans*) on Macquarie Island and the effects of mortality from longline fishing. *Polar Biol.* 14, 231–242. doi: 10.1007/bf00239171

Delord, K., Besson, D., Barbraud, C., and Weimerskirch, H. (2008). Population trends in a community of large Procellariiforms of Indian Ocean: potential effects of environment and fisheries interactions. *Biol. Conserv.* 141, 1840–1856. doi: 10.1016/j.biocon.2008.05.001

DPIPWE (2014). *The Conservation and Status of Albatrosses and Giant Petrels on Macquarie Island: Report on the 2013/14 Field Season*. Hobart, TAS: Australian Government, Department of Primary Industries Parks Water and Environment.

Favero, M., Blanco, G., Copello, S., Pon, J. P. S., Patterlini, C., Mariano-Jelicich, R., et al. (2013). Seabird bycatch in the Argentinean demersal longline fishery, 2001-2010. *Endanger. Species Res.* 19, 187–199. doi: 10.3354/esr00478

Fielding, S., Watkins, J. L., Trathan, P. N., Enderlein, P., Waluda, C. M., Stowasser, G., et al. (2014). Interannual variability in Antarctic krill (*Euphausia superba*) density at South Georgia, Southern Ocean: 1997-2013. *ICES J. Mar. Sci.* 71, 2578–2588. doi: 10.1093/icesjms/fsu104

Forcada, J., and Trathan, P. N. (2009). Penguin responses to climate change in the Southern Ocean. *Glob. Chang. Biology* 15, 1618–1630. doi: 10.1111/j.1365-2486.2009.01909.x

Gilman, E., Boggs, C., and Brothers, N. (2003). Performance assessment of an underwater setting chute to mitigate seabird bycatch in the Hawaii pelagic longline tuna fishery. *Ocean Coast. Manag.* 46, 985–1010. doi: 10.1016/j.ocecoaman.2003.12.001

Gimenez, O., Lebreton, J. D., Gaillard, J. M., Choquet, R., and Pradel, R. (2012). Estimating demographic parameters using hidden process dynamic models. *Theor. Popul. Biol.* 82, 307–316. doi: 10.1016/j.tpb.2012.02.001

Granadeiro, J. P., Brickle, P., and Catry, P. (2014). Do individual seabirds specialize in fisheries' waste? The case of black-browed albatrosses foraging over the Patagonian Shelf. *Anim. Conserv.* 17, 19–26. doi: 10.1111/acv.12050

Grosbois, V., Gimenez, O., Gaillard, J. M., Pradel, R., Barbraud, C., Clobert, J., et al. (2008). Assessing the impact of climate variation on survival in vertebrate populations. *Biol. Rev.* 83, 357–399. doi: 10.1111/j.1469-185x.2008.00047.x

ICCAT (2010). *ICCAT By-Catch Database* [Online]. Available online at: https://www.iccat.int/en/bycatch.html (accessed November 07, 2016)

Inchausti, P., and Weimerskirch, H. (2001). Risks of decline and extinction of the endangered Amsterdam albatross and the projected impact of long-line fisheries. *Biol. Conserv.* 100, 377–386. doi: 10.1016/s0006-3207(01)00044-1

Jenouvrier, S., Desprez, M., Fay, R., Barbraud, C., Weimerskirch, H., Delord, K., et al. (2018). Climate change and functional traits affect population dynamics of a long-lived seabird. *J. Anim. Ecol.* 87, 906–920. doi: 10.1111/1365-2656.12827

Jiménez, S., Abreu, M., Pons, M., Ortiz, M., and Domingo, A. (2010). Assessing the impact of the pelagic longline fishery on albatrosses and petrels in the southwest Atlantic. *Aquat. Living Resour.* 23, 49–64. doi: 10.1051/alr/2010002

Jouventin, P., and Dobson, F. S. (2002). Why breed every other year? The case of albatrosses. *Proc. R. Soc. B Biol. Sci.* 269, 1955–1961. doi: 10.1098/rspb.2002.2080

Lea, M. A., Guinet, C., Cherel, Y., Duhamel, G., Dubroca, L., Pruvost, P., et al. (2006). Impacts of climatic anomalies on provisioning strategies of a Southern Ocean predator. *Mar. Ecol. Prog. Ser.* 310, 77–94. doi: 10.3354/meps310077

Lebreton, J. D., Burnham, K. P., Clobert, J., and Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62, 67–118. doi: 10.2307/2937171

Lefebvre, W., and Goosse, H. (2005). Influence of the Southern annular mode on the sea ice-ocean system: the role of the thermal and mechanical forcing. *Ocean Sci.* 1, 145–157. doi: 10.5194/os-1-145-2005

Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., et al. (1997). Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387, 897–900. doi: 10.1038/43174

Lovenduski, N. S., and Gruber, N. (2005). Impact of the Southern annular mode on Southern Ocean circulation and biology. *Geophys. Res. Lett.* 32:L11603.

Maree, B. A., Wanless, R. M., Fairweather, T. P., Sullivan, B. J., and Yates, O. (2014). Significant reductions in mortality of threatened seabirds in a South African trawl fishery. *Anim. Conserv.* 17, 520–529. doi: 10.1111/acv.12126

Marshall, G. J. (2003). Trends in the Southern annular mode from observations and reanalyses. *J. Clim.* 16, 4134–4143. doi: 10.1175/1520-0442(2003)016<4134:titsam>2.0.co;2

McInnes, J. C., Jarman, S. N., Lea, M. A., Raymond, B., Deagle, B. E., Phillips, R. A., et al. (2017). DNA metabarcoding as a marine conservation and management tool: a circumpolar examination of fishery discards in the diet of threatened albatrosses. *Front. Mar. Sci.* 4:277. doi: 10.3389/fmars.2017.00277

McMahon, C. R., Harcourt, R. G., Burton, H. R., Daniel, O., and Hindell, M. A. (2017). Seal mothers expend more on offspring under favourable conditions and less when resources are limited. *J. Anim. Ecol.* 86, 359–370. doi: 10.1111/1365-2656.12611

Meredith, M. P., and Hogg, A. M. (2006). Circumpolar response of Southern Ocean eddy activity to a change in the Southern annular mode. *Geophys. Res. Lett.* 33:L16608.

Mills, M. S. L., and Ryan, P. G. (2005). Modelling impacts of long-line fishing: what are the effects of pair-bond disruption and sex-biased mortality on albatross fecundity? *Anim. Conserv.* 8, 359–367. doi: 10.1017/s1367943005002386

Milot, E., Weimerskirch, H., Duchesne, P., and Bernatchez, L. (2007). Surviving with low genetic diversity: the case of albatrosses. *Proc. R. Soc. B Biol. Sci.* 274, 779–787. doi: 10.1098/rspb.2006.0221

Moreno, C. A., Arata, J. A., Rubilar, P., Hucke-Gaete, R., and Robertson, G. (2006). Artisanal longline fisheries in Southern Chile: lessons to be learned to avoid incidental seabird mortality. *Biol. Conserv.* 127, 27–36. doi: 10.1016/j.biocon.2005.07.011

Moreno, C. A., Castro, R., Mújica, L. J., and Reyes, P. (2008). Significant conservation benefits obtained from the use of a new fishing gear in the Chilean Patagonian toothfish fishery. *CCAMLR Sci.* 15, 79–91.

Nicol, S., Pauly, T., Bindoff, N. L., Wright, S., Thiele, D., Hosle, G. W., et al. (2000). Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. *Nature* 406, 504–507. doi: 10.1038/35020053

Otley, H. M., Reid, T. A., and Pompert, J. (2007). Trends in seabird and Patagonian toothfish *Dissostichus eleginoides* longliner interactions in Falkland Island waters, 2002/03 and 2003/04. *Mar. Ornithol.* 35, 47–55.

Pardo, D., Barbraud, C., Authier, M., and Weimerskirch, H. (2013). Evidence for an age-dependent influence of environmental variations on a long-lived seabird's life-history traits. *Ecology* 94, 208–220. doi: 10.1890/12-0215.1

Pardo, D., Forcada, J., Wood, A. G., Tuck, G. N., Ireland, L., Pradel, R., et al. (2017). Additive effects of climate and fisheries drive catastrophic declines in an albatross community. *Proc. Natl. Acad. Sci. U.S.A.* 144, 10829–10837.

Parkinson, C. L. (2019). A 40-y record reveals gradual Antarctic sea ice increases followed by decreases at rates far exceeding the rates seen in the Arctic. *Proc. Natl. Acad. Sci. U.S.A.* 116, 14414–14423. doi: 10.1073/pnas.1906556116

Pascoe, S., Wilcox, C., and Donlan, C. J. (2011). Biodiversity offsets: a cost-effective interim solution to seabird bycatch in fisheries? *PLoS One* 6:e25762. doi: 10.1371/journal.pone.0025762

Pennycuick, C. J. (1982). The flight of petrels and albatrosses (*Procellariiformes*), observed in South Georgia and its vicinity. *Philos. Trans. R. Soc. B Biol. Sci.* 300, 75–106. doi: 10.1098/rstb.1982.0158

Petyt, C. (1995). Behaviour of seabirds around fishing trawlers in New Zealand subantarctic waters. *Notornis* 42, 99–115.

Phillips, R. A., Gales, R., Baker, G. B., Double, M. C., Favero, M., Quintana, F., et al. (2016). The conservation status and priorities for albatrosses and large petrels. *Biol. Conserv.* 201, 169–183. doi: 10.1016/j.biocon.2016.06.017

Phillips, R. A., Silk, J. R. D., and Croxall, J. P. (2005). Foraging and provisioning strategies of the light-mantled sooty albatross at South Georgia: competition and co-existence with sympatric pelagic predators. *Mar. Ecol. Prog. Ser.* 285, 259–270. doi: 10.3354/meps285259

Poncet, S., Wolfaardt, A. C., Black, A., Browning, S., Lawton, K., Lee, J., et al. (2017). Recent trends in numbers of wandering (*Diomedea exulans*), black-browed (*Thalassarche melanophris*) and grey-headed (*T. chrysostoma*) albatrosses breeding at South Georgia. *Polar Biol.* 40, 1347–1358. doi: 10.1007/s00300-016-2057-0

R Core Team (2016). *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing.

Richard, Y., Abraham, E. R., and Berkenbusch, K. (2011). *Counts of Seabirds Around Commercial Fishing Vessels within New Zealand Waters*. Wellington: Unpublished report held by the Department of Conservation.

Rivalan, P., Barbraud, C., Inchausti, P., and Weimerskirch, H. (2010). Combined impacts of longline fisheries and climate on the persistence of the Amsterdam Albatross *Diomedia amsterdamensis*. *Ibis* 152, 6–18. doi: 10.1111/j.1474-919x.2009.00977.x

Robertson, G., Candy, S. G., Wienecke, B., and Lawton, K. (2010). Experimental determinations of factors affecting the sink rates of baited hooks to minimize seabird mortality in pelagic longline fisheries. *Aquat. Conserv.* 20, 632–643. doi: 10.1002/aqc.1140

Robertson, G., Moreno, C., Arata, J. A., Candy, S. G., Lawton, K., Valencia, J., et al. (2014). Black-browed albatross numbers in Chile increase in response to reduced mortality in fisheries. *Biol. Conserv.* 169, 319–333. doi: 10.1016/j.biocon.2013.12.002

Rolland, V., Barbraud, C., and Weimerskirch, H. (2008). Combined effects of fisheries and climate on a migratory long-lived marine predator. *J. Appl. Ecol.* 45, 4–13. doi: 10.1111/j.1365-2664.2007.01360.x

Rolland, V., Barbraud, C., and Weimerskirch, H. (2009). Assessing the impact of fisheries, climate and disease on the dynamics of the Indian yellow-nosed Albatross. *Biol. Conserv.* 142, 1084–1095. doi: 10.1016/j.biocon.2008.12.030

Scales, K. L., Miller, P. I., Embling, C. B., Ingram, S. N., Pirotta, E., and Votier, S. C. (2014). Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *J. R. Soc. Interface* 11, 1–9.

Schoombie, S., Crawford, R. J. M., Makhado, A. B., Dyer, B. M., and Ryan, P. G. (2016). Recent population trends of sooty and light-mantled albatrosses breeding on Marion Island. *Afr. J. Mar. Sci.* 38, 119–127. doi: 10.2989/1814232x.2016.1162750

Sokolov, S., and Rintoul, S. R. (2007). On the relationship between fronts of the Antarctic circumpolar current and surface chlorophyll concentrations in the Southern Ocean. *J. Geophys. Res.* 112, 1–17. doi: 10.1007/s13131-012-0248-2

Sokolov, S., and Rintoul, S. R. (2009). Circumpolar structure and distribution of the antarctic circumpolar current fronts: 2. Variability and relationship to sea surface height. *J. Geophys. Res.* 114, 1–15. doi: 10.1007/s13131-012-0248-2

Springer, K. (2016). Methodology and challenges of a complex multi-species eradication in the sub- Antarctic and immediate effects of invasive species removal. *N. Z. J. Ecol.* 40, 273–278. doi: 10.20417/nzjecol.40.30

Stammerjohn, S. E., Martinson, D. G., Smith, R. C., Yuan, X., and Rind, D. (2008). Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño-Southern Oscillation and Southern annular mode variability. *J. Geophys. Res.* 113, 1–20.

Stammerjohn, S., Massom, R., Rind, D., and Martinson, D. (2012). Regions of rapid sea ice change: an inter-hemispheric seasonal comparison. *Geophys. Res. Lett.* 39:L06501.

Tamini, L. L., Chavez, L. N., Góngora, M. E., Yates, O., Rabuffetti, F. L., and Sullivan, B. (2015). Estimating mortality of black-browed albatross (*Thalassarche melanophris*, Temminck, 1828) and other seabirds in the Argentinean factory trawl fleet and the use of bird-scaring lines as a mitigation measure. *Polar Biol.* 38, 1867–1879. doi: 10.1007/s00300-015-1747-3

Terauds, A., Gales, R., and Alderman, R. (2005). Trends in numbers and survival of Black-browed (*Thalassarche melanophrys*) and Grey-headed (*T. chrysostoma*) Albatrosses breeding on Macquarie Island. *Emu* 105, 159–167. doi: 10.1071/mu05026

Terauds, A., Gales, R., Baker, G. B., and Alderman, R. (2006). Population and survival trends of Wandering Albatrosses (*Diomedea exulans*) breeding on Macquarie Island. *Emu* 106, 211–218. doi: 10.1071/mu06007

Trathan, P. N., Forcada, J., and Murphy, E. J. (2007). Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Philos. Trans. R. Soc. B Biol. Sci.* 362, 2351–2365. doi: 10.1098/rstb.2006.1953

Tuck, G. N., Polacheck, T., and Bulman, C. M. (2003). Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. *Biol. Conserv.* 114, 1–27. doi: 10.1016/s0006-3207(02)00378-6

Tuck, G. N., Polacheck, T., Croxall, J. P., and Weimerskirch, H. (2001). Modelling the impact of fishery by-catches on albatross populations. *J. Appl. Ecol.* 38, 1182–1196. doi: 10.1046/j.0021-8901.2001.00661.x

Turner, J., Chenoli, S. N., Abu Samah, A., Marshall, G., Phillips, T., and Orr, A. (2009). Strong wind events in the Antarctic. *J. Geophys. Res. Atmos.* 114, 1–25. doi: 10.11646/zootaxa.3625.1.1

Vargas, F. H., Lacy, R. C., Johnson, P. J., Steinfurth, A., Crawford, R. J. M., Dee Boersma, P., et al. (2007). Modelling the effect of El Niño on the persistence of small populations: the Galápagos penguin as a case study. *Biol. Conserv.* 137, 138–148.

Waluda, C. M., Trathan, P. N., and Rodhouse, P. G. (1999). Influence of oceanographic variability on recruitment in the Illex argentinus (*Cephalopoda: Ommastrephidae*) fishery in the South Atlantic. *Mar. Ecol. Prog. Ser.* 183, 159–167. doi: 10.3354/meps183159

Waugh, S. M., Weimerskirch, H., Moore, P. J., and Sagar, P. M. (1999). Population dynamics of Black-browed and Grey-headed Albatrosses *Diomedea melanophrys* and *D. chrysostoma* at Campbell Island, New Zealand, 1942-96. *Ibis* 141, 216–225. doi: 10.1111/j.1474-919x.1999.tb07544.x

Weimerskirch, H., and Jouventin, P. (1998). "Changes in population sizes and demographic parameters of six albatross species breeding on the French sub-Antarctic islands," in *Albatross Biology and Conservation*, eds G. Robertson and R. Gales (Chipping Norton: Surrey Beatty & Sons), 84–91.

Weimerskirch, H., Clobert, J., and Jouventin, P. (1987). Survival in five southern albatrosses and its relationship with their life history. *J. Anim. Ecol.* 56, 1043–1055. doi: 10.2307/4965

Weimerskirch, H., Louzao, M., De Grissac, S., and Delord, K. (2012). Changes in wind pattern alter albatross distribution and life-history traits. *Science* 335, 211–214. doi: 10.1126/science.1210270

Weller, F., Cecchini, L. A., Shannon, L., Sherley, R. B., Crawford, R. J. M., Altwegg, R., et al. (2014). A system dynamics approach to modelling multiple drivers of the African penguin population on Robben Island, South Africa. *Ecol. Modell.* 277, 38–56. doi: 10.1016/j.ecolmodel.2014.01.013

Yeh, Y. M., Huang, H. W., Dietrich, K. S., and Melvin, E. (2013). Estimates of seabird incidental catch by pelagic longline fisheries in the South Atlantic Ocean. *Anim. Conserv.* 16, 141–152. doi: 10.1111/j.1469-1795.2012.00588.x

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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in Marine Science

ORIGINAL RESEARCH
published: 09 March 2021
doi: 10.3389/fmars.2021.579946

Comparative Modeling of Cod-Capelin Dynamics in the Newfoundland-Labrador Shelves and Barents Sea Ecosystems

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The Atlantic cod (*Gadus morhua*) stocks in the Newfoundland-Labrador Shelves (NL) and Barents Sea (BS) ecosystems have shown divergent trajectories over the last 40 years. Both stocks experienced either an important decline (BS) or a collapse (NL) in the mid-1980s and early 1990s, respectively. After these population reductions, the BS stock quickly rebounded and it is currently at record high levels, while the NL stock, despite showing some improvement since the mid-2000s, remains at low levels. Fishing and environmental conditions are known to be important drivers of cod dynamics in both ecosystems, especially the availability of high energy prey like capelin (*Mallotus villosus*), however, the question of how different or similar these two stocks truly are remains. Could, for example, the NL cod stock rebuild if presented to conditions like the ones experienced by BS cod? To explore such questions, we developed a simple biomass dynamic model for cod using a bioenergetic-allometric approach. This model includes fisheries catches and capelin availability as external drivers and was implemented for both ecosystems. Despite the contrasting trends, the model produced very good fits, and showed some remarkably similar estimated parameters in both systems. We explored these similarities by (a) performing the thought experiment of transferring cod stocks between ecosystems by switching estimated key parameters between models and comparing the output, and (b) implementing an integrated model architecture which allowed fitting common parameters for both stocks to evaluate the similarity of key vital rates. Our results indicate that cod trajectories in NL and BS can be reliably described using simple bioenergetic-allometric arguments, fishery catches, and capelin availability. Model parameters that encapsulate intrinsic vital rates were not significantly different between stocks. This indicates that NL and BS cod stocks are biologically similar, and that the differences in their trajectories are driven by the ecosystem context in which these stocks are embedded, and suggests that the NL stock would be expected to rebuild if enough capelin were available. This also indicates that capelin status and trend should be an important consideration for effective management of these cod stocks.

Keywords: trophic interactions, predator-prey, ecosystem approach to fisheries, bottom-up regulation, food web ecology, bioenergetic-allometric model

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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: *03 July 2020*
Accepted: *03 February 2021*
Published: *09 March 2021*

Citation:
Koen-Alonso M, Lindstrøm U and Cuff A (2021) Comparative Modeling of Cod-Capelin Dynamics in the Newfoundland-Labrador Shelves and Barents Sea Ecosystems. Front. Mar. Sci. 8:579946. doi: 10.3389/fmars.2021.579946

INTRODUCTION

The Newfoundland and Labrador Shelves (NL) and the Barents Sea (BS) are considered typical high-latitude shelf ecosystems (**Figure 1**), implying strong seasonality in physics (e.g., sea ice, temperature) and biological production, high productivity, and low biological diversity (e.g., Dayton et al., 1994; Wassmann et al., 2006; Gaichas et al., 2014). Both regions have marine communities historically dominated by groundfish, with Atlantic cod (*Gadus morhua*) as the dominant fish predator, small pelagic fish like capelin (*Mallotus villosus*) and herring (*Cuplea harengus*) acting as key forage species by connecting primary and secondary production with upper trophic levels, and with marine mammals as important top predators (e.g., Wassmann et al., 2006; Gaichas et al., 2014; Bernier et al., 2018; Koen-Alonso and Cuff, 2018). The annual production cycle in both ecosystems is dominated by the spring bloom, where sea ice dynamics play an important regulatory role, and characterized by an important bentho-pelagic coupling (e.g., Wassmann et al., 2006; Thompson et al., 2008; Bernier et al., 2018).

While similar in many respects, these two ecosystems also display major physical differences (Drinkwater et al., 2013). The oceanography of the NL ecosystem is characterized by the unidirectional north to south flow of the cold Labrador current, while the BS oceanography is characterized by a more counter-clockwise flow within its basin, defined by the warm continuation of the Atlantic current, the Norwegian current, and inflows from the Arctic (**Figure 1**). Another important difference is that, while both ecosystems are showing warming signals in recent decades, NL has shown a more cyclic pattern in ocean conditions, with a very cold period in the late 1980s and early 1990s, clear warming trends from the mid-2000s to the mid-2010s, and a return to average conditions since (e.g., Colbourne, 2004; Drinkwater et al., 2013; Lind et al., 2018; Cyr et al., 2020). On the other hand, the BS ecosystem also experienced a cold period in ocean conditions in the 1980s but has seen a strong and directional warming since the mid-2000s. This change has led to a reduction in the domain of Arctic waters in BS, triggering an expansion of boreal fish communities and a reduction in Arctic ones (Fossheim et al., 2015).

Another important contrast between these two ecosystems is the trajectory and status of their fish communities. Both ecosystems have a long history of fishing, traditionally targeting Atlantic cod as the staple catch, but also other groundfish and pelagic fishes (e.g., flatfishes, capelin, herring). They both experienced significant fishing pressure to the point of overfishing resources between the 1960s and 1980s (e.g., Hutchings and Myers, 1994; Myers et al., 1996; Lilly et al., 2013; Koen-Alonso et al., 2013; Haug et al., 2017; Popov and Zeller, 2018; ICES, 2019). The compounding effects of environmental conditions and fishing led to a regime shift in NL, with the collapse of groundfish stocks and capelin, and the increase in shellfish species like Northern shrimp (*Pandalus borealis*) and snow crab (*Chionoecetes opilio*) (e.g., Koen-Alonso et al., 2010; Buren et al., 2014a; Pedersen et al., 2017; Koen-Alonso and Cuff, 2018). Today, after experiencing two decades of shellfish dominance, the NL fish community is showing modest signals of groundfish rebuilding, likely tied to an also modest capelin rebuilding, and is still far below its pre-collapse levels (Koen-Alonso and Cuff, 2018). In contrast, the BS capelin stock typically displays decadal fluctuation (Gjøsæter et al., 2009; Carscadden et al., 2013; ICES, 2019). This stock has "collapsed" four times in the past four decades (mid-1980s, 1990s, 2000s, and 2010s; ICES, 2020) but it is only the capelin collapse in the mid-1980s that had major ecosystem consequences. During this time significant reductions in groundfish abundance, and an invasion of southern areas by starving harp seals (*Pagophilus groenlandicus*) were observed (Haug et al., 1991; Gjøsæter et al., 2009). Unlike NL, the BS fish community recovered in a few years after these collapses (Johannesen et al., 2012), and has built-up record levels of groundfish biomass despite the four capelin collapses.

Against this backdrop of broader ecosystem change, the cod stocks in NL and BS have played a central role in defining these changes, showing very divergent trajectories over the last 40 years (Cadigan, 2015; ICES, 2018, 2019, 2020; DFO, 2019, 2020). Both stocks experienced either a significant decline (BS) or a collapse (NL) in the mid-1980s and early 1990s, respectively. After these important population declines, the BS stock quickly rebounded and it is currently experiencing an all times high level (e.g., Bogstad et al., 2015; ICES, 2019). The NL stock, despite showing improvements since the mid-2000s, continues to be at a low level to this day (DFO, 2019, 2020).

While there is little question that fishing played a significant role in the declines of these stock (e.g., Hutchings and Myers, 1994; Myers et al., 1996; Lilly et al., 2013), current understanding also indicates that environmental conditions are important drivers of cod dynamics in both ecosystems, especially the availability of high energy prey like capelin (Rose and O'Driscoll, 2002; Buren et al., 2014b; Mullowney and Rose, 2014; Bogstad et al., 2015). These general similarities, together with the major differences in their trajectories, beg the question about how different or similar these two stocks truly are. Are these different responses more linked to ecosystem conditions, or are there more intrinsic biological/physiological differences between these stocks what have allowed BS cod to rebuild while preventing recovery of NL cod? To explore these questions, we did a comparative analysis of the NL and BS cod dynamics using the same modeling framework for both stocks, and contrasted the results obtained between ecosystems. More specifically, we modeled the biomass dynamics using a bioenergetic-allometric approach (Yodzis and Innes, 1992; Koen-Alonso and Yodzis, 2005; Buren et al., 2014b), and considered the same external drivers for both cod stocks (i.e., fisheries catches and capelin availability). Furthermore, we proceeded to imagine transferring cod stocks between ecosystems by switching estimated parameter between models and comparing the output. Further, we investigated more formally the similarities in vital rates between stocks by implementing an integrated model architecture which allowed estimating common parameters between stocks.

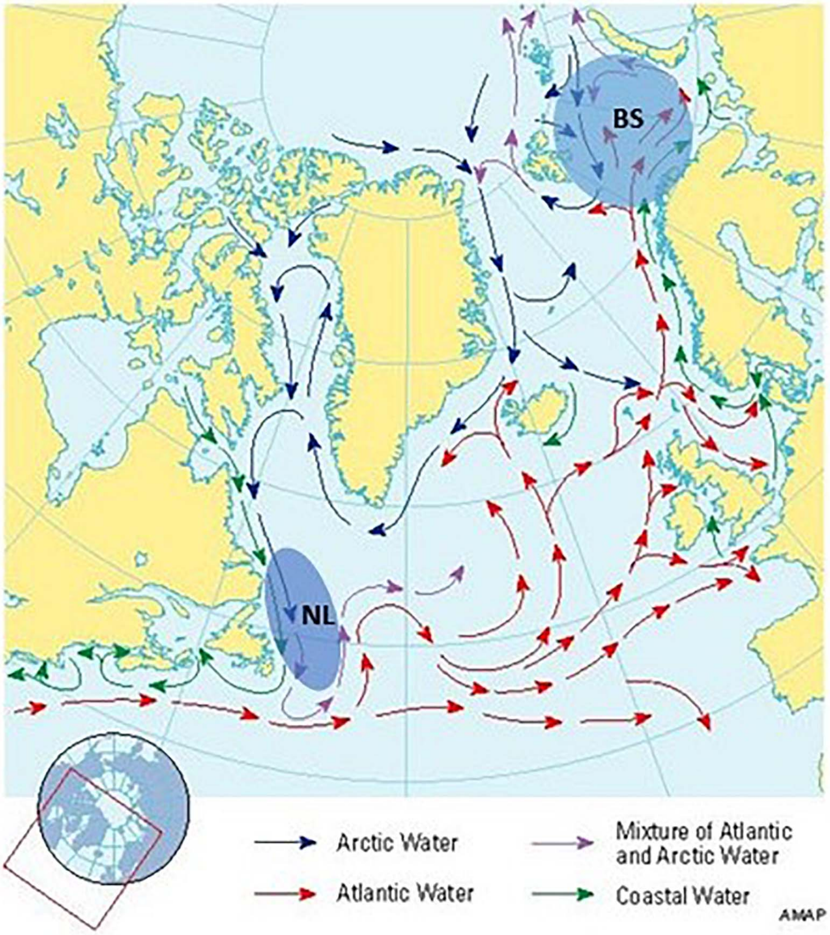

FIGURE 1 | Location of the two ecosystems, Newfoundland-Labrador shelves (NL) and Barents Sea (BS) (marked with ellipses), for which cod stocks are being compared in this study, with indication of major surface currents in the north Atlantic Ocean (AMAP 1998).

MATERIALS AND METHODS

Concept and Modeling Approach

There are many possible ways in which the NL and BS cod stocks could be compared, from traditional morphometric analyses, genetics, and reproductive biology, effectively focusing on fish biological characteristics and traits, all the way to population and ecosystem modeling analyses focused on the dynamics of the stocks, and how they have responded to specific combinations of external drivers and perturbations (e.g., Cole et al., 1991). Our analysis here follows the latter, but also considers some intrinsic biological characteristics, more in line with the former, by using a bioenergetic-allometric rationale to approach model structure and parameterization (Yodzis and Innes, 1992; Yodzis, 1998; Koen-Alonso and Yodzis, 2005; Buren et al., 2014b).

The basic premise of this analysis is to describe the biomass dynamics of each cod stock by fitting the same simple biomass dynamic model to both stocks and comparing the resulting model fits and estimated parameters. The model describes the changes in cod stock biomass as a function of losses through respiration, density-dependent natural mortality, and harvesting (i.e., fishing), and gains from consumption of capelin and other prey. Both capelin biomass and fishery catches are inputs into the model, serving as external drivers of the cod dynamics. Some model parameters are fixed using the bioenergetic-allometric rationale (Yodzis and Innes, 1992; Yodzis, 1998; Koen-Alonso and Yodzis, 2005; Buren et al., 2014b), while others are estimated by fitting the model to data (see below). The basic model equation is:

$$B^{p}_{t+1} = \left(B^{o}_{t} + B^{o}_{t}\left(-T + \mathbf{e}J_{max}\left(\frac{\mathbf{a}\left(C_{t} + \mathbf{c}pr\right)^{2}}{J_{max} + \mathbf{a}\left(C_{t} + \mathbf{c}pr\right)^{2}}\right)\right)\right.$$

$$\left. - \mathbf{m}\left(B^{o}_{t}\right)^{2} - H_{t}\right)\varepsilon_{t} \qquad (1)$$

where B^{p}_{t+1} is the predicted cod biomass in year t+1, and B^{o}_{t}, C_{t}, and H_{t} are the observed biomasses of cod and capelin, and the cod catch in year *t,* respectively. This model implementation assumes a multiplicative process error ε_t following a lognormal distribution (the process error assumption is the reason behind the use of observed cod biomass in year *t*, B_t^o, to predict cod biomass in year *t*+1, B_{t+1}^p). The parameters in this equation are either fixed based on the bioenergetic-allometric framework used or estimated by the model fitting procedure.

The fixed parameters are *T*, the mass-specific respiration rate for the stock, and J_{max}, the maximum mass-specific ingestion rate for the stock. Both rates are derived from allometric equations (Yodzis and Innes, 1992; Koen-Alonso and Yodzis, 2005; Buren et al., 2014b) and assuming an average individual cod body mass of 1 kg in NL and 1.23 kg in BS, derived from data (Buren et al., 2014b; ICES, 2019). The resulting values of *T* and J_{max} were 2.30 and 8.9 for NL, and 2.18 and 8.44 for BS respectively. The estimated parameters are *e*, *a*, *cpr,* and *m*, which denote the fraction of the ingested energy/biomass available at the metabolizable level ("assimilation coefficient"), the functional response coefficient ("*attack rate*"), alternative prey biomass (i.e., the "*capelin prey replacement*"), and the density-dependent mortality coefficient, respectively, as well as the initial cod biomass at the beginning of the time series (B_0), which is an initialization parameter, and the standard deviation of the process error (*S*).

Some key assumptions embedded in the model structure are a type 3 functional response for cod, an always available and constant alternative food source for cod, and a quadratic density-dependent natural mortality. While these are important assumptions, they are in line with what we know about cod, and high trophic level predators more generally (e.g., Smout and Lindstrøm, 2007; Kempf et al., 2008; Buren et al., 2014b). Capelin is a key prey for cod, but is certainly not the only cod prey, and type 3 is therefore a fairly common phenomenological emergent form for functional responses under a diverse range of ecological mechanisms (e.g., prey switching, prey refuges; Koen-Alonso, 2007). Quadratic density-dependent mortality is a standard representation for density-dependent mortality and consistent with similar modeling exercises (Koen-Alonso and Yodzis, 2005; Buren et al., 2014b).

The bioenergetic-allometric modeling approach used here has been previously applied to the study of the main drivers of NL cod (Buren et al., 2014b). While this analysis builds on this prior work, the models are different. In contrast to Buren et al. (2014b), the model used here incorporates alternative prey, and it is implemented as a discrete model formulation (instead of using differential equations) assuming a different error structure (process error in this analysis vs. observation error in the previous study).

Model Fitting

The model was implemented assuming a multiplicative lognormal process error as mentioned above (i.e., additive Gaussian residuals in log scale), and was fitted to data using a maximum likelihood approach. The model was coded using R (R Core Team, 2017) and TMB (Kristensen et al., 2016), and the minimization of the negative loglikelihood was done using the nlminb function within R.

Considering a process error only formulation effectively creates a more restricted parameter space during the fitting procedure, which markedly improves convergence. The associated cost of this modeling choice is the assumption that there is no observation error in cod biomass, which is not correct. While an in-depth examination of model error structure and assumptions is beyond this study, a quick examination of the operational implications of different error structures can help understand the choice made here. Assuming process error only implies that cod biomass is measured without error, and that the differences between predicted and observed cod biomasses for a given year fully reflect real changes driven by factors not included in the model. On the other hand, assuming observation error only implies that the differences between predicted and observed cod biomasses are purely driven by problems in our way of measuring cod biomass, while effectively assuming that the model captures all relevant factors that drive the underlying cod dynamics. A state-space approach is the most realistic one, assuming that both types of errors occur, but splitting the variance between the two types of error requires highly informative and contrasting data. Without sufficiently contrasting data achieving convergence and/or reliable parameter estimates within a state-space framework can be problematic (e.g., Auger-Méthé et al., 2016), and preliminary explorations using a state-space approach to this analysis showed convergence problems (i.e., our data is not informative enough to reliably split the process and observation variances within this model architecture without imposing additional constrains on the magnitude of the variances).

The prior study on NL cod using this modeling approach but considering observation error only estimated that the catchability coefficient for total biomass was no different than 1 (Buren et al., 2014b), indicating that scientific surveys typically sample very well medium to large size fish, which are the ones that mostly define the total biomass index used as response variable in the analysis. This indicates that the scaling associated with the observation process (i.e., catchability) does not appear to be a substantial issue for the total biomass estimates used here, and suggests that assuming total biomass survey estimates as reasonable proxies for total stock biomass does not present major shortcomings for this analysis. Also, given the simple structure of the model, it is reasonable to expect that some other factors not included in the model (e.g., temperature, ocean climate) can also influence cod dynamics. Therefore, using a process error only structure would allow considering these other effects on cod, at least in terms of capturing their influence on the variability of total cod biomass. Given all these considerations, assuming process error only emerges as a sensible and practical choice for this analysis. The adequacy of the model fits was evaluated using standard procedures like the coefficient of determination (r^2), and the examination of the standardized residuals. In addition, the consistency of the model predictions was examined through a retrospective pattern analysis (Mohn, 1999; Hurtado-Ferro et al., 2015), comparing the model fit obtained for the full times series, with those obtained by fitting the model to subsets of the full dataset obtained by sequentially removing the data for the terminal year, 1 year at a time. The subsets considered for this analysis removed ("peeled off") the last 1–5 years of data. Mohn's *rho* statistic for predicted cod biomass, calculated as Hurtado-Ferro et al. (2015), was the metric used for this analysis, and the rules of thumb for this statistic developed by Hurtado-Ferro et al. (2015) were used to gauge the consistency/stability of model predictions. These rules of thumb, developed from age-structure model simulations, indicate that, for long live species like cod, Mohn's *rho* values outside the −0.15 to 0.2 range are likely indicative of retrospective patterns in the model (i.e., instability/inconsistency in model prediction in the terminal year).

Comparisons Between Ecosystems

The evaluation of similarities and differences between NL and BS cod was done in an iterative way. The first step involved fitting independent models to each cod stock and evaluating the ability of the model to describe the cod dynamics, while comparing the estimated parameter values. If the common model structure can reasonably describe both NL and BS cod stock trajectories, the basic idea that both stocks are effectively driven by availability of key prey (i.e., capelin) and fishing would be supported. A simple comparison of the estimated parameters also provides an initial insight on how similar or different the biology of these stocks may be; some estimated parameters like the assimilation coefficient (e), and the attack rate (a) would be expected to be more reflective of the cod biology and behavior (i.e., more intrinsic to the stock), while others like the capelin prey replacement (cpr) (i.e., availability of alternative prey) and the density-dependent mortality coefficient (m) would be expected to be more influenced by ecological factors associated to the ecosystem where the stocks are embedded.

Considering this nominal distinction between parameters intrinsic to the stock, and parameters more associated to ecosystem conditions, the second step was simply to run these models with some parameters exchanged between them. For example, running the NL model using the T, J_{max}, e, and a estimated for BS cod would be a modeling proxy for transplanting BS cod into the NL ecosystem and seeing how that stock would have fared under NL conditions (more accurately, it reflects transplanting the biology and behavioral characteristics of BS cod). Similarly, running the BS model using these parameters as estimated from the NL case would approximate how NL cod would have responded to BS ecosystem conditions.

Finally, a more formal comparison was implemented by integrating the equations for each stock into a single model architecture and fitting both models together and simultaneously, and where the function being minimized in the model fitting procedure was the sum of the negative loglikelihood from each of the originally independent models. When this integrated model is fitted to data assuming fully independent stocks (i.e., no common parameter values between stocks), the results are, as it should be, identical to those obtained from the independent model fits. However, this integrated architecture permits estimating common parameters for both stocks, which allows testing hypothesis of similar parameter values between stocks by using likelihood ratio tests. More specifically, two hypotheses were compared this way; the first one was that e, a, and m were common to both stocks, which implies that basic biological intrinsic parameters and the background density-dependent natural mortality were similar between ecosystems, and the second one where only e, and a were assumed common between stocks, implying that the basic biological and behavioral characteristics of the two stocks were similar after accounting for differences in fish body size.

Data

The data used to fit these models were total cod biomass, capelin biomass, and cod fisheries catches (**Figure 2**). Data series are displayed in log scale to facilitate visualization of the dynamics at both high and low biomass levels. In the NL ecosystem cod biomass was estimated as the total standard biomass index for random stratified survey designs calculated from Fisheries and Oceans Canada (DFO) fall bottom trawl surveys in the Northwest Atlantic Fisheries Organization (NAFO) divisions 2J3KL for the period 1981–2017, and where the data for the 1981–1994 period were adjusted to correct for a change in gear in the research survey (e.g., Buren et al., 2014b). Capelin availability was obtained from the DFO spring capelin acoustic survey in NAFO Div. 3L (Buren et al., 2014b, 2019), and where the gaps (1983–1984, 1993–1995, 1997–1998, 2006, and 2016) in this time series were filled by simple linear interpolation (see Buren et al., 2014b), or assumed similar to a nearby year (1981 assumed similar to 1982). Cod catches were obtained from DFO and NAFO catch statistics.

In the BS ecosystem cod biomass was estimated using data from the Norwegian acoustic survey of North East Arctic cod on the spawning grounds off Lofoten (Korsbrekke, 1997) and the joint Norwegian-Russian winter bottom trawl survey (e.g., Fall et al., 2020), which has been conducted annually since 1982 and 1981, respectively. Because the Lofoten survey cover the mature stock and the winter bottom trawl survey in the Barents Sea cover the immature stock, the biomass estimates (swept area and acoustic) derived from these surveys were added in order to get an estimate of the entire cod stock. The capelin biomass time series was obtained from the stock assessment report (ICES, 2019).

The timing/season of the different surveys and fisheries were considered when defining the proper time index for the different inputs and outputs in the modeling exercise. For example, the NL cod survey takes place at the end of the calendar year, so it more closely reflects the cod biomass state at the beginning of the following year (i.e., the fishing within that calendar year and the impact of capelin in that calendar year have already impacted the cod stock at the time of the survey), while this is not the case in BS. These technical aspects were considered when setting up the models for each ecosystem.

RESULTS

Model Fit

The results indicate good model fits for the NL and BS cod stocks (**Figure 3**). Both models explain more than 80% of the variance in their respective datasets ($r^2_{NL} = 0.92$ and

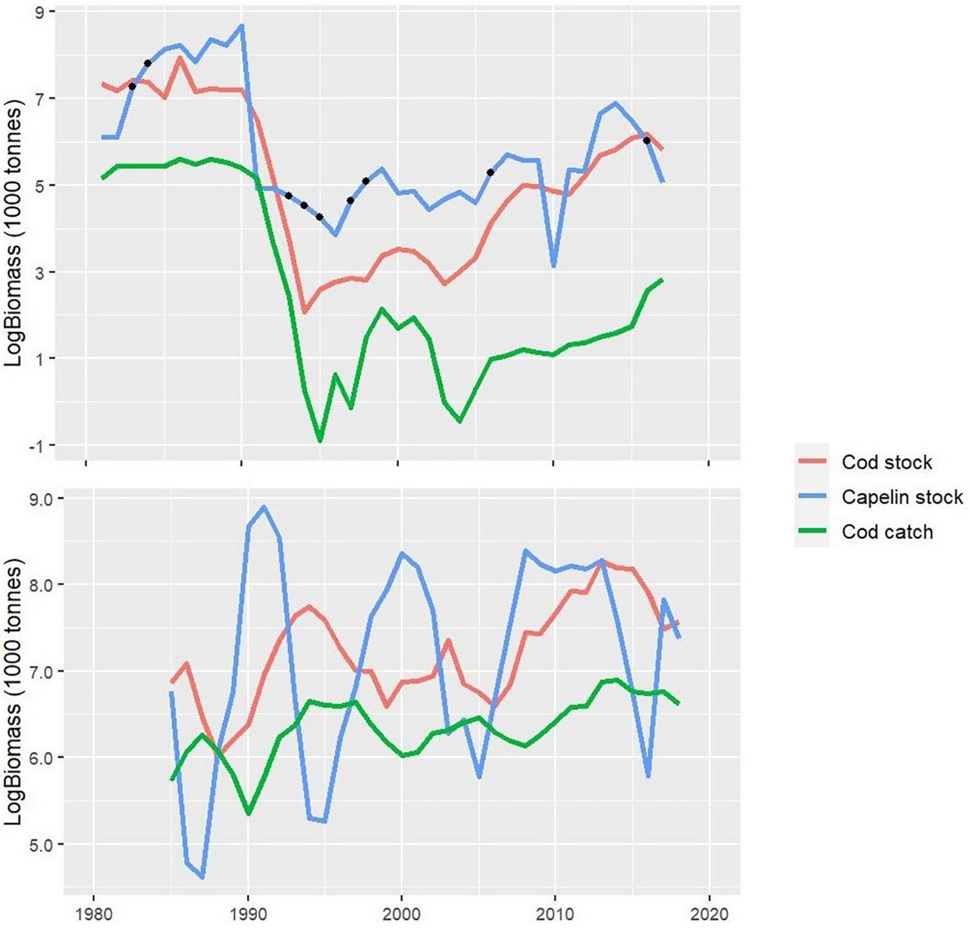

FIGURE 2 | Input time series data (log scale) for cod, capelin, and cod catches used for the Newfoundland-Labrador shelves (NL) (top panel) and Barents Sea (BS) (bottom panel) cod models. The black dots in the capelin time series in NL represent the interpolated years (see text for details).

$r^2_{BS} = 0.81$), and show reasonable distributions of the residuals (**Figure 4**). Most residuals are contained within the one standard deviation envelope; the only ones departing beyond that are the negative residuals for NL cod in 1992–1994, which correspond to the aftermath of the stock collapse; even these residuals are contained within two standard deviations. Both models show high stability/consistency in their predictions (**Supplementary Appendix**), with Mohn's *rho* values (NL: 0.025, BS: −0.014) well within the range associated with no retrospective pattern problems (−0.15 to 0.2), indicating that there is stability/consistency in the terminal year predictions.

While the underlying structure is simple and uses basic representations of core biological/ecological rates (i.e., respiration, food consumption, mortality), the model is still capable of adequately describing two very contrasting stock trajectories, indicating that the key processes and drivers that define cod dynamics are reasonably captured by the model structure and consistent between the NL and BS ecosystems. Several of the parameters related to intrinsic factors of the stocks (i.e., species biology and behavior), like the assimilation coefficient, and attack rate, have very similar estimated values in both models, while those parameters more related to extrinsic factors (mortality coefficient, process error) show more clear differences between models (**Table 1**). This indicates that both stocks respond to the drivers considered (capelin availability and fishing) in very similar ways, and the differences in cod trajectory between NL and BS are more associated to external factors (i.e., ecosystem conditions, fishing) than intrinsic biological differences between the stocks.

Comparisons Between Ecosystems

The similarity in the estimated values for parameters more associated with intrinsic factors (i.e., cod biology and behavior), prompts the question of how these stocks may have responded if exposed to each other's ecological contexts. We explored this thought experiment by switching some parameters between models and observing how different the predicted trajectories were. More specifically, switching the parameter values for T, J_{max}, e, and a between models allows characterizing the response to drivers in one ecosystem with the key biological/behavioral traits of the cod stock from the other ecosystem, while

FIGURE 3 | Model fits (log scale) for the Newfoundland-Labrador shelves (NL) (blue line) and Barents Sea (BS) (red line) cod stocks and 95% confidence intervals (shaded areas). These fits correspond to fully independent stocks (i.e., no common parameters between stocks).

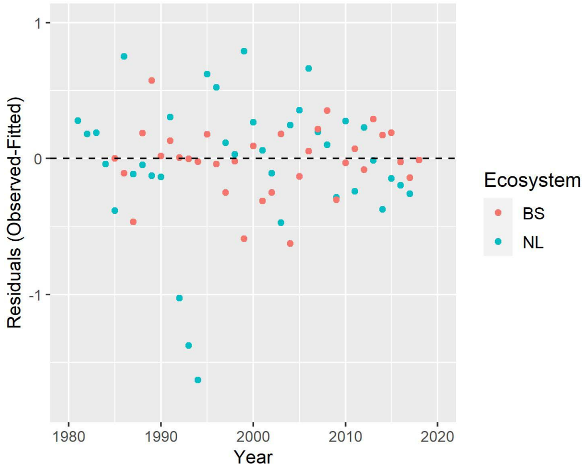

FIGURE 4 | Standardized residuals for the Newfoundland-Labrador shelves (NL) (blue dots) and Barents Sea (BS) (red dots) cod models assuming fully independent stocks (i.e., no common parameters between stocks).

keeping the original estimates for the remaining parameters (and data) represents the ecosystem context in which the "switched stock behavior" is being embedded. This exploration approximates the thought experiment of putting NL cod in the BS ecosystem, and vice versa.

The results of this exploration indicate that the BS cod would have been expected to collapse if exposed to the conditions in the NL ecosystem, while the NL cod would have been expected to rebuild in the more favorable conditions of the BS ecosystem (**Figure 5**). Still, this simple exploration also suggests that the larger sized cod from BS would have sustained a larger biomass in the pre-collapse period and recovered better than NL cod did in the NL ecosystem, while NL cod showed more severe declines and weaker increases in the BS ecosystem than BS cod did in its own system (**Figure 5**). As thought provoking and informative as this exploration can be, it remains illustrative. A more statistically sound approach is needed to further investigate these observations.

A formal evaluation of the similarities and differences in parameter values between stocks was done using likelihood ratio tests based on an integrated implementation of the NL and BS cod models. This architecture allows estimating parameters simultaneously for both stocks and implementing restrictions in model parameters (i.e., estimating common/shared parameter values for both stocks). Within this approach, the estimation of parameters assuming fully independent stocks correspond to a general model, while estimations assuming common parameter values between stocks correspond to a restricted version of the general model, and hence, the adequacy of likelihood ratio tests for this analysis.

Two hypotheses were evaluated using likelihood ratio tests. The first one considered that intrinsic parameters (*e* and *a*) and

TABLE 1 | Estimated parameters and goodness of fit for the general integrated model, assuming fully independent NL and BS cod stocks (no common parameters between stocks), and the restricted model assuming similar intrinsic biological traits between stocks (common *a* and *e* parameters).

	Model scenario			
	Independent NL and BS cod stocks (no common parameters)		**Similar intrinsic biological characteristics between stocks (common *a* and *e* parameters)**	
Parameter (units)	**Newfoundland-Labrador Shelves**	**Barents Sea**	**Newfoundland-Labrador Shelves**	**Barents Sea**
Initial biomass: B_0 (kt)	1669.0 (1096.8)	953.0 (238.0)	1575.9 (1064.6)	953.0 (238.9)
Assimilation coefficient: *e* (dimensionless)	0.365 (0.031)	0.386 (0.014)	0.385 (0.012)	
Attack rate: *a* (kt^{-2})	0.00011 (0.00011)	0.00019 (0.00025)	0.00011 (0.00008)	
Density-dependent natural mortality coefficient: *m* (kt^{-1})	0.00048 (0.00012)	0.00027 (0.00004)	0.00054 (0.00008)	0.00026 (0.00004)
Capelin prey replacement: *cpr* (kt)	353.25 (205.93)	358.91 (307.35)	323.34 (142.82)	515.88 (235.37)
Standard deviation of process error: *S* (dimensionless)	0.505 (0.059)	0.250 (0.030)	0.508 (0.059)	0.250 (0.030)
Model fit (r^2)	0.92	0.81	0.92	0.81
Joint negative loglikelihood	28.31		28.70	

The standard deviation of the estimates is given in parentheses.

FIGURE 5 | Exploration of the thought experiment of transferring NL cod (blue line) into the Barents Sea (BS) ecosystem and BS cod (red line) into the Newfoundland-Labrador shelves (NL) ecosystem by switching intrinsic parameters (*T, Jmax, e*, and *a*) of the corresponding models between areas (see text for details).

a key extrinsic parameter (*m*) were common to both stocks; the second one corresponded to only the intrinsic parameters being similar between stocks. The results show that the first hypothesis (common *e, a* and *m*) can be rejected, but not the second one (common *e, and a*) (**Table 2**). The "common e and a" model explained as much as the independent stocks model ($r^2_{NL} = 0.92$ and $r^2_{BS} = 0.81$), and did not show any indication of potential retrospective pattern problems (Mohn's *rho* values of 0.013 for NL and −0.013 for BS, see **Supplementary Figure A1**). This indicates that there is no support in the data for assuming differences in the intrinsic parameters *e* and *a* between stocks, suggesting a common scaling of the corresponding vital rates with body size, and no significant improvement in model fit from assuming fully independent stocks (**Figures 3**, **6**). These results imply that the basic biology and behavior of NL and BS cod stocks, at least as summarized by these model parameters, is similar, while the differences in stock trajectory are driven by the ecosystem context in which these stocks are embedded.

DISCUSSION

Understanding how ecosystems respond to change, and the underlying mechanisms behind these responses, are not just

TABLE 2 | Test of hypothesis for common parameters between the NL and BS cod models using likelihood ratio tests.

	Negative loglikelihood				
Hypothesis	**General model**	**Restricted model**	**Degrees of freedom**	**χ^2**	***p*-value**
I. Both intrinsic biological traits and key extrinsic factors are similar between stocks (common parameters: *a*, *e*, *m*)	28.31	32.86	3	9.098	0.028
II. Only intrinsic biological traits are similar between stocks (common parameters: *a*, *e*)	28.31	28.70	2	0.774	0.679

The general model assumes that the two cod models have no common parameters.

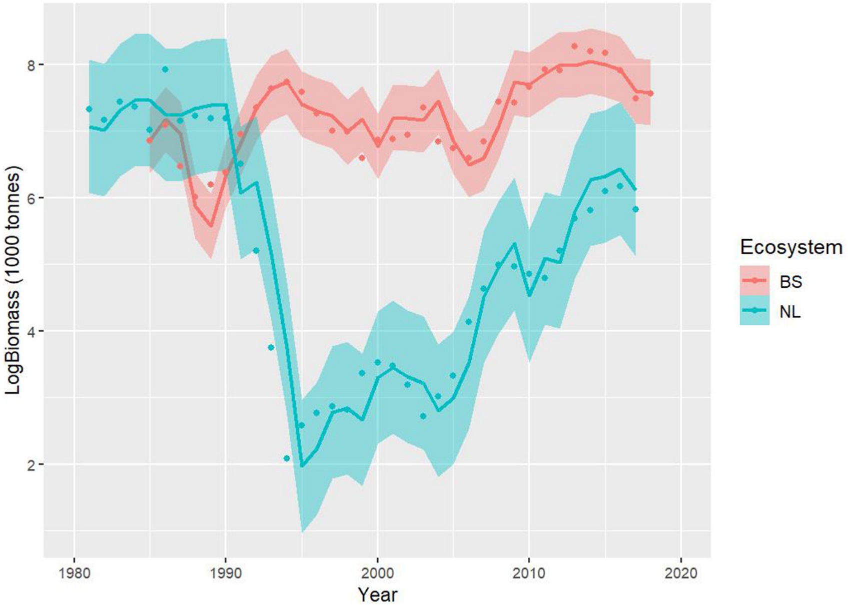

FIGURE 6 | Model fits (log scale) for the Newfoundland-Labrador shelves (NL) (blue line) and Barents Sea (BS) (red line) cod stocks and 95% confidence intervals (shaded areas). These fits correspond to the model assuming *a* and *e* as common parameters to both stocks.

fundamental questions in ecology, but also key practical questions in our pursuit for more sustainable ways of managing renewable natural resources (e.g., Fogarty, 2014; Link, 2017; Koen-Alonso et al., 2019). Within fisheries, ecosystem approaches are slowly but surely complementing and broadening the scope of traditional single species management frameworks (Fogarty, 2014; Link, 2017; Koen-Alonso et al., 2019). At the core of these transitions is the recognition that, beyond the direct effects of fishing, changes in ecosystem conditions play a major role in defining stock responses and trajectories (e.g., Cushing, 1982; Glantz, 1992; Koen-Alonso et al., 2010; Fossheim et al., 2015; Dempsey et al., 2017; Pedersen et al., 2017; Koen-Alonso and Cuff, 2018).

Given the complexity of natural ecosystems, elucidating what are the main drivers of ecosystem change, and understanding the mechanisms behind these changes, are often approached using comparative analyses (e.g., Cole et al., 1991; Megrey et al., 2009; Murawski et al., 2010; Bundy et al., 2012; Gaichas et al., 2012; Holsman et al., 2012). These studies typically involve using similar methods in different ecosystems, different analytical and/or modeling approaches applied to a single ecosystem, or some combination of the two (Murawski et al., 2010; Mantzouni et al., 2010). The basic premise behind these comparative approaches is simple; those conclusions that remain valid across ecosystems and/or methodological approaches are more likely to be robust and reliable. It separates the ecological chaff from the wheat.

While studies of NL and BS cod dynamics typically take demographic approaches (i.e., age structured population models) (e.g., Shelton and Lilly, 2000; Cadigan, 2015; Rose and Walters, 2019; ICES, 2019, 2020), our study relies upon a bioenergetic-allometric framework (Yodzis and Innes, 1992). This theoretical approach is one of the pillars of the metabolic theory of ecology, which has proven useful in describing general ecological patterns, ecosystem organization, and dynamics (e.g., Gillooly et al., 2001; Brown et al., 2004; Brose et al., 2008; Brose, 2010; Schramski et al., 2015). A fundamental feature of this approach is the basic concept that metabolic rates scale allometrically with individual body mass (Peters, 1983; Yodzis and Innes, 1992; Gillooly et al., 2001), which helps simplifying model parameterization, but more fundamentally focuses on physiological constraints expected to be shared across species and/or levels of biological and ecological organization (Yodzis and Innes, 1992; Brown et al., 2004; Vasseur and McCann, 2005; Brose, 2010; Schramski et al., 2015).

Our results provide further support of the utility of this general theoretical approach to ecological functioning and organization. The commonality found in key model parameters associated with intrinsic traits of the stocks indicates that NL and BS cod are more similar than different in their basic functional biology once accounting for variation in body size (i.e., reflecting the differences in size structure between stocks), while their differences appear more associated to factors related to the specific ecosystem conditions experienced by each stock. Furthermore, these models explain a large fraction of the variance in cod biomass (**Table 1**), suggesting that the basic relationships and external factors considered here are sufficient to characterize the key processes that regulate the dynamics of these stocks.

Capelin availability and fishing are common and important drivers of cod dynamics in NL and BS (e.g., Rose and O'Driscoll, 2002; Lilly et al., 2013; Buren et al., 2014b; Kjesbu et al., 2014; Mullowney and Rose, 2014). While excessive fishing has been an historical problem for both stocks (Lilly et al., 2013; Cadigan, 2015), important declines in BS cod and the collapse of the NL stock have occurred at times of capelin collapses, while stock build-ups often follow from improvements in capelin (**Figure 2**).

After its collapse in the early 1990s, the NL cod stock showed consistent signals of rebuilding only after modest increases in capelin started to be observed in the mid-2000s (Buren et al., 2019). In the intervening years, the forage species pool in the NL ecosystem was dominated by northern shrimp, which constituted the main prey in cod diets (Dawe et al., 2012; Mullowney and Rose, 2014). In terms of nutritional quality, northern shrimp has lower energy density than capelin, and thus, a shrimp dominated diet is expected to impose additional energetic constraints to the scope for growth of the NL cod stock (Lawson et al., 1998; Rose and O'Driscoll, 2002; Sherwood et al., 2007; Dawe et al., 2012; Buren et al., 2014b; Mullowney and Rose, 2014). Another way of looking at this question is by considering the ratio of capelin availability to total food availability derived from the model results for each ecosystem, $cr_t = C_t/\left(C_t + cpr\right)$, as a coarse approximation to the proportion or energy coming from capelin vs. other sources in year *t*. While the distribution of these capelin ratios indicate that both stocks show an important reliance on capelin as prey, they also indicate that NL cod, which is the stock that has yet to rebuild, has derived a lower fraction of energy from capelin than BS cod has over the time periods considered in this study (**Figure 7**). These differences in capelin ratios are also generally consistent with the proportions of capelin observed in the diet compositions of cod in these ecosystems (e.g., Dawe et al., 2012; ICES, 2018).

While BS cod showed an important decline in the 1980s which was associated to both fishing and a capelin collapse (1985–1989), the next three capelin collapses observed in this ecosystem (1993–1997, 2003–2007, and 2014–2016) did not trigger comparable cod declines (Gjøsæter et al., 2009; ICES, 2020). The likely reason behind this difference, in addition to lower fishing mortalities, especially during the last two capelin collapses (the level of cod fishing mortality in the mid-late 1990s was comparable to the one in the 1970s and early 1980s) (Lilly et al., 2013), is that during the most recent capelin collapses, suitable prey replacements for capelin were available in BS; herring, polar cod (*Boreogadus saida*), and juvenile fishes (0-group) remained abundant in these periods, while if we consider herring and polar cod as indicators, this alternative prey pool was also low during the 1980s capelin collapse (Eriksen et al., 2011, 2017; Jelmert et al., 2020).

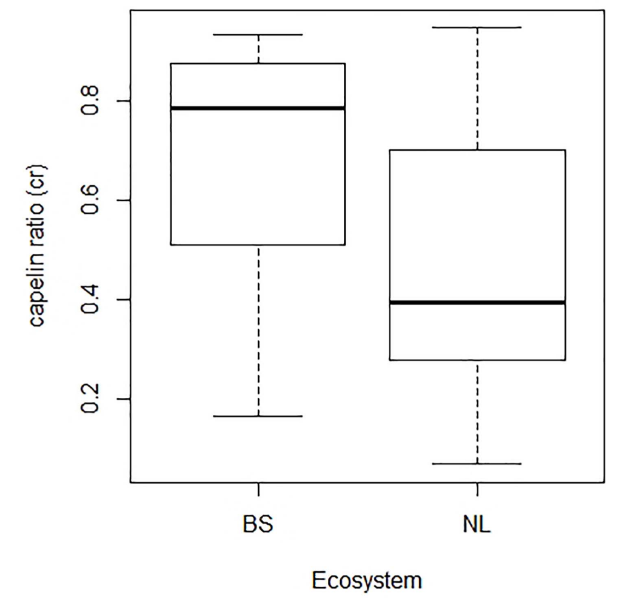

FIGURE 7 | Box plots of the annual capelin ratios (i.e., the fraction of capelin in relation to total food availability for cod derived from model results) in the Barents Sea (BS) and Newfoundland-Labrador shelves (NL) ecosystems. These ratios correspond to the model assuming *a* and *e* as common parameters to both stocks, and can be interpreted a coarse approximation to the proportion of energy that cod derives from capelin in each ecosystem.

These differences in availability of alternative prey to capelin appear reflected in two ways in the model results. The BS model has a slightly higher *cpr* estimate than the NL model (**Table 1**), suggesting a somewhat higher average biomass of alternative prey in the BS ecosystem than in the NL ecosystem. However, this difference is rather marginal and it also dependents on how comparable the capelin estimates truly are between NL and BS. The capelin estimates used here are both derived from acoustic surveys (Buren et al., 2019; ICES, 2019), and reliably reflect the relative changes in capelin level, but they are not intended to be precise estimates of absolute biomass. In our work here, these estimates are assumed to be good indicators of the order of magnitude of the capelin biomass level, and in this sense, comparable enough between ecosystems for the use given within these models. The fact that estimates of *cpr* are similar for both ecosystems, but nominally larger for BS, is consistent with this assumption about the capelin indices, and with the expectations of a better alternative prey availability in BS in comparison to NL (e.g., Eriksen et al., 2011, 2017; Buren et al., 2019; Jelmert et al., 2020).

The other result that can also be interpreted as evidence of better foraging conditions in BS is the lower density-dependent natural mortality coefficient estimated for BS cod (**Tables 1**, **2**). If low prey availability is an issue, poor cod condition would be on average more prevalent, and expected to increase the odds of dying by natural causes, chiefly starvation, but also through increased susceptibility to diseases, and predation. This could also affect reproductive performance (e.g., reduced egg quality, quantity, and/or survival). All these factors, in the context of the simple model structure used here, are expected to be reflected in a larger m, and this is what was found for NL cod (**Tables 1**, **2**).

This result is also consistent with available observations. During the collapse, the NL cod showed clear signals of reduced condition, especially in the northern areas (NAFO divisions 2J3K) (Buren et al., 2014b; Morgan et al., 2018), providing compelling evidence that food availability was a likely factor in the stock collapse. Condition signals improved by 2006–2012, a period when the stock was starting to show signals of rebuilding and capelin was showing modest improvement, and while the role of condition (and related mechanisms) in limiting stock growth at present remains a matter of debate (Morgan et al., 2018), there is little question that the stock has experience low productivity since the collapse (Shelton et al., 2006; Sherwood et al., 2007; Fudge and Rose, 2008). On the other hand, despite its considerable stock size, the BS cod has not displayed any sign of starvation in the past decades, in contrast to some of its competitors (e.g., Durant et al., 2014; Bogstad et al., 2015), however, this appears to be changing because the growth of juvenile cod has dropped much in 2020 (Bogstad pers. comm.) suggesting reduced feeding conditions.

The above interpretation of m is consistent with the expectations from differences in the prey field between these ecosystems (i.e., natural mortality mainly driven by bottom-up processes), but the role of predation by marine mammals is a frequent argument put forward to explain high natural mortality and/or lack of recovery in cod stocks (e.g., Hansen and Harding, 2006; Trzcinski et al., 2006; Swain and Benoît, 2015; Swain et al., 2015). On this issue, the evidence on the role of marine mammal predation in controlling cod stocks does not paint a uniform picture. Studies on the likely causes for the lack of recovery of the cod stock in the southern Gulf of St Lawrence, Canada, have found that predation by gray seals (*Halichoerus grypus*) is the most likely driver (Chouinard et al., 2005; Benoît et al., 2011; Swain and Benoît, 2015), and predation by harp seals can become a factor for cod recovery in the northern Gulf of St. Lawrence under certain environmental conditions (Chassot et al., 2009; Bousquet et al., 2014). On the other hand, an examination of this issue in BS focused on harp seal and minke whale (*Balaenoptera acutorostrata*) predation concluded that marine mammals were more likely to influence BS cod through competition for food than predation (e.g., Øigård et al., 2013; Bogstad et al., 2015). In the case of NL cod, a direct examination of harp seal predation, capelin availability, and fishing as drivers concluded that in contrast to capelin availability and fishing, seal predation was not a significant driver of the dynamics of NL cod (Buren et al., 2014b). The importance of marine mammal predation in controlling cod dynamics appears to be ecosystem-specific, and likely dependent on the history of the ecosystem and prevailing environmental conditions. In the case of NL and BS cod stocks, predation by marine mammals does not appear to be a major driver, with our results further supporting that prey availability in general, and capelin availability in particular, together with fishing, are the dominant factors in controlling their dynamics.

These results are also relevant in a practical sense. After the collapse of the NL cod stock, a commercial fishing moratorium was established in 1992, which has remained in place since. In practice this has implied that the NL cod fishery has been essentially restricted to a stewardship fishery and a recreational fishery for the past three decades (Lilly et al., 2013; Cadigan, 2015; DFO, 2019, 2020). Notwithstanding this moratorium the NL stock has not recovered, but it has been showing signals of rebuilding since 2006 (Buren et al., 2014b; Cadigan, 2015; DFO, 2019, 2020), and the start of this recovery coincided with a modest improvement in the availability of capelin (Buren et al., 2014a, 2019). In recent years the role of capelin and food availability is becoming a frequent topic of discussion in NL cod stock-assessments (e.g., DFO, 2020), and the current assessment-model for NL cod allows for time-varying natural mortality (Cadigan, 2015), but the model projections used for advice provision are not capelin-informed (DFO, 2019), and the management framework for the stock does not explicitly account for capelin level (or any other explicit ecosystem consideration) as a control lever. Fisheries and Oceans Canada (DFO), the federal department in Canada responsible for fisheries management, is formally committed to the adoption of ecosystem approaches, but implementation on the ground remains patchy and limited. Even though many scientific assessments do include and discuss ecosystem effects (e.g., DFO, 2020), most stock-level decision-making management frameworks to date remain traditional single-species approaches. While work toward implementation of ecosystem approaches in DFO is ongoing, our findings here emphasize the importance for this transition to gain momentum by making evident that management and rebuilding plans for NL cod would benefit from formally incorporating capelin as an explicit factor in these plans.

In contrast, the size of the capelin stock has been part of the decision-making process for the management of the BS cod fishery since 1989–1990, after the Total Allowable Catch (TAC) for BS cod was significantly reduced in response to the collapse of capelin and low availability of other forage species (Lilly et al., 2013). Since then, reference points for BS cod have been set conservatively to accommodate for ecosystem conditions. Both environmental and biological factors have for many years been included in predictions of cod recruitment (ICES, 2020). Cod cannibalism and its inverse relationship with capelin abundance is one important factor affecting cod recruitment (e.g., Yaragina et al., 2009, 2018). More generally, considerations of trophic interactions and their impacts on important stocks like cod, haddock, and capelin, and their incorporation into stock-assessment and/or strategic models, have been in operation in fisheries decision-making frameworks in the BS since the 1990s (Howell and Bogstad, 2010; Bogstad and Filin, 2011).

CONCLUSION

The NL and BS cod stocks have shown very contrasting trajectories over the past 40 years; the NL cod stock collapsed in the 1990s and has not recovered despite a long lasting commercial fishing moratorium, while the BS cod stock has rapidly recovered after an important decline in the late 1980s and 1990's, and has increased to record high levels in the 2010s. These differences have been attributed to the impacts of fishing, and to changes in stock productivity linked to ecosystem and environmental conditions.

This analysis supports this general perspective. It shows that simple bioenergic-allometric models, accounting for capelin availability and fisheries catches as drivers, can adequately describe the biomass dynamics of both stocks. Furthermore, this study shows that basic biological and behavioral traits appear similar between the stocks, implying that NL cod would be expected to recover under favorable ecosystem conditions, namely sufficiently large availability of capelin, while BS cod would be expected to decline if low availability of capelin and low alternative prey occur simultaneously, as was the case in the 1980s and, to some extent in the 1990s.

These clear dependencies between predator and prey further emphasize the need to address ecosystem interactions in the context of fisheries management. While specific details are expected to be case-dependent (i.e., type of interaction, data availability), decision-making management frameworks need to formally and explicitly incorporate ecosystem interactions more broadly. Paradoxically, the widespread overfishing of the past meant that controlling fishing was often enough to reverse declining stock trajectories; we had made fishing the dominant driver of many exploited fish stocks. As we reduce fishing pressure and learn to fish more sustainably, the importance of ecosystem factors as regulators of stock productivity and its variability over time becomes more prominent. Sustainable fisheries are no longer just about which level of fishing pressure is acceptable, but also how that level may need to change when ecosystem conditions and interactions change. This also implies that fishing on multiple interacting stocks requires explicit management of the emergent trade-offs between the corresponding fisheries. To no one's surprise, these are basic tenets of ecosystem approaches (e.g., Fogarty, 2014; Link, 2017; Koen-Alonso et al., 2019), and their implementation is never simple nor easy (Koen-Alonso et al., 2019). However, in a world rapidly changing due to climate change, it is not only important to implement ecosystem-based management, it is rather urgent too.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this was a modeling study using historical fish data and as such we did not need ethical review and approval.

AUTHOR CONTRIBUTIONS

MKA and UL contributed equally to the ideas in this manuscript, implemented the models for NL and BS, and drafted the manuscript. MKA developed the initial model concept and structure. AC and MKA integrated the NL and BS models into a single architecture. MKA, UL, and AC contributed to the data. AC provided edits to the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

The Norway-Canada collaborative project "A Transatlantic innovation arena for sustainable development in the Arctic" (CoArc) provided partial support for this work (project number 8048 at Akvaplan-niva and QZA-15/0457 at Norwegian Ministry of Foreign Affairs). Additional support was provided by Fisheries and Oceans Canada (DFO), and the Norwegian Institute of Marine Research (IMR) through operating and project funds to MKA and UL, respectively.

ACKNOWLEDGMENTS

This study builds upon the work of many people, and benefited from the many discussions we have had on cod, capelin, seals, and fisheries over the years in different fora, particularly a series of workshops on cod-seal interactions organized by DFO in 2007–2008, the annual meetings of the Northwest Atlantic Fisheries Organization (NAFO) Scientific Council (SC) Working Group on Ecosystem Science and Assessment (WGESA) since 2008, and most recently the CoArc project workshops in 2016–2019. We are especially grateful to G. Stenson, T. Haug, A. Buren, F. Mowbray, G. Evans, P. Regular, E. Pedersen, P. Pepin, M. Fogarty, A. Bundy, and P. Renaud for their insights, contributions, and willingness to serve as sounding board as the ideas contained this paper took shape. We also thank to the reviewers of this manuscript for their input and suggestions.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.579946/full#supplementary-material

REFERENCES

Auger-Méthé, M., Field, C., Albertsen, C. M., Derocher, A. E., Lewis, M. A., Jonsen, I. D., et al. (2016). State-space models' dirty little secrets: even simple linear Gaussian models can have estimation problems. *Sci. Rep.* 6:26677. doi: 10.1038/srep26677

Benoît, H. P., Swain, D. P., Bowen, W. D., Breed, G. A., Hammill, M. O., and Harvey, V. (2011). Evaluating the potential for grey seal predation to explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence. *Mar. Ecol. Prog. Ser*. 442, 149–167. doi: 10.3354/meps09454

Bernier, R. Y., Jamieson, R. E., and Moore, A.M. (eds.) (2018). *State of the Atlantic Ocean Synthesis Report*. Canadian Technical Report of Fisheries and Aquatic Sciences 3167. Moncton, NB: Fisheries and Oceans Canada, iii, 149.

Bogstad, B., and Filin, A. A. (2011). "Chapter 12.1: multispecies and ecosystem modelling as tools for fishery management," in *The Barents Sea. Ecosystem, resources, management. Half a century of Russian-Norwegian cooperation*, eds T. Jakobsen and V. K. Ozhigin (Trondheim: Tapir Academic Press), 647–664.

Bogstad, B., Gjøsæter, H., Haug, T., and Lindstrøm, U. (2015). A review of the battle for food in the Barents Sea: cod vs. marine mammals. *Front. Ecol. Evol*. 3:29. doi: 10.3389/fevo.2015.00029

Bousquet, N., Chassot, E., Duplisea, D. E., and Hammill, M. O. (2014). Forecasting the major influences of predation and environment on cod recovery in the northern Gulf of St. Lawrence. *PLoS One* 9:e82836. doi: 10.1371/journal.pone.0082836

Brose, U. (2010). Body-mass constraints on foraging behavior determine population and food-web dynamics. *Funct. Ecol*. 24, 28–34. doi: 10.1111/j.1365-2435.2009.01618.x

Brose, U., Ehnes, R. B., Rall, B. C., Vucic-Pestic, O., Berlow, E. L., and Scheu, S. (2008). Foraging theory predicts predator-prey energy fluxes. *J. Anim. Ecol.* 77, 1072–1078. doi: 10.1111/j.1365-2656.2008.01408.x

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Metabolic theory of ecology. *Ecology* 87, 1771–1789.

Bundy, A., Bohaboy, E. C., Hjermann, D. O., Mueter, F. J., Fu, C., and Link, J. S. (2012). Common patterns, common drivers: comparative analysis of aggregate surplus production across ecosystems. *Mar. Ecol. Prog. Ser.* 459, 203–218. doi: 10.3354/meps09787

Buren, A. D., Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B., Stenson, G., et al. (2014a). Bottom-up regulation of capelin, a keystone forage species. *PLoS One* 9:e87589. doi: 10.1371/journal.pone.0087589

Buren, A. D., Koen-Alonso, M., and Stenson, G. (2014b). The role of harp seals, fisheries and food availability in driving the dynamics of northern cod. *Mar. Ecol. Prog. Ser*. 511, 265–284. doi: 10.3354/meps10897

Buren, A. D., Murphy, H. M., Adamack, A. T., Davoren, G. K., Koen-Alonso, M., Montevecchi, W. A., et al. (2019). The collapse and continued low productivity of a keystone forage fish species. *Mar. Ecol. Prog. Ser*. 616, 155–170. doi: 10.3354/meps12924

Cadigan, N. (2015). A state-space stock assessment model for northern cod, including under-reported catches and variable natural mortality rates. *Can. J. Fish. Aquat. Sci.* 73, 296–308. doi: 10.1139/cjfas-2015-0047

Carscadden, J. E., Gjøsæter, H., and Vilhjálmsson, H. (2013). Recruitment in the Barents Sea, Icelandic, and eastern Newfoundland/Labrador capelin (*Mallotus villosus*) stocks. *Prog. Oceanogr.* 114, 84–96. doi: 10.1016/j.pocean.2013.05.006

Chassot, E., Duplisea, D., Hammill, M. O., Caskenette, A., Bousquet, N., Lambert, Y., et al. (2009). The role of predation by harp seals (*Pagophilus groenlandicus*) in the collapse and non-recovery of northern Gulf of St. Lawrence cod (*Gadus morhua*). *Mar. Ecol. Prog. Ser*. 379, 279–297. doi: 10.3354/meps07897

Chouinard, G. A., Swain, D. P., Hammill, M. O., and Poirier, G. A. (2005). Correspondence between changes in grey seal population abundance and variation in natural mortality of southern Gulf of St. Lawrence cod. *Can. J. Fish. Aquat. Sci.* 62, 1991–2000. doi: 10.1139/f05-107

Colbourne, E. B. (2004). Decadal changes in the ocean climate in Newfoundland and Labrador waters from the 1950s to the 1990s. *J. Northwest Atl. Fish. Sci.* 34, 43–61. doi: 10.2960/j.v34.m478

Cole, J. J., Lovett, G., and Findlay, S. E. G. (1991). *Comparative analysis of ecosystems: Patterns, Mechanisms, and Theory*. New York, NY: Springer Verlag, 375.

Cushing, D. H. (1982). *Climate and Fisheries*. London: Academic Press.

Cyr, F., Colbourne, E., Galbraith, P. S., Gibb, O., Snook, S., Bishop, C., et al. (2020). *Physical Oceanographic Conditions on the Newfoundland and Labrador Shelf during 2018*. DFO Canadian Science Advisory Secretariat Research. Document No. 2020/018. Ottawa ON: Fisheries and Oceans Canada, iv, 48.

Dawe, E., Koen-Alonso, M., Chabot, D., Stansbury, D., and Mullowney, D. (2012). Trophic interactions between key predatory fishes and crustaceans: comparison of two Northwest Atlantic systems during a period of ecosystem change. *Mar. Ecol. Prog. Ser*. 469, 233–248.

Dayton, P. K., Mordida, B. J., and Bacon, F. (1994). Polar marine communities. *Am. Zool*. 34, 90–99. doi: 10.1093/icb/34.1.90

Dempsey, D. P., Koen-Alonso, M., Gentleman, W. C., and Pepin, P. (2017). Compilation and discussion of driver, pressure, and state indicators for the Grand Bank ecosystem, Northwest Atlantic. *Ecol. Indic.* 75, 331–339. doi: 10.1016/j.ecolind.2016.12.011

DFO (2019). *Stock Assessment of Northern Cod (NAFO divisions 2J3KL) in 2019*. Canadian Science Advisory Secretariat Report. 2019/050. Ottawa ON: Fisheries and Oceans Canada.

DFO (2020). *Stock Status Update for Northern Cod*. DFO Canadian Science Advisory Secretariat Research No. 2020/nnn. Ottawa ON: Fisheries and Oceans Canada.

Drinkwater, K., Colbourne, E., Loeng, H., Sundby, S., and Kristiansen, T. (2013). Comparison of the atmospheric forcing and oceanographic responses between the Labrador Sea and the Norwegian and Barents seas. *Prog. Oceanogr*. 114, 11–25. doi: 10.1016/j.pocean.2013.03.007

Durant, J. M., Skern-Mauritzen, M., Krasnov, Y. V., Nikolaeva, N. G., Lindstrøm, U., and Dolgov, A. (2014). Temporal Dynamics of Top Predators Interactions in the Barents Sea. *PLoS One* 9:e110933. doi: 10.1371/journal.pone.0110933

Eriksen, E., Bogstad, B., and Nakken, O. (2011). Ecological significance of 0-group fish in the Barents Sea ecosystem. *Polar. Biol*. 34, 647–657. doi: 10.1007/s00300-010-0920-y

Eriksen, E., Skjoldal, H. R., Gjøsæter, H., and Primicerio, R. (2017). Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. *Progr. Oceanogr*. 151, 206–226. doi: 10.1016/j.pocean.2016.12.009

Fall, J., de Lange Wenneck, T., Bogstad, B., Fuglebakk, E., Gjøsæter, H., Seim, S. E., et al. (2020). *Fish Investigations in the Barents Sea Winter 2020*. Joint Report. Series. (https://www.hi.no/resources/Winter_survey_report_2020_IMR_PINRO.pdf)*****accessqur

Fogarty, M. (2014). The art of ecosystem-based fishery management. *Can. J. Fish. Aquat. Sci.* 71, 479–490. doi: 10.1139/cjfas-2013-0203

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M., and Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat. Clim. Change* 5, 673–677. doi: 10.1038/nclimate2647

Fudge, S. B., and Rose, G. A. (2008). Life history co-variation in a fishery depleted Atlantic cod stock. *Fish. Res.* 92, 107–113. doi: 10.1016/j.fishres.2008.02.005

Gaichas, S., Gamble, R., Fogarty, M., Benoit, H., Essington, T., Fu, C., et al. (2012). Assembly rules for aggregate-species production models: simulations in support of management strategy evaluation. *Mar. Ecol. Prog. Ser*. 459, 275–292. doi: 10.3354/meps09650

Gaichas, S., Reiss, C., and Koen-Alonso, M. (2014). "Chapter 10: ecosystem-Based Management in High Latitude Ecosystems," in *The Sea*, Vol. 16, eds M. J. Fogarty and J. J. McCarthy (Cambridge: Harvard University Press), 277–324.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., and Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science* 293, 2248–2251. doi: 10.1126/science.1061967

Gjøsæter, H., Bogstad, B., and Tjelmeland, S. (2009). Ecosystem effects of the three capelin stock collapses in the Barents Sea. *Mar. Biol. Res.* 5, 40–53. doi: 10.1080/17451000802454866

Glantz, M. H. (1992). *Climate Variability, Climate Change and Fisheries*. Cambridge: UniversityPress, Cambridge.

Hansen, J. L., and Harding, K. C. (2006). On the potential impact of harbour seal predation on the cod population in the eastern North Sea. *J. Sea Res.* 56, 329–337. doi: 10.1016/j.seares.2006.06.004

Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallfredsson, E. H., Høines, A. S., et al. (2017). Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents Seas: a review of possibilities and constraints. *Fish. Res.* 188, 38–57. doi: 10.1016/j.fishres.2016.12.002

Haug, T., Krøyer, A. B., Nilssen, K. T., Ugland, K. I., and Aspholm, P. E. (1991). Harp seal (*Phoca groenlandica*) invasions in Norwegian coastal waters: age composition and feeding habits. *ICES J. Mar. Sci.* 48, 363–371. doi: 10.1093/icesjms/48.3.363

Holsman, K. K., Essington, T., Miller, T. J., Koen-Alonso, M., and Stockhausen, W. J. (2012). Comparative analysis of cod and herring production dynamics across 13 northern hemisphere marine ecosystems. *Mar. Ecol. Prog. Ser.* 459, 231–246. doi: 10.3354/meps09765

Howell, D., and Bogstad, B. (2010). A combined Gadget / FLR model for management strategy evaluations of the Barents Sea fisheries. *ICES J. Mar. Sci.* 67, 1998–2004. doi: 10.1093/icesjms/fsq135

Hurtado-Ferro, F., Szuwalski, C. S., Valero, J. L., Anderson, S. C., Cunningham, C. J., Johnson, K. F., et al. (2015). Looking in the rear-view mirror: bias and retrospective patterns in integrated, age-structured stock assessment models. *ICES J. Mar. Sci.* 72, 99–110. doi: 10.1093/icesjms/fsu198

Hutchings, J. A., and Myers, R. A. (1994). What can be learned from the collapse of a renewable resource? Atlantic Cod, *Gadus morhua*, of Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.* 51, 2126–2146. doi: 10.1139/f94-214

ICES (2018). *Interim Report of the Working Group on the Integrated Assessments of the Barents Sea (WGIBAR)*. WGIBAR 2018 REPORT 9-12 March 2018. ICES CM 2018/IEASG:04. Tromsø: ICES, 210.

ICES (2019). *Report of the Arctic Fisheries Working Group (AFWG)*. ICES Scientific. Report No. 30.Burnaby, BC: ICES, 934.

ICES (2020). *Arctic Fisheries Working Group (AFWG)*. ICES Scientific. Report No. 2:52. Burnaby, BC: ICES, 577. doi: 10.17895/ices.pub.6050

Jelmert, A., Sandø, A. B., Bogstad, B., Frie, A. K., Grøsvik, B. E., Eriksen, E., et al. (2020). *Status of the Environment of the Barents Sea (eds. P. Arneberg, Gro van der Meeren, Sylvia Frantzen and Ida Vee)*. Report. Institute. Marine. Resarch., no. 2020-13. Bergen: Norwegian Institute of Marine Research, 114.

Johannesen, E., Ingvaldsen, R. B., Bogstad, B., Dalpadado, P., Eriksen, E., Gjøsæter, H., et al. (2012). Changes in Barents Sea ecosystem state, 1970–2009: climate fluctuations, human impact, and trophic interactions. *ICES J. Mar. Sci.* 69, 880–889. doi: 10.1093/icesjms/fss046

Kempf, A., Floeter, J., and Temming, A. (2008). Predator–prey overlap induced Holling type III functional response in the North Sea fish assemblage. *Mar. Ecol. Prog. Ser.* 367, 295–308. doi: 10.3354/meps07555

Kjesbu, O. S., Bogstad, B., Devine, J. A., Gjøsæter, H., Howell, D., Ingvaldsen, R. B., et al. (2014). Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Proc. Nat. Acad. Sci. U.S.A.* 111, 3478–3483. doi: 10.1073/pnas.1316342111

Koen-Alonso, M. (2007). "A process-oriented approach to the multispecies functional response," in *From Energetics to Ecosystems: The dynamics and structure of ecological systems*, eds N. Rooney, K. S. McCann, and D. L. G. Noakes (Dordrecht: Springer Netherlands), 1–36. doi: 10.1007/978-1-4020-5337-5_1

Koen-Alonso, M., and Cuff, A. (2018). *Status and trends of the fish community in the Newfoundland Shelf (NAFO Div. 2J3K), Grand Bank (NAFO Div. 3LNO) and Southern Newfoundland Shelf (NAFO Div. 3Ps) Ecosystem Production Units*. NAFO SCR Document 18/070. Dartmouth, NS: Northwest Atlantic Fisheries Organization, 1–11.

Koen-Alonso, M., Fogarty, M., Pepin, P., Hyde, K., and Gamble, R. (2013). *Ecosystem production potential in the Northwest Atlantic*. NAFO SCR 13/075. Dartmouth, NS: Northwest Atlantic Fisheries Organization, 1–13.

Koen-Alonso, M., Pepin, P., Fogarty, M. J., Kenny, A., and Kenchington, E. (2019). The northwest Atlantic fisheries organization roadmap for the development and implementation of an ecosystem approach to fisheries: structure, state of development, and challenges. *Mar. Pol.* 100, 342–352. doi: 10.1016/j.marpol.2018.11.025

Koen-Alonso, M., Pepin, P., and Mowbray, F. (2010). *Exploring the Role of Environmental and Anthropogenic Drivers in the Trajectories of Core Fish Species of the Newfoundland-Labrador Marine Community*. NAFO SCR 10/37. Dartmouth, NS: Northwest Atlantic Fisheries Organization, 1–16.

Koen-Alonso, M., and Yodzis, P. (2005). Multispecies modelling of some components of the marine community of northern and central Patagonia. *Can. J. Fish. Aquat. Sci.* 62, 1490–1512. doi: 10.1139/f05-087

Korsbrekke, K. (1997). *Norwegian Acoustic Survey of Norteast Arctic Cod on the Spawning Grounds off Lofoten*. ICES CM 1997/Y:18. Burnaby, BC: ICES, 18.

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. M. (2016). TMB: automatic differentiation and laplace approximation. *J. Stat. Softw.* 70, 1–21.

Lawson, J. W., Magalhães, A. M., and Miller, E. H. (1998). Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. *Mar. Ecol. Prog. Ser.* 164, 13–20. doi: 10.3354/meps164013

Lilly, G. R., Nakken, O., and Brattey, J. (2013). A review of the contributions of fisheries and climate variability to contrasting dynamics in two Arcto-boreal Atlantic cod (*Gadus morhua*) stocks: persistent high productivity in the Barents Sea and collapse on the Newfoundland and Labrador Shelf. *Prog. Oceanogr.* 114, 106–125. doi: 10.1016/j.pocean.2013.05.008

Lind, S., Ingvaldsen, R. B., and Furevik, T. (2018). Arctic warming hotspot in the northern Barents Sea linked to declining sea-ice import. *Nat. Clim. Change* 8, 634–639. doi: 10.1038/s41558-018-0205-y

Link, J. S. (2017). System-level optimal yield: increased value, less risk, improved stability, and better fisheries. *Can. J. Fish. Aquat. Sci.* 75, 1–16. doi: 10.1139/cjfas-2017-0250

Mantzouni, I., Sørensen, H., O'Hara, R. B., and MacKenzie, B. R. (2010). Hierarchical modelling of temperature and habitat size effects on population dynamics of North Atlantic cod. *ICES J. Mar. Sci.* 67, 833–855. doi: 10.1093/icesjms/fsp291

Megrey, B. A., Link, J. S., Hunt, G. L., and Moksness, E. (2009). Comparative marine ecosystem analysis: applications, opportunities, and lessons learned. *Progr. Oceanogr.* 81, 2–9. (and associated papers in this special issue), doi: 10.1016/j.pocean.2009.04.002

Mohn, R. (1999). The retrospective problem in sequential population analysis: an investigation using cod fishery and simulated data. *ICES J. Mar. Sci.* 56, 473–488. doi: 10.1006/jmsc.1999.0481

Morgan, J. M., Koen-Alonso, M., Rideout, R. M., Buren, A. D., and Maddock Parsons, D. (2018). Growth and condition in relation to the lack of recovery of northern cod. *ICES J. Mar. Sci.* 75, 631–641. doi: 10.1093/icesjms/fsx166

Mullowney, D. R. J., and Rose, G. A. (2014). Is recovery of northern cod limited by poor feeding? The capelin hypothesis revisited. *ICES J. Mar. Sci.* 71, 784–793. doi: 10.1093/icesjms/fst188

Murawski, S. A., Steele, J. H., Taylor, P., Fogarty, M. J., Sissenwine, M. P., Ford, M., et al. (2010). Why compare marine ecosystems? *ICES J. Mar. Sci.* 67, 1–9. doi: 10.1093/icesjms/fsp221

Myers, R. A., Barrowman, N. J., Hoenig, J. M., and Quhe, Z. (1996). The collapse of cod in Eastern Canada: the evidence from tagging data. *ICES J. Mar. Sci.* 53, 629–640. doi: 10.1006/jmsc.1996.0083

Øigård, T. A., Lindstrøm, U., Nilssen, K. T., and Haug, T. (2013). Functional relationship between harp seal body condition, environment and prey in the Barents Sea. *Mar. Ecol. Prog. Ser.* 484, 287–301. doi: 10.3354/meps10272

Pedersen, E. J., Thompson, P. L., Aaron Ball, R., Fortin, M.-J., Gouhier, T. C., Link, H., et al. (2017). Signatures of the collapse and incipient recovery of an overexploited marine ecosystem. *R. Soc. Open Sci.* 4:170215. doi: 10.1098/rsos.170215

Peters, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.

Popov, S., and Zeller, D. (2018). Reconstructed Russian fisheries catches in the Barents Sea: 1950-2014. *Front. Mar. Sci.* 5:266. doi: 10.3389/fmars.2018.00266

R Core Team (2017). *R: A language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rose, G. A., and O'Driscoll, R. L. (2002). Capelin are good for cod: can the northern stock rebuild without them? *ICES J. Mar. Sci.* 59, 1018–1026. doi: 10.1006/jmsc.2002.1252

Rose, G. A., and Walters, C. J. (2019). The state of Canada's iconic Northern cod: a second opinion. *Fish. Res.* 219:105314. doi: 10.1016/j.fishres.2019.105314314

Schramski, J. R., Dell, A. I., Grady, J. M., Sibly, R. M., and Brown, J. H. (2015). Metabolic theory predicts whole-ecosystem properties. *Proc. Natl. Acad. Sci. U.S.A.* 112, 2617–2622. doi: 10.1073/pnas.1423502112

Shelton, P. A., and Lilly, G. R. (2000). Interpreting the collapse of the northern cod stock from survey and catch data. *Can. J. Fish. Aquat. Sci.* 57, 2230–2239. doi: 10.1139/f00-191

Shelton, P. A., Sinclair, A. F., Chouinard, G. A., Mohn, R., and Duplisea, D. E. (2006). Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 63, 235–238. doi: 10.1139/f05-253

Sherwood, G. D., Rideout, R. M., Fudge, S. B., and Rose, G. A. (2007). Influence of diet on growth, condition and reproductive capacity in Newfoundland and Labrador cod (*Gadus morhua*): insights from stable carbon isotopes (δ13C). *Deep-Sea Res. 2 Top. Stud. Oceanogr.* 54, 2794–2809. doi: 10.1016/j.dsr2.2007.08.007

Smout, S., and Lindstrøm, U. (2007). Multispecies functional response of the minke whale *Balaenoptera acutorostrata* based on small-scale foraging studies. *Mar. Ecol. Prog. Ser.* 341, 277–291. doi: 10.3354/meps341277

Swain, D. P., and Benoît, H. P. (2015). Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem. *Mar. Ecol. Prog. Ser.* 519, 165–182. doi: 10.3354/meps11012

Swain, D. P., Benoît, H. P., and Hammill, M. O. (2015). Spatial distribution of fishes in a Northwest Atlantic ecosystem in relation to risk of predation by a marine mammal. *J. Anim. Ecol.* 84, 1286–1298. doi: 10.1111/1365-2656.12391

Thompson, R. J., Deibel, D., Redden, A. M., and McKenzie, C. H. (2008). Vertical flux and fate of particulate matter in a Newfoundland fjord at sub-zero water temperatures during spring. *Mar. Ecol. Prog. Ser.* 357, 33–49. doi: 10.3354/meps07277

Trzcinski, M. K., Mohn, R., and Bowen, W. D. (2006). Continued decline of an Atlantic cod population: how important is gray seal predation? *Ecol. Appl.* 16, 2276–2292. doi: 10.1890/1051-0761(2006)016[2276:cdoaac]2.0.co;2

Vasseur, D. A., and McCann, K. S. (2005). A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *Am. Nat.* 166, 184–198. doi: 10.1086/431285

Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M. L., Hop, H., et al. (2006). Food webs and carbon flux in the Barents Sea. *Prog. Oceanogr.* 71, 232–287. doi: 10.1016/j.pocean.2006.10.003

Yaragina, N. A., Bogstad, B., and Kovalev, Y. (2009). Variability in cannibalism in Northeast Arctic cod (*Gadus morhua*) during the period 1947–2006. *Mar. Biol. Res.* 5, 75–85. doi: 10.1080/17451000802512739

Yaragina, N. A., Kovalev, Y., and Chetyrkin, A. (2018). Extrapolating predation mortalities back in time: an example from North-east Arctic cod cannibalism. *Mar. Biol. Res.* 14, 1–14. doi: 10.1080/17451000.2017.1396342

Yodzis, P. (1998). Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *J. Anim. Ecol.* 67, 635–658. doi: 10.1046/j.1365-2656.1998.00224.x

Yodzis, P., and Innes, S. (1992). Body size and consumer-resource dynamics. *Am. Nat.* 139, 1151–1175. doi: 10.1086/285380

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.

frontiers
in Marine Science

ORIGINAL RESEARCH
published: 27 April 2021
doi: 10.3389/fmars.2021.646733

Appraising the Status of Fish Community Structure in the Yellow Sea Based on an Indicator-Testing Framework

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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: 28 December 2020
Accepted: 06 April 2021
Published: 27 April 2021

Citation:
Li Y, Ma S, Fu C, Tian Y, Li J, Sun P, Ye Z and Liu Y (2021) Appraising the Status of Fish Community Structure in the Yellow Sea Based on an Indicator-Testing Framework.
Front. Mar. Sci. 8:646733.
doi: 10.3389/fmars.2021.646733

Fish community structure (FCS) of the Yellow Sea (YS) is affected by multiple pressures. Quantifying the responses of indicators of FCS (IFCSs) to pressures is a key aspect of ecosystem-based fisheries management. Quantitative methodology has hitherto been rarely applied to evaluate the performance of ecological indicators in response to physical and anthropogenic pressures and management actions. In this study, we adopted a quantitative and flexible framework to quantify the performance of IFCSs in the YS as well as to identify a suite of operational IFCSs to evaluate the status of the FCS via two state-space approaches. A total of 22 IFCSs were tested for their responses to three types of pressures including anthropogenic activities (fishing), large-scale climate change, and regional environmental variables. Our results indicate that the majority of IFCSs have good performance in terms of sensitivity in their responses to pressures, but weak performance in terms of robustness. The IFCSs tend to respond stronger to fishing than to large-scale climatic indices and regional environmental indices both in terms of sensitivity and robustness. A final indicator suite of five best-performing IFCSs was identified. The five IFCSs include total catch (ToC), mean trophic level (MTL), the ratio of catch of large predatory groups to total catch (LPC/ToC), mean temperature of catch (MTC) [or alternatively catch of small pelagic groups (SPC)], and functional evenness based on thermal groups (T-J′FD), all of which show regime shift patterns consistent with climate change. Compared to a reference period (1960–1964), the status of the current FCS has been obviously changed, and the long-term trajectories of the final indicator suite is consistent with that of fishing pressure. This study demonstrates the applicability of the indicator-testing framework in appraising the status of FCS, and facilitates moving towards ecosystem-based fisheries management in the YS.

Keywords: indicator-testing framework, state-space approach, ecological indicator, fish community structure, Yellow Sea, over-exploitation

INTRODUCTION

Threats to marine ecosystems consist of anthropogenic activities such as fishing, shipping, pollution, and species introductions (Jennings and Kaiser, 1998; Halpern et al., 2008), regional environmental changes in the pH (ocean acidification), chlorophyll-a concentration, and sea surface temperature (Fabry et al., 2008; Solanki et al., 2015), and climate change (Hoegh-Guldberg and Bruno, 2010; Gissi et al., 2021). The combination of multiple pressures has resulted in considerable variability in marine fish community structure (FCS; Möllmann et al., 2009; Zhang et al., 2020). For instance, overfishing typically caused miniaturization in the body size and truncation in age structure (Conover et al., 2005; Shan et al., 2012). The resources of some commercial fish species like rockfish (*Sebastes* spp.) showed obvious decline in recent decades (Link et al., 2009). The mean trophic level in Indian States and Union Territories steadily declined at an average rate of 0.058 per decade (Bhathal and Pauly, 2008). Similar phenomena have been extensively discovered around the world (Tsikliras et al., 2015). Aside from overfishing, global warming has accelerated species extinction and altered biodiversity, further jeopardizing ecosystem structure (Urban, 2015). The ubiquitous biodiversity loss caused by climate change was pervasive in terrestrial, freshwater and marine ecosystems (Weiskopf et al., 2020). Undoubtedly, extreme declines of fisheries resources and changes in compositions of fishery catches have threatened the sustainability of ecosystems and human well-being (Vörösmarty et al., 2010).

To sustain fisheries resources under a changing world, ecosystem-based fisheries management (EBFM) has been increasingly advocated (Garcia and Cochrane, 2005; Sherman et al., 2005; Large et al., 2015); however, fisheries management have been implemented primarily based on single-species stock assessment with the objective of achieving sustainable exploitation of single-species (Munyandorero, 2012; Burgess et al., 2017).Single-species-based fisheries management often do not fully incorporate ecosystem considerations such as ecological interactions and environmental processes (Link et al., 2002; Pikitch et al., 2004). As a result, fisheries management objectives based on single-species are not necessarily beneficial to the whole ecosystem; the sustainability of a few limited fish species does not represent the sustainability of the whole ecosystem. Therefore, developing EBFM is extremely urgent (Pikitch et al., 2004; Large et al., 2015). Implementing EBFM follows three steps including pre-defined management goals, an assessment of ecosystem status, and decision criteria to achieve management objectives (Sainsbury et al., 2000). Similar to traditional decision criteria based on single-species management methods, ecological indicators as synthetic and quantifiable attributes that represent ecosystem status can also be translated into decision criteria to assist management decision making in EBFM (Jennings, 2005; Link, 2005; Levin et al., 2009).

Identifying suitable indicators to represent the status of an ecosystem has been an important research topic in the last two decades (Shin et al., 2010; Otto et al., 2018a). However, such task is challenging because of the complexity of ecosystem dynamics (Bjørnstad and Grenfell, 2001; Jørgensen et al., 2016). For example, trophic interaction, one of the most typical characteristics of an ecosystem, can modify the responses of ecological indicators to pressures and interfere interpretive ability of indicators to changes in various pressures (Kadin et al., 2019). Efforts have been taken, through comparative multi-model multi-ecosystem simulation experiments, to explore various ecological indicators to determine whether the ecological indicators selected can track changes in the ecosystems and reveal their emergent properties under multiple pressures (Shin et al., 2018; Fu et al., 2019). To reflect the complexity of ecosystems, effects of different pressures, and management objectives, multiple ecological indicators are needed as a single indicator represents only finite components of ecosystems and responds to limited pressures and management measures (Rochet and Trenkel, 2009; Ottersen et al., 2011). In addition, the performances of ecological indicators need to be rigorously evaluated before they can be used for making policy decisions when implementing EBFM. Although hundreds of ecological indicators have hitherto been proposed, only a limited number of them have been evaluated for a very limited number of ecosystems (e.g., Otto et al., 2018a; Fu et al., 2019). There are considerable gaps in the using of complementary indicator suites to assess the dynamics of FCS (Rossberg et al., 2017) and in the evaluation of their performances to assist fisheries management decision making.

Indicator-testing framework proposed by Otto et al. (2018a) is a useful methodology for validating the performance of ecological indicators and for evaluating the state of ecosystem based on a robust indicator suite. Using this methodology, Otto et al. (2018a) validated the performance of food web indicators in the Baltic Sea and selected a final indicator suite as proxies for the state of the food web in different regions. This framework features a score criterion with objectivity and covers information about trophic interactions as well as threshold responses. More importantly, it has great flexibility that supports the development of operational ecological indicators for different types of ecosystem and management objectives.

The Yellow Sea (YS) is one of the most productive regions for marine fisheries in the Northwestern Pacific (Tang et al., 2016). Over the past several decades, the FCS in the YS has been undergoing dramatic changes (Tang, 2009) driven by multiple pressures including large-scale climate variability and climate change (the Arctic Oscillation, El Niño-Southern Oscillation and global warming, Wei et al., 2013; Cai et al., 2016; Ma et al., 2019), regional environmental changes (SST, Nurani et al., 2015), and overfishing (Mu et al., 2007). Especially, continuous intensive fishing selectively removed larger individuals or higher trophic levels species, and reduced the abundance of vulnerable species, resulting in a decrease in biomass and the mean body size as well as changes in species composition (Xu and Jin, 2005). With multiple pressures continually impacting the YS, there are increasing concerns on the decline and miniaturization of fishery ecosystem resources in this region. The ecosystem function of fishery production has been predicted to be declining (Tang et al., 2016), which poses a great threat to food availability for human beings around the YS and beyound. Therefore, developing sustainable fisheries based on ecosystem management in the YS is extremely urgent (Tang et al., 2016), especially in optimizing management by utilizing suitable ecological indicators of the FCS (IFCSs). However, relevant studies on the FCS fluctuations, suitable IFCSs, and optimal management of fisheries resources in the YS are still scant.

In this paper, we applied the indicator-testing framework (Otto et al., 2018a) to quantify and visualize the performances of the FCS in the YS, in order to select an operational indicator suite. Through comparing the dynamics of the FCS in the YS based on the final indicator suite and previous relevant studies (Jin, 2003; Chen, 2004; Lin et al., 2013; Tian et al., 2013; Ma et al., 2018, 2019), we aimed to: (i) demonstrate the applicability of the indicator-testing framework for the FCS in the YS; (ii) choose an operational indicator suite to represent the status of the FCS in the YS; and (iii) provide a solid foundation for the selection of indicators and suggest their applications in fisheries management.

MATERIALS AND METHODS

Study Area

The YS is one of marginal seas of northwestern North Pacific, adjacent to the Bohai Sea in the north and the East China Sea in the south (**Figure 1**). The YS covers an area of about 400,000 km^2 with an average depth of 44 m. The YS is highly productive, contributing to more than 20% of marine fishery production in China and comprised of various species associated with different niches. Under the dual pressures of climate variability and overfishing, species composition in the total catch have changed greatly (Ma et al., 2019). In particular, the proportion of warm-water species increased significantly, while the proportion of cold-water species decreased significantly (Liang et al., 2018). In addition, the fishery species composition changed from demersal fish at high trophic levels to small pelagic fish at low trophic levels (Ma et al., 2018).

Ecological Indicators of Fish Community Structure

In this study, we used a series of selection criteria suggested in Otto et al. (2018a) to select candidate indicators. As fishery-independent data from research surveys are rare in the YS (e.g., Liang et al., 2020), we took advantage of the YS catch time-series data from 1960 to 2014 obtained through the Sea Around Us project[1] (Pauly and Zeller, 2016) to derive ecological indicators. Catch data were summarized to species, genus, family, order, and class. All species were classified into four functional groups, namely the large predatory, small pelagic, demersal, and invertebrate groups according to their trophic levels, biological characteristics, and previous studies (Tian et al., 2006, 2013). All the species were also categorized into three thermal groups, namely warm-water, temperate-water, and cold-water groups according to their optimal temperature (Ma et al., 2019). Based on the catch data of the corresponding groups, we calculated 22 IFCSs that represent the YS large marine ecosystem (**Table 1**). These 22 IFCSs include 5 indicators based on all species (termed "total-IFCSs"), 11 indicators based on functional groups ("functional-IFCSs") and six indicators based on thermal groups ("thermal-IFCSs"). Specifically, total-IFCSs include total catch (ToC), the mean trophic level (MTL), the mean temperature of catch (MTC), Whilm species diversity (H''), and McNaughton dominance (Dom). Functional-IFCSs contain catch of large predatory groups (LPC), catch of small pelagic groups (SPC), catch of demersal groups (DeC), catch of invertebrate groups (InC), the ratio of LPC to ToC (LPC/ToC), the ratio of SPC to ToC (SPC/ToC), the ratio of the ratio of DeC to ToC (DeC/ToC), the ratio of InC to ToC (InC/ToC), the ratio of DeC to SPC (DeC/SPC), the ratio of LPC to SPC (LPC/SPC), and functional evenness based on functional groups (F-J$'$FD). Thermal-IFCSs consist of catch of warm-water groups (WWC), catch of cold-water groups (CWC), the ratio of WWC to ToC (WWC/ToC), the ratio of CWC to ToC (CWC/ToC), the ratio of WWC to CWC (WWC/CWC), and functional evenness based on thermal groups (T-J$'$FD).

Prior to the calculation of each indicator, multiple imputation with Bayesian linear regression techniques (Buuren and Groothuis-Oudshoorn, 2011) was used to fill the missing values of the catch data in the YS (1.43%). Multiple imputation was performed using the packages "mice" within the "R" statistical and programming environment (R Core Team, 2019), with each imputed value derived from five iterations and each iteration consisting of 100 imputations.

Pressure Variables

A total of eight large-scale climate indices were tested for their effects on all IFCSs, including the Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), Arctic Oscillation Index (AOI), Pacific-North America Index (PNA), North Pacific Index (NPI), Southern Oscillation Index (SOI), Asian Monsoon Index (MOI), and Sea Surface Temperature in Nino 4 Region (Nino 4). Descriptions, data sources, and spatial-temporal resolutions of these climate indices are provided in **Supplementary Table 1**. These climatic variables are well documented and largely associate with the ecosystems and their fish communities in the North Pacific (Boeing and Duffy-Anderson, 2008; Ceballos et al., 2009; Litzow et al., 2014; Kidwell et al., 2017).

In addition to the large-scale climate indices, seven well-documented environmental indices in the YS, including sea surface temperature (SST), sea surface salinity (SSS), sea level pressure (SLP), scalar wind (SW), wind direction (WD), air temperature (AT), and precipitable water content (PWC), were also selected to represent regional environmental conditions (Cui and Zorita, 1998; Park et al., 2015; Zheng et al., 2015) and to test the responses of IFCSs. More details on these environmental indices are provided in **Supplementary Table 1**.

Anthropogenic pressures in the YS were approximated by fishing efforts (FE) in the following statistical analyses to understand the responses of IFCSs. Engine power data for the total number of Chinese marine fishing boats in the YS were derived from Chinese Fishery Statistics from 1960 to 2014 to represent fishing efforts (Zhao et al., 2015). Due to the lack of

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[1] http://www.seaaroundus.org/

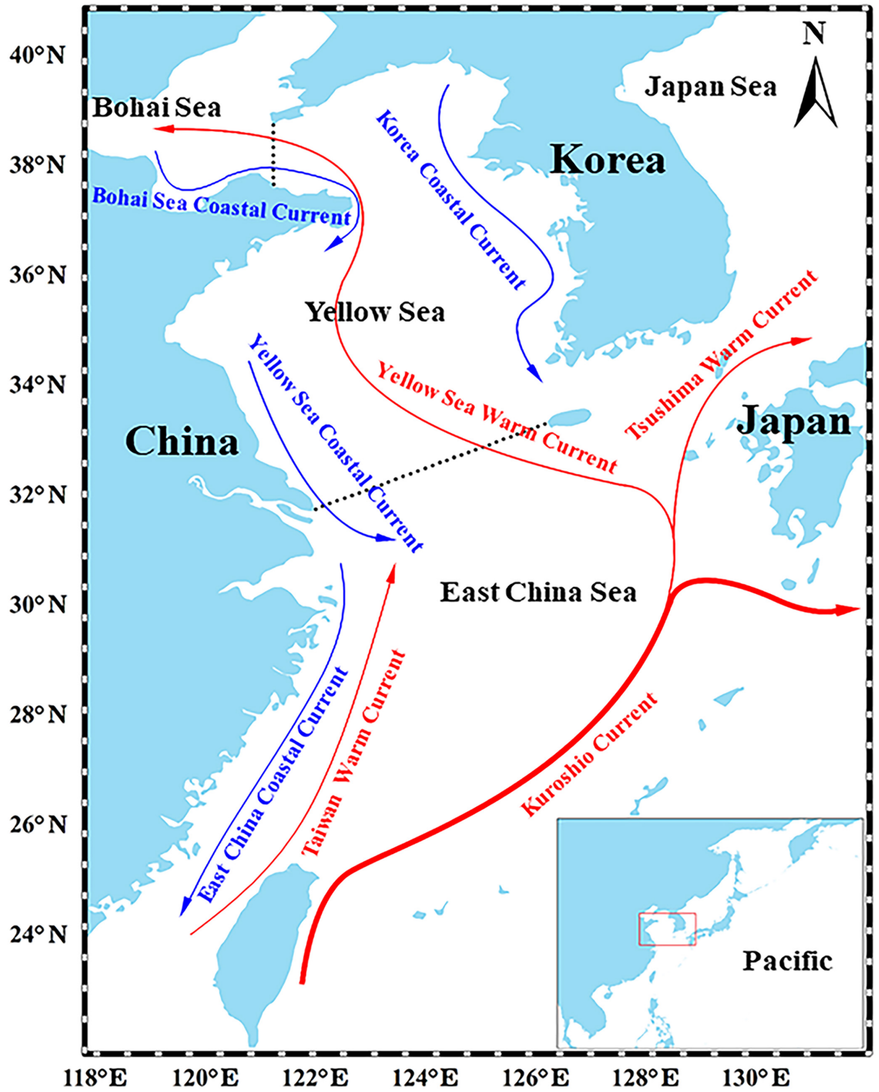

FIGURE 1 | Map of the East China Continental Shelf Sea. Red and blue lines represent the primary warm currents and cold currents that affect the YS, respectively. The panel at the bottom-right shows the location of the YS in the Northwest Pacific (Ma et al., 2018).

other accurate fishing effort indices for specific species/groups, we assumed fishing efforts were the same across all fish species.

Indicator-Testing Framework

The indicator-testing framework of Otto et al. (2018a) was used to assess the performances of IFCSs and further choose a set of complementary and robust indicators for representing the FCS in the YS. Before conducting statistical analyses, all the 22 IFCSs were standardized by zero-mean normalization. All calculations were done using the package "INDperform" (Otto et al., 2018b) within the R environment (R Core Team, 2019). The indicator-testing framework, combined with score criteria (**Supplementary Table 2**), is a seven-step process with the first five steps being used to validate and quantify the performances of IFCSs in their responses to pressures (**Supplementary Table 1**).

Specifically, Step 1 identifies indicators' trends and links to the score criterion 1. Generalized additive models (GAMs; Hastie and Tibshirani, 1990) are applied to model the long-term changes of IFCSs in response to one pressure (explanatory variable) at a time. When there are significant temporal auto-correlation in residuals, the alternative Generalized Additive Mixed Models (GAMMs) are used. A score of 1 is given if an IFCS shows a significant trend, otherwise, score 0. Step 2 identifies the responses of IFCSs to pressures and links to sub-criterion 2.1 and the first two sub-criteria of criterion 3. Step 3 measures the robustness of an IFCS in relation to one specific pressure based on the degree of fit for the last 3 years between predictions from the model using the training dataset (i.e., excluding the last 3 years) and the test dataset (i.e., the last 3 years). The score of sub-criterion 3.3 is according to the value of the normalized root mean square error (NRMSE) on the test dataset.

TABLE 1 | List of fishery community structural indicators tested for YS.

IFCS categories	Fishery community structural indicators	Abbreviation	Definition	Examples of applications
Indicators based on the total species	Total Catch	ToC		Tang et al., 2016
	The Mean Trophic Level	MTL	$MTL_{yr} = \frac{\sum_i^n C_{i,yr} \times TL_i}{\sum_i^n C_{i,yr}}$	Tian et al., 2013; Ma et al., 2019
	The Mean Temperature of Catch	MTC	$MTC_{yr} = \frac{\sum_i^n C_{i,yr} \times T_i}{\sum_i^n C_{i,yr}}$	Tian et al., 2013; Ma et al., 2019
	Whilm species diversity	H''	$H'' = -\sum_{i=1}^{S} (\frac{w_i}{W}) \ln(\frac{w_i}{W})$	Wilhm, 1968
	McNaughton Dominance	Dom	$(N1+N2)/N$	Dornelas et al., 2014
Indicators based on the functional groups	Catch of Large Predatory groups	LPC		Ma et al., 2019
	Catch of Small Pelagic groups	SPC		Tian et al., 2008; Ma et al., 2018
	Catch of Demersal groups	DeC		Tian et al., 2011; Ma et al., 2019
	Catch of Invertebrate groups	InC		Tian et al., 2008; Ma et al., 2019
	Catch of Large Predatory groups/Total catch	LPC/ToC		
	Catch of Small Pelagic groups/Total catch	SPC/ToC		
	Catch of Demersal groups/Total catch	DeC/ToC		Tian et al., 2011
	Catch of Invertebrate groups/Total catch	InC/ToC		
	Catch of Invertebrate groups/ Catch of Small Pelagic groups	DeC/SPC		
	Catch of Large Predatory groups/ Catch of Small Pelagic groups	LPC/SPC		
	Functional evenness based on Functional groups	F-J′FD	$J'_{FD} = -\sum_{i=1}^{n} (p_i \log_2 p_i)$	Gamtto and Furtado, 2009
Indicators based on the thermal groups	Catch of Warm-Water groups	WWC		Tian et al., 2011
	Catch of Cold-Water groups	CWC		Tian et al., 2011
	Catch of Warm-Water groups/Total catch	WWC/ToC		Tian et al., 2011
	Catch of Cold-Water groups/Total catch	CWC/ToC		
	Catch of Warm-Water groups/ Catch of Cold-Water groups	WWC/CWC		
	Functional evenness based on Thermal groups	T-J′FD	$J'_{FD} = -\sum_{i=1}^{n} (p_i \log_2 p_i)$	Gamtto and Furtado, 2009

S, the number of fish species of each sample; W, the total biomass of one sample; w_i*, the total biomass of the ith species;* p_i*, percentage of the total biomass of the ith functional groups to total catch; n, 4 in formula of F-J′FD and 3 in formula of T-J′FD and the total number of species in other formulas; N1 and N2 are the biomass of the first and second most weighty species;* $C_{i,yr}$*, is the catch of species i in year yr;* TL_i*, the trophic level of species i;* T_i*, the optimal temperature of species i.*

In the case of non-linear responses of IFCSs to pressures, the method of finite differences (Trenkel and Rochet, 2009) is used to test the first derivative of the smoothing function, representing the instantaneous change rate of IFCSs to that of the pressures in Step 4. Confidence intervals (CI) of the first derivative are generated by carrying out a conditional bootstrap by resampling from the GAM (or GAMM) residuals. The IFCSs' responses to changes in pressures are not considered to be statistically significant when zero is contained within the CI of the first derivative. Subsequent scoring sub-criterion 2.2 was done via counting the proportion of points inside the CI. In Step 5, the threshold GAM (TGAM; Ciannelli et al., 2004) is used to detect interactions between pressures corresponding to criterion 3.4. A zero score for sub-criterion 3.4 is given if interactions with other pressure(s) are detected. The IFCS with summed scores of sensitivity and robustness > 50% of maximum score is considered to have good performances in their responses to pressures.

In Step 6, Nightingale rose diagrams are used to visualize the overall performance of the IFCSs. Finally, in Step 7, a hierarchical group-average cluster analysis (Legendre and Legendre, 1998) is carried out based on the sub-criteria scores of sensitivity (criterion 2), robustness (criterion 3), and the other two criteria

(criteria 1 and 4) to recognize redundant IFCSs. Then a final indicator suite is identified based on the following criteria (Otto et al., 2018a): (1) responsiveness to at least one pressure, (2) non-redundancy, i.e., the IFCSs is not grouped with other IFCSs at the lowest level in the cluster analysis, or having higher scores in sensitivity and robustness than their redundant counterpart in the same cluster, (3) good performance (the sum scores of sensitivity and robustness >50% of the maximum score), and (4) complement, i.e., the IFCS covers the full types of pressures together with other IFCSs.

State Space Approaches and Regime Shift Detection

For the final indicator suite, two state-space approaches were applied to analyze the temporal dynamics of the FCS. One approach is to calculate the Euclidean distance between each year and a reference year (de Berg et al., 2008), and the referent year is set as the initial year 1960 in this study. The other one is the convex hull method (Swenson, 2014), in which we first calculated the convex hull for a reference period (1960–1964) based on the first two axes obtained from a Principal Component Analysis (PCA), then calculated the convex hull of the current period (2010–2014) to determine whether there was overlap between the two closed spaces.

The PCA was applied to identify the most important patterns of common variability in the FCS. Only the first two PCs (PC1 and PC2) for the IFCSs were retained for representing the most important modes of variability in the final indicator suite. The sequential *t*-test analysis of regime shift (STARS; Rodionov, 2004; Rodionov and Overland, 2005) was then used to detect trends and regime shifts in the derived PCs. STARS was written in Visual Basic for Application (VBA) for Microsoft Excel and was available at www.BeringClimate.noaa.gov. To assist visualizing the trends in the time series of PCs, the cumulative sum (CuSum) was calculated by a simple addition of a datum to the sum of all previous data points (Beamish et al., 1999; Tian et al., 2004). In addition, because the results of STARS are easily affected by the cut-off length, sensitivity analysis on the cut-off length was also conducted. Specifically, the STARS was run successively with the value of the cut-off length changing from 10 to 20 with an increment of 0.01, then the frequencies of time nodes being selected as potential regime shifts were summed to identified the time node with the highest frequency as the regime shift.

RESULTS

The Performances of the IFCSs in the YS

The IFCSs in different categories tended to have differing responses to pressures (**Table 2**). All total-IFCSs were insensitive to climate indices while being highly affected by fishing efforts. The functional-IFCSs responded selectively to fishing efforts but not to environmental indices showing primarily low performances. By contrast, the thermal-IFCSs, especially the index T-J′FD, showed high sensitivity in their responses to all three types of pressures. All IFCSs responded significantly to at least one pressure except Dom and H′′ (**Table 2**) with only H′′ showing no trend (**Supplementary Figure 1**). However, none of the IFCSs showed a direct response to the regional environmental index (WD) and three large-scale climate indices (NPI, MOI, and Nino 4). Therefore, these four pressure indices were excluded from the subsequent analysis. Among the 22 IFCSs that responded to one or more pressures, half showed good performances in their responses to pressures (**Table 2**). In terms of sensitivity, a majority of IFCSs (18 out of 22) showed good performance with scores >50%. By contrast, none of the IFCSs scored more than 50% of the total score in terms of robustness, which resulted in weak performance for many IFCSs (**Table 2**). Among all IFCSs, the indicators of LPC/ToC, CWC, and WWC/ToC showed significant linear responses to all their pressures. In contrast, relevant non-linear responses to all their significant pressures were found for SPC/ToC, DeC/ToC, InC/ToC, DeC/SPC, LPC/SPC, and F-J′FD (**Table 2** and **Supplementary Figure 2**). Another striking feature across all IFCSs was that one or more threshold interactions were found for every IFCS (**Supplementary Figure 2**). For example with T-J′FD, there was a threshold interaction with PNA: under lower PNA conditions (<0.97) the negative effect of fishing efforts remained constant and linear, but under higher PNA conditions (>0.97) there were no significant responses (**Supplementary Figure 2**).

Indicator Suite for the YS

Based on the performances of the 22 IFCSs and the need to reduce redundancies found amongst the 22 IFCSs (**Figure 2**), we identified two combinations (Combinations I and II) with each consisting of five indicators. Either combination can be considered as a final robust indicator suite. Combination I comprised one thermal-IFCS (T-J′FD), one functional-IFCS (LPC/ToC) and three total-IFCS (ToC, MTL, MTC). Combination II consisted of one thermal-IFCS (T-J′FD), two functional-IFCSs (LPC/ToC, SPC) and two total-IFCSs (ToC, MTL). Together, these IFCSs would allow the evaluation of impacts from large-scale climatic and regional environmental changes as well as fishing effort. The total-IFCSs are suitable for detecting the impacts of fishing efforts and climate variability with ToC and MTC showing strong responses to PDO and PNA, respectively. By contrast, MTL showed a specific response to fishing efforts. As a synthetic indicator of thermal-IFCSs, T-J′FD showed a strong and robust response to climate indices (i.e., PDO and AO), environmental indices (i.e., SSS and SW), as well as fishing efforts. For the functional-IFCSs, LPC/ToC only responded to environmental indices, but not to fishing efforts and climate indices, while SPC showed strong response to fishing efforts and two climatic indices (**Table 2**).

The Dynamics of the FCS in the YS

Both robust combinations of IFCSs showed that the FCS in the YS has departed substantially from their reference state (**Figure 3**). Although the Euclidean distance scalar of combination I suggested the YS returning to the earlier state after 2000 (**Figure 3A**), the state approach based on the PCA indicated clearly that the last five years of the current period are outside the reference domain in terms of PC1 dimensions (**Figure 3B**). There were also true for Combination II (**Figures 3C,D**). The first two

TABLE 2 | Overview of performance scores of fishery ecosystem structure indicators for each criterion in the YS.

IFCS categories	IFCS	1-Reflects changes	4-Link to management	Pressure-dependent scores													
				Pressure	p value	2-Sensitivity			Sensitivity performance (%)	3-Robustness					Robustness performance (%)	Total performance (%)	Model type
						2.1	2.2	Sum		3.1	3.2	3.3	3.4	Sum			
Indicators based on the total stock	ToC *	1	0	PDO.winter.DJF	0.010887	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR1)
				SOI.winter.DJF	0.020086	1	0	1	17	1	0	0	0	1	17	17	GAMM(AR1)
				YS.PWC.winter.JFM	0.000779	1	0	1	17	1	0	0	0	1	17	17	GAMM(AR1)
				YS.fishing.efforts.KW.	0.000000	3	3	6	100	2	0	0	0	2	33	67	GAM
	MTL*	1	1	NPGO.winter.DJF	0.004615	1	0	1	17	1	0	0	0	1	17	17	GAMM(AR1)
				YS.fishing.efforts.KW.	0.025457	2	3	5	83	2	1	0	0	3	50	67	GAMM(AR1)
	MTC*	1	0	YS.fishing.efforts.KW.	0.000000	3	3	6	100	1	0	0	0	1	17	58	GAM
				PNA.winter.DJF	0.047547	1	3	4	67	1	1	0	0	2	33	50	GAMM(ARMA11)
	H′′	0	2														
	Dom	1	2														
Indicators based on the functional groups	LPC	1	2	PDO.winter.DJF	0.039323	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR1)
				YS.fishing.efforts.KW.	0.000000	3	3	6	100	2	0	1	0	3	50	67	GAM
	SPC*	1	0	PNA.winter.DJF	0.039565	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR1)
				YS.AT.winter.JFM	0.000003	1	0	1	17	1	0	0	0	1	17	17	GAMM(ARMA12)
				YS.fishing.efforts.KW.	0.000000	3	3	6	100	2	0	0	0	2	33	67	GAM
	DeC	1	2	PDO.winter.DJF	0.025482	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR1)
				SOI.winter.DJF	0.021999	1	0	1	17	1	0	0	0	1	17	17	GAMM(AR1)
				YS.SST.winter.JFM	0.009685	1	0	1	17	1	0	0	0	1	17	17	GAMM(AR1)
	InC	1	2	PDO.winter.DJF	0.015048	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR1)
				YS.PWC.winter.JFM	0.044135	1	0	1	17	1	0	0	0	1	17	17	GAMM(AR1)
				YS.fishing.efforts.KW.	0.000000	3	3	6	100	2	0	0	0	2	33	50	GAM
	LPC/ToC*	1	2	YS.AT.winter.JFM	0.013745	1	3	4	67	1	1	0	0	2	33	50	GAMM(ARMA11)
				YS.SLP.winter.JFM	0.006074	1	3	4	67	1	1	0	0	2	33	50	GAM
	SPC/ToC	1	0	YS.AT.winter.JFM	0.001636	1	0	1	17	1	0	0	0	1	17	17	GAMM(ARMA12)
				YS.fishing.efforts.KW.	0.000000	3	2	5	83	0	0	0	0	0	0	42	GAM
	DeC/ToC	1	2	YS.AT.winter.JFM	0.034638	1	0	1	17	1	0	0	0	1	17	17	GAMM(AR1)
	InC/ToC	1	2	YS.fishing.efforts.KW.	0.000000	3	2	5	83	0	0	0	0	0	0	42	GAM
	DeC/SPC	1	0	PNA.winter.DJF	0.027280	1	0	1	17	1	0	0	0	1	17	17	GAMM(AR1)
				YS.SST.winter.JFM	0.010380	1	0	1	17	1	0	0	0	1	17	17	GAMM(AR1)
	LPC/SPC	1	0	YS.fishing.efforts.KW.	0.000000	3	2	5	83	0	0	0	0	0	0	42	GAM
				YS.AT.winter.JFM	0.000468	1	1	2	33	1	0	0	0	1	17	25	GAMM(ARMA11)
	F-J'_{FD}	1	2	YS.fishing.efforts.KW.	0.000000	3	3	6	100	2	0	0	0	2	33	67	GAM
Indicators based on the thermal groups	WWC	1	0	PDO.winter.DJF	0.001297	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR1)
				AO.winter.DJF	0.048372	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR1)
				YS.PWC.winter.JFM	0.003745	1	0	1	17	1	0	0	0	1	17	17	GAMM(AR1)
				YS.SSS.winter.JFM	0.022286	1	0	1	17	1	0	0	0	1	17	17	GAMM(AR1)

(Continued)

TABLE 2 | Continued

IFCS categories	IFCS	1-Reflects changes	4-Link to management	Pressure-dependent scores													
				Pressure	p value	2-Sensitivity			Sensitivity performance (%)	3-Robustness					Robustness performance (%)	Total performance (%)	Model type
						2.1	2.2	Sum		3.1	3.2	3.3	3.4	Sum			
				YS.fishing.efforts.KW.	0.000000	3	2	5	83	2	0	0	0	2	33	58	GAMM(ARMA11)
	CWC	1	0	YS.SW.winter.JFM	0.021314	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR1)
				YS.fishing.efforts.KW.	0.000000	3	3	6	100	2	1	0	0	3	50	75	GAMM(AR1)
	WWC/ToC	1	1	PDO.winter.DJF	0.017833	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR1)
				YS.AT.winter.JFM	0.022084	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR1)
	CWC/ToC	1	1	PDO.winter.DJF	0.008086	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR2)
				YS.fishing.efforts.KW.	0.000000	3	3	6	100	0	0	0	0	0	0	50	GAM
	WWC/CW**c**	1	1	PDO.winter.DJF	0.000346	1	3	4	67	1	1	0	0	2	33	50	GAMM(ARMA11)
				AO.winter.DJF	0.000177	2	3	5	83	1	1	0	0	2	33	58	GAM
				YS.SSS.winter.JFM	0.005129	2	3	5	83	1	1	0	0	2	33	58	GAMM(AR1)
				YS.fishing.efforts.KW	0.000000	3	3	6	100	0	0	0	0	0	0	50	GAM
	T-J′FD*	1	1	PDO.winter.DJF	0.005241	1	3	4	67	1	1	0	0	2	33	50	GAMM(ARMA11)
				AO.winter.DJF	0.000267	2	3	5	83	1	1	0	0	2	33	58	GAM
				YS.SST.winter.JFM	0.000259	2	1	3	50	0	0	0	0	0	0	25	GAM
				YS.SW.winter.JFM	0.043082	1	3	4	67	1	1	0	0	2	33	50	GAMM(AR1)
				YS.SSS.winter.JFM	0.041274	2	3	5	83	1	1	0	0	2	33	58	GAMM(AR1)
				YS.fishing.efforts.KW.	0.000031	3	3	6	100	2	1	0	0	3	50	75	GAMM(AR1)

*Complementary indicators with a good performance suggested for the YS based on this framework are indicated in *.*

PCs accounted for 85.5 and 88.5% of the final IFCSs variances for the Combinations I and II, respectively (**Figures 3B,D**).

For Combination I, step-like changes occurred in 1971/72, 1985/86, and 2003/04 for PC1 and 1976/77 and 1990/91 for PC2 (**Figures 4**, **5**); similar results were found in Combination II (**Supplementary Figures 3, 4**). As all five robust IFCSs have high loadings on one or both PCs (**Figure 6** and **Supplementary Figure 5**), this can be interpreted as a deviation from the reference period in all components of the FCS represented by the suites with values of ToC and MTC (alternatively SPC) being lower while MTL, LPC/ToC and particularly T-J′FD being higher during the reference period (**Figure 6** and **Supplementary Figures 1, 5**).

DISCUSSION

Performance of IFCSs in the YS

In general, the first five steps of the indicator-testing framework have indicated that the majority of the 22 IFCSs of the YS showed good performances in terms of their sensitivity to pressures, but weak performances in terms of robustness. Regime shifts of marine fish community are frequent occurrences accompanying climate regime shifts (Tian et al., 2006, 2008; Litzow and Ciannelli, 2007; Möllmann and Diekmann, 2012), and such abrupt changes can only be explained by non-linear state changes in response to sudden changes in pressures (Petersen et al., 2008; Fu et al., 2015). However, the IFCS-pressure relationships in our study were largely linear (27 of the 51 significant pressure responses), which contribute to low scores in one of the robustness criteria i.e., Criterion 3.2. Such linear relationships may partly be due to the standardization of data as suggested by Otto et al. (2018a). In addition, all IFCSs that had significant responses to at least one pressure were found to have one or more threshold interactions, which was a primary reason for the low scores in the robustness aspect. Threshold interactions are often used to test non-additive interactions between two types of pressures, which are important for assessing population dynamics (Ciannelli et al., 2004). Threshold responses in potential interactions between pressures provide guidance for potential reference points for fisheries management (Fu et al., 2019). From a conservation perspective, a threshold may represent a risk point where the risk of species loss increases sharply (Toms and Villard, 2015). For example, overfishing cod (*Gadus morhua*) may change the dynamics of predation-prey relationships between cod and zooplankton, and thus damage the population dynamics of cod (Casini et al., 2009). Therefore, thresholds may offer critical insight and useful guidelines when developing ecosystem-based conservation objectives (Samhouri et al., 2010). From this point, IFCSs that show threshold interactions in their responses to pressures proved their utility for EBFM.

Although 22 IFCSs were considered from different population perspectives, only five indicators were contained in the final indicator suite which were identified based on the performance of each IFCS and the need to reduce redundancies, which were ubiquitous among the IFCSs derived from the unitary data

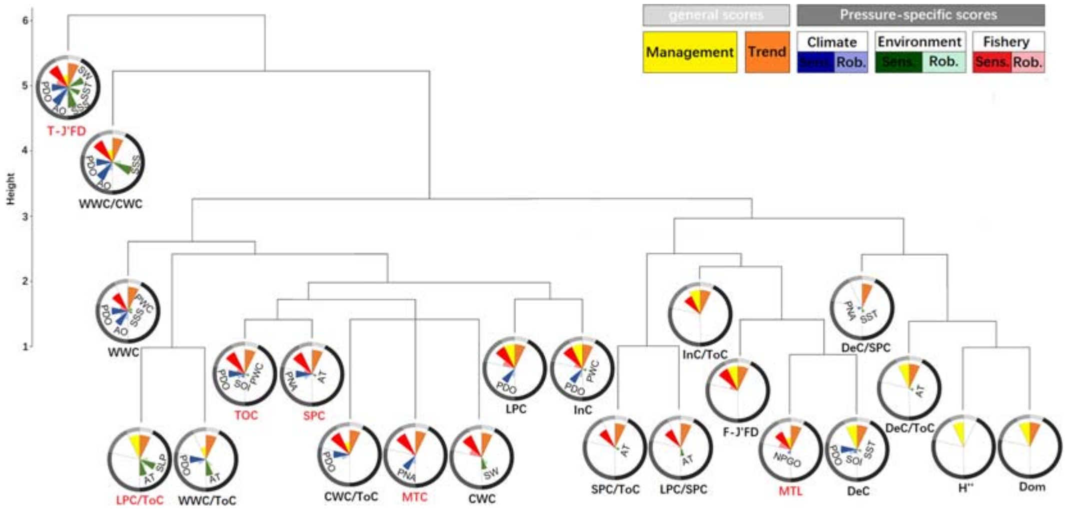

FIGURE 2 | Dendrograms from hierarchical cluster analyses of fishery ecological structure indicators of the YS. For each indicator nightingale rose diagrams are displayed to visualize their performance scores. Sensitivity (opaque color) and robustness (transparent color) scores are shown individually for each significant pressure. The length of the bars represents the percentage of achieved score from the maximum with the boundary line indicating the 100%.

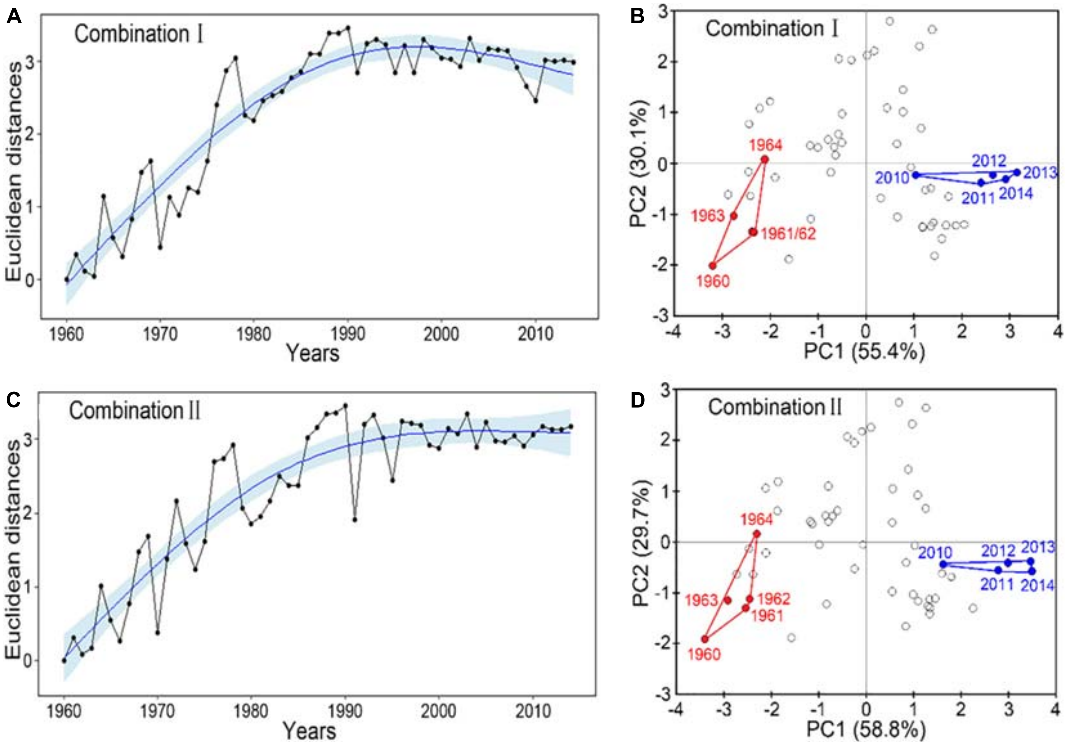

FIGURE 3 | Evaluation of the current fishery community structural state based on the final indicator suite. Panels **(A,C)** show the time trajectories of Euclidean distance in indicator state space from arbitrary reference year 1960, including a fitted trend with 95% confidence interval. The distance was calculated as the square root of the sum of squared distances between each standardized indicator value in a specific year and its reference value. Panels **(B,D)** show the location of the last 5 years in the time series (blue) in the 2-dimensional principal component (1st and 2nd) space in comparison to the state domain of the reference period 1960–1964 (red). Combination I consists of ToC, LPC/ToC, MTL, MTC, T-J′FD; combination II consists of ToC, LPC/ToC, MTL, SPC, T-J′FD.

(i.e., only catch data). The five indicators within Combination I, the thermal-IFCS T-J′FD jointly with the functional-IFCS LPC/ToC and the total-IFCSs MTL, ToC and MTC, would allow the evaluation of management measures related to all significant pressures. In particular, the introduction of comprehensive indices MTL and MTC helped improve

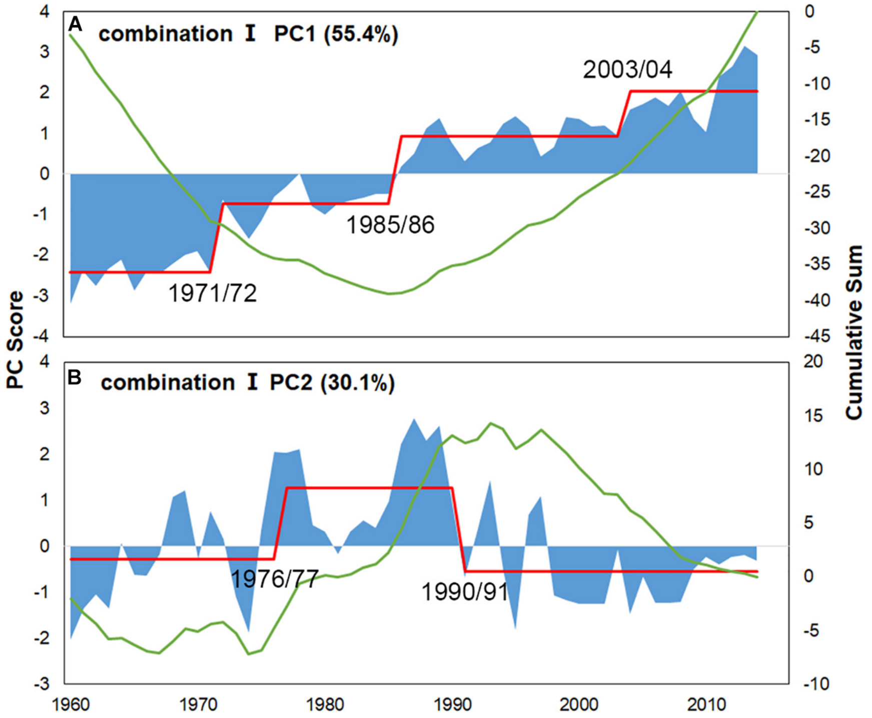

FIGURE 4 | PC scores for the final indicator suite (consist of ToC, LPC/ToC, MTL, MTC, T-J′FD). Blue areas represent scores, green lines denote cumulative sums for scores and red lines represent regime means detected by STARTS.

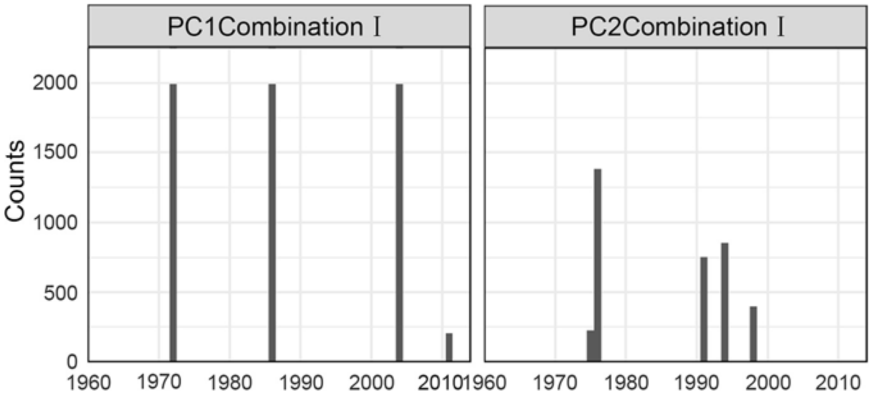

FIGURE 5 | Sensitivity results of STARTS to cut-off length for the final indicator suite (consist of ToC, LPC/ToC, MTL, MTC, T-J′FD). Gray bars represent time nodes with considerable probability of regime shifts.

the data dimension (going beyond catch data only) by incorporating biological characteristics of fish. The MTL and MTC indicators have been widely used in related research to reflect the trophic level and optimal temperature of species, respectively (Tsikliras and Stergiou, 2014; Hermida and Delgado, 2016). In Combination II, SPC was included in the place of MTC as both of them responded to the same pressure PNA with the same performance. Although the results of the two combinations are similar, we focused on Combination I in our result presentation and discussion as the final indicator suite to reflect long-term trajectory of the FCS in the YS as the indicator MTC incorporates biological characteristics of fish while SPC is unitary (based on catch data only). To facilitate the move towards EBFM in the YS by employing and evaluating more comprehensive ecological indicators in terms of their responses to management-related key pressures, we advocate continuous and consistent research surveys to collect pluralistic data, such as length (Large et al., 2013), abundance (Shannon et al., 2009), and age structure (Shin et al., 2010), which are largely lacking in the YS.

In previous studies, LPC (Myers and Worm, 2005) and DeC (Newman et al., 2015, 2016) were found most suitable and subsequently implemented in fisheries management. However,

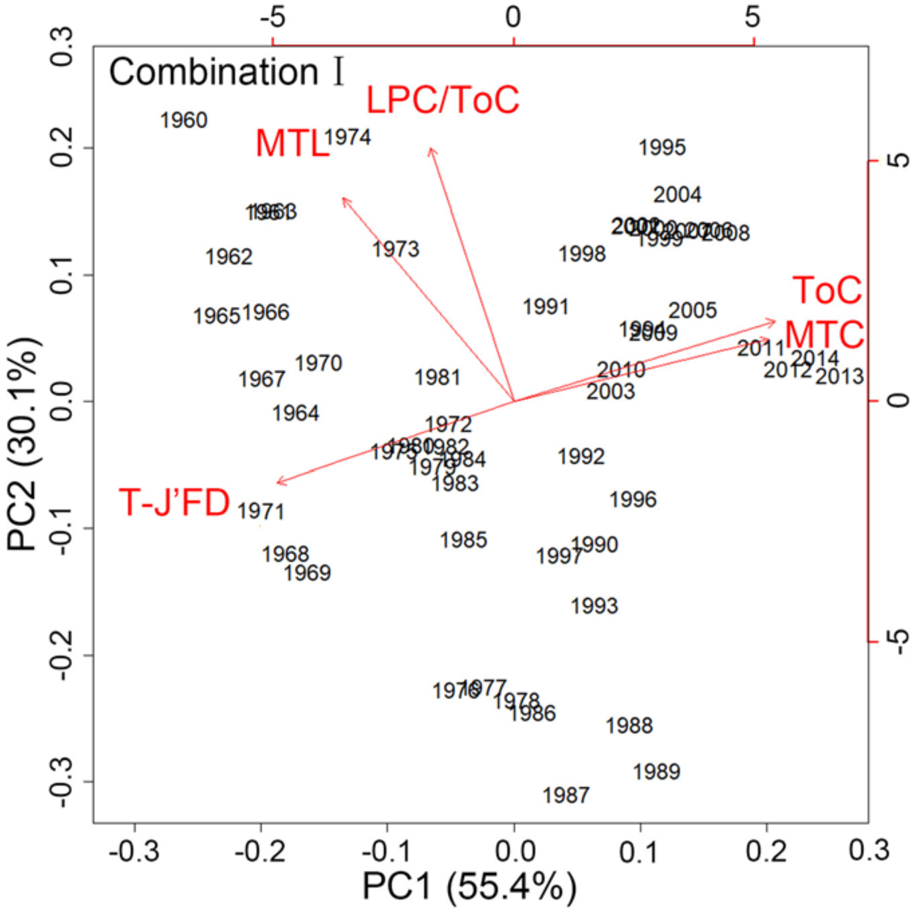

FIGURE 6 | Results of the standardized principal component analysis (PCA) using the final indicator suite (consist of ToC, LPC/ToC, MTL, MTC, T-J′FD). Red lines describing the indicator loadings on the first and second principal components (PC).

these indicators did not perform necessarily best for the study period (1960–2014) in the YS. Specifically, LPC had high redundancy with ToC and T-J′FD within the final indicator suit in terms of its response to fishing efforts and PDO. In addition, the relationship between DeC and its significant pressures was less robust than LPC/ToC. Such results demonstrate that not all indicators are suitable for fisheries management in all ecosystems, even if they are sensitive in their responses to relevant pressures. We would encourage that the evaluation of indicator performances is done on an ecosystem-specific basis because of the unique characterizes of an ecosystem and the diverse fishery exploitation history (Fu et al., 2019).

Furthermore, the final indicator suite would not be applicable for evaluating the impact of four pressures (i.e., WD, NPI, MOI, Nino 4) as all IFCSs were not found significant in their response to them. Therefore, more comprehensive ecological indicators are needed to evaluate the impacts of these four pressures, and the performance of candidate indicators should be validated before they can be used for assessing ecosystem dynamics and guiding fisheries management.

Optimal Indicators for Reflecting Relative Pressures

Among multiple pressures that impact marine ecosystems, climate change plays one of the most important roles (Barange et al., 2014; Kirkman et al., 2015; Kadin et al., 2019). For instance, climate change was found to be important factor in evaluating the responses of small pelagic fish, an important functional group in marine fish communities, to fishing pressure and decadal variations (Tian et al., 2013; Ma et al., 2018). However, climate change was not identified as important in our study. The SPC was shown to have significant response only to one climate index (i.e., PNA) with weak robustness contrary to previous studies. Moreover, some indicators such as MTC commonly used to reflect climate changes (Tsikliras and Stergiou, 2014) showed no sensitivity to any climate indices. As a whole, 13 of the 22 IFCSs tested significant in their response to one or more climate indices (**Table 2**). The response mechanism of fish communities to climate change is complex. Climate change may impact the dynamics of marine ecosystems via complex "Atmosphere-ocean-ecosystem" processes (Ma et al., 2019), causing increases in sea water temperature, which further alters reproduction effectiveness (Palomera et al., 2007), survival (Martins et al., 2012), distributional shifts along latitudinal and depth gradients (Perry et al., 2005; Simpson et al., 2011), and other behavioral variations (Goniea et al., 2006; Audzijonyte et al., 2020). It is generally acknowledged that the responses of marine fish communities to climate change can vary among regions (Barange et al., 2014; Guenette et al., 2014), resulting in regional specificity in the performances of IFCSs. Again, our results advocate that it is imperative to validate indicators in different ecosystems before using them in management decisions, as suggested by Östman et al. (2017).

In general, IFCSs have different sensitivity in their responses to different environment variables, and significant responses to regional environment variables mainly occurred in functional-IFCSs and thermal-IFCSs (**Table 2**). Regional environmental conditions affect FCS directly by limiting the distribution of organisms within their tolerance range or indirectly by altering species interactions (Ochoa-Hueso, 2016). For example, Ocean warming has modified marine biology community structure by increasing biodiversity and miniaturizing the plankton ecosystem, which negatively affects demersal Atlantic cod (Beaugrand et al., 2010). Younger copepodites have strong sensitivity to midwater temperature in spring and summer, while there is a strong positive correlation between females and older copepodites and deep water salinity from spring till autumn (Otto et al., 2020). Moreover, potential threshold interactions among pressures can also alter the shape of the relationships between responses and pressures (Pang et al., 2018). Therefore, considering species compositions in specific food webs is important when employing ecosystem indicators in the evaluation of pressures and management measures.

Marine ecosystems are affected by multiple human pressures (Halpern et al., 2008). Early fisheries studies around the world have provided sufficient proof that several fish groups have declined markedly in population sizes even resulting in local extinction of some vulnerable species, both as target and by-catch species (Stevens et al., 2000). Continuous overfishing also resulted in miniaturization of important commercial species and reconstruction of total fish communities (Conover et al., 2005). Consequently, fishery-based ecosystem indicators are commonly sensitive to fishing efforts (Gascuel et al., 2016). Although we only used engine power data as proxies for the total number of Chinese marine fishing boats in the YS, our results showed that 15 of 22 IFCSs were sensitive to fishing efforts. In particular, the indicators MTL, LPC and T-J′FD were found to have highest sensitivity and robustness compared with other indicators within the final indicator suite. In contrast, the indicators DeC, LPC/ToC, DeC/ToC, DeC/SPC, WWC/ToC showed no significant responses to fishing efforts. The responses of indicators to fishing can be altered by species interactions. For example, small pelagic forage fish often increases apparently accompanying the decline of large predatory fish due to overfishing, which in turn results in the decrease of the biomass of zooplankton and phytoplankton (Frank et al., 2005). Therefore, Using fishing mortality of specific species is optimal when assessing the influences of fishing. In future studies, we intend to introduce more accurate mortality rate of specific species as proxies for anthropogenic pressures.

Long-Term Changes of the FCS in the YS

Combining the scores of IFCSs with the hierarchical group-average cluster analysis, we identified five IFCSs forming a final indicator suite as a proxy for the FCS in the YS. Although only 5 of 22 IFCSs were retained in the final indicator suite and the basic data were simple, our analysis sheds light on the dynamics of the FCS in the YS, proving sufficiency of the five IFCSs in the final indicator suite to represent synthetical information on fish community dynamics. Regime shifts detected in the mid-1970s and the early 1990s (**Figure 4**) coincided with the climate regime shifts based on the integrated trend analysis using many climate indices, while detected shifts in the final indicator suite in the mid-1980s coincided with the regime shifts of regional environment variables (Ma et al., 2019). The shift detected in the early 1970s was not accompanied by any types of pressures, which may result from the fact that no indicators tested in this study were sensitive to the four pressures (i.e., WD, NPI, MOI, Nino 4), indicating that the final indicator suite was unsuitable for evaluating the impacts of these four pressures.

Both state space approaches indicated that the status of the FCS of the YS deviated obviously from the reference year, despite some level of returning to the earlier state after 2000 (**Figure 3A**). There is ample evidence that the dynamics of the FCS in the YS synchronized with other regions in the world based on more relevant indices (Perry et al., 2005; Atkinson et al., 2011; Kirkman et al., 2015). The long-term trajectory of the final indicators suite in the study period derived from Euclidean distances analysis was highly consistent with fishing effort in the YS, suggesting that the final indicators suite could reflect fishing efforts appropriately. The PCA convex hull analysis for the final indicator suite showed that SPC contributed most to the observed changes in the IFCSs state space, reflecting the declines of large predatory fish biomass in global ocean (Ransom and Worm, 2003) and also reflecting the increases of small pelagic fish because of reduced predation mortality by large predatory fish (Cury et al., 2000). Moreover, the fluctuation of small pelagic fishes varied with species in the YS (Ma et al., 2018), implying that the increases of small pelagic fish were not only due to the reduction of predators. Therefore, our results also indirectly indicated that environmental conditions may have changed compared to the reference period as small pelagic fish are highly dependent on external environmental conditions (Merino et al., 2010). Such dynamics are also reflected in the decline of the mean trophic level (Zhang et al., 2007), supported by our result concerning MTL. In combination I, MTC plays the most important role, reflecting that global warming is more friendly to warm-water species than cold-water species (Almodóvar et al., 2012; O'Gorman et al., 2016). Global warming caused water temperature range to gradually fluctuate away from the niche of cold-water species, which is adverse to cold-water species but advantageous to warm-water species. Such results were also reflected in another important indicator, i.e., T-J′FD, contributing to the observed changes. Its long-term changes indicated that the resources distribution of three thermal groups trends more evenness with CWC/ToC gradually declining while WWC/ToC generally increasing within the observation period (**Supplementary Figure 1**). ToC ranked second in its contribution to changes in the IFCS state space, reflecting the rapid increasing of total catch (FAO, 2016).

As the YS ecosystem is continually facing impacts from overfishing and climate change, resulting in serious declines of fishery resources and miniaturization, it is imperative to move towards EBFM. The great change of the FCS in the YS has been proven by our final indicator suite, which can subsequently be used as an effective tool in ecosystem monitoring to reach management targets (Levin et al., 2009). In particular, the increase of SPC has been identified as one of the most outstanding changes of the FCS in the YS. Therefore, we advocate that the management objective of increasing size of fish should be include in the EBFM in the YS, which can potentially be achieved by enlarging mesh size.

CONCLUSION

In this study, we use a quantitative and flexible framework to verify the performance of IFCSs that represent various aspects of the FCS in the YS. As different regions have different management objectives, we used nightingale rose diagrams to exhibit the performance of IFCSs in relation to pressure management visually. Five indicators, ToC, MTL, LPC/ToC, MTC (or alternatively SPC) and T-J′FD, were determined to form the final indicator suite as a proxy for the FCS in the YS. The five indicators are suitable to detect different pressures with LPC/ToC to SLP and AT; ToC to PWC and SOI; MTC to NPGO; MTC (and SPC) to PNA; T-J′FD to SW, SST, AO and SSS, respectively, while PDO can be detected by both ToC and T-J′FD. Fishing effort can be detected by five indicators of the final indicator suite except LPC/ToC. Based on the final indicator suite, we found the FCS in the YS is deviate distinctly from an earlier reference period, suggesting the impact of over-fishing. The indicator-testing framework has been demonstrated to be applicable to the FCS in the YS. Future fishery and ecosystem management should use the indicator-testing framework for selecting suites of complementary indicators under given management objectives.

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 authors.

AUTHOR CONTRIBUTIONS

YL performed the data analyses and wrote the manuscript. CF participated in data analysis. SM conceived the idea for the study. YT and YL helped design the study, and critically revised the manuscript. JL, PS, and ZY edited the manuscript. All authors listed have made a direct and substantial contribution to this work, gave final approval for publication, and agreed to be held accountable for the work performed therein.

FUNDING

This study was supported by the National Key R&D Program of China (No. 2018YFD0900902), Shandong Key R&D Program (No. 2019GHY112014), and the National Natural Science Foundation of China (NSFC) (Grant Nos. 41930534, 41861134037, and 41876177).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.646733/full#supplementary-material

REFERENCES

Almodóvar, A., Nicola, G. G., Ayllón, D., and Elvira, B. (2012). Global warming threatens the persistence of Mediterranean brown trout. *Glob. Chang. Biol.* 18, 1549–1560. doi: 10.1111/j.1365-2486.2011.02608.x

Atkinson, L. J., Leslie, R. W., Field, J. G., and Jarre, A. (2011). Changes in demersal fish assemblages on the west coast of South Africa, 1986–2009. *Afr. J. Mar. Sci.* 33, 157–170. doi: 10.2989/1814232X.2011.572378

Audzijonyte, A., Richards, S. A., Stuart-Smith, R. D., Pecl, G., Edgar, G. J., Barrett, N. S., et al. (2020). Fish body sizes change with temperature but not all species shrink with warming. *Nat. Ecol. Evol.* 4, 809–814. doi: 10.1038/s41559-020-1171-0

Barange, M., Merino, G., Blanchard, J. L., Scholtens, J., Harle, J., Allison, E. H., et al. (2014). Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nat. Clim. Chang.* 4, 211–216. doi: 10.1038/nclimate2119

Beamish, R. J., Noakes, D. J., McFarlane, G. A., Klyashtorin, L., Ivanov, V. V., and Kurashov, V. (1999). The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 56, 516–526. doi: 10.1139/f98-200

Beaugrand, G., Edwards, M., and Legendre, L. (2010). Marine biodiversity, ecosystem functioning and the carbon cycles. *Proc. Natl. Acad. Sci. U.S.A.* 107, 10120–10124. doi: 10.1073/pnas.0913855107

Bhathal, B., and Pauly, D. (2008). 'Fishing down marine food webs' and spatial expansion of coastal fisheries in India, 1950–2000. *Fish. Res.* 91, 26–34. doi: 10.1016/j.fishres.2007.10.022

Bjørnstad, O. N., and Grenfell, B. T. (2001). Noisy clockwork: time series analysis of population fluctuations in animals. *Science* 293, 638–643. doi: 10.1126/science.1062226

Boeing, W. J., and Duffy-Anderson, J. T. (2008). Ichthyoplankton dynamics and biodiversity in the Gulf of Alaska: responses to environmental change. *Ecol. Indic.* 8, 292–302. doi: 10.1016/j.ecolind.2007.03.002

Burgess, M. G., Giacomini, H. C., Szuwalski, C. S., Costello, C., and Gaines, S. D. (2017). Describing ecosystem contexts with singlr-species models: a theoretical synthesis for fisheries. *Fish Fish.* 18, 264–284. doi: 10.1111/faf.12179

Buuren, S. V., and Groothuis-Oudshoorn, K. (2011). Mice: multivariate imputation by chained equations in R. *J. Stat. Softw.* 45, 1–68.

Cai, R., Tan, H., and Qi, Q. (2016). Impacts of and adaptation to inter-decadal marine climate change in coastal China seas. *Int. J. Climatol.* 36, 3770–3780. doi: 10.1002/joc.4591

Casini, M., Hjelm, J., Molinero, J. C., Lövgren, J., Cardinale, M., Bartolino, V., et al. (2009). Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* 106, 197–202. doi: 10.1073/pnas.0806649105

Ceballos, L. I., Lorenzo, E. D., Hoyos, C. D., Schneider, N., and Taguchi, B. (2009). North Pacific gyre oscillation synchronizes climate fluctuations in the eastern and western boundary systems*. *J. Clim.* 22, 5163–5174. doi: 10.1175/2009JCLI2848.1

Chen, C. (2004). Ammodytes personatus resources in the Yellow Sea and its sustainable utilization. *J. Fish. China* 28, 603–607. (in Chinese),

Ciannelli, L., Chan, K. S., Bailey, K. M., and Stenseth, N. C. (2004). Nonadditive effects of the environment on the survival of a large marine fish population. *Ecology* 85, 3418–3427. doi: 10.1890/03-0755

Conover, D. O., Arnott, S. A., Walsh, M. R., and Munch, S. B. (2005). Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). *Can. J. Fish. Aquat. Sci.* 62, 730–737. doi: 10.1139/F05-069

Cui, M., and Zorita, E. (1998). Analysis of the sea-level variability along the Chinese coast and estimation of the impact of a CO2-perturbed atmospheric circulation. *Tellus A* 50, 333–347. doi: 10.3402/tellusa.v50i3.14530

Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Qui?ones, R. A., Shannon, L. J., et al. (2000). Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES J. Mar. Sci.* 57, 603–618. doi: 10.1006/jmsc.2000.0712

de Berg, M., Cheong, O., van Kreveld, M., and Overmars, M. (2008). *Computational Geometry- Algorithms and Applications*. Berlin: Springer.

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., et al. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344, 296–299. doi: 10.1126/science.1248484

Fabry, V. J., Seibel, B. A., Feely, R. A., and Orr, J. C. (2008). Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J. Mar. Sci.* 65, 414–432. doi: 10.1093/icesjms/fsn048

FAO (2016). *The State of World Fisheries and Aquaculture 2016. Contributing to Food Security and Nutrition for all*. Rome: FAO.

Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308, 1621–1623. doi: 10.1126/science.1113075

Fu, C., Large, S., Knight, B., Richardson, A. J., Bundy, A., Reygondeau, G., et al. (2015). Relationships among fisheries exploitation, environmental conditions, and ecological indicators across a series of marine ecosystems. *J. Mar. Syst.* 148, 101–111. doi: 10.1016/j.jmarsys.2015.01.004

Fu, C., Xu, Y., Bundy, A., Grüss, A., Coll, M., Heymans, J. J., et al. (2019). Making ecological indicators management ready: assessing the specificity, sensitivity, and threshold response of ecological indicators. *Ecol. Indic.* 105, 16–28. doi: 10.1016/j.ecolind.2019.05.055

Gamtto, S., and Furtado, R. (2009). Feeding diversity in macroinvertebrate communities: a contribution to estimate the ecological status in shallow waters. *Ecol. Indic.* 9, 1009–1019. doi: 10.1016/j.ecolind.2008.11.012

Garcia, S. M., and Cochrane, K. L. (2005). Ecosystem approach to fisheries: a review of implementation guidelines. *ICES J. Mar. Sci.* 62, 311–318. doi: 10.1016/j.icesjms.2004.12.003

Gascuel, D., Coll, M., Fox, C., Guénette, S., Guitton, J., Kenny, A., et al. (2016). Fishing impact and environmental status in European seas: a diagnosis from stock assessments and ecosystem indicators. *Fish Fish.* 17, 31–55. doi: 10.1111/faf.12090

Gissi, E., Manea, E., Mazaris, A. D., Fraschetti, S., Almpanidou, V., Bevilacqua, S., et al. (2021). A review of the combined effects of climate change and other local human stressors on the marine environment. *Sci. Total Environ.* 755:142564. doi: 10.1016/j.scitotenv.2020.142564

Goniea, T. M., Keefer, M. L., Bjormn, T. C., Peery, C. A., Bennett, D. H., and Stuehrenberg, L. C. (2006). Behavioral thermoregulation and slowed migration by adult fall chinook salmon in response to high Columbia River water temperatures. *Trans. Am. Fish. Soc.* 135, 408–419. doi: 10.1577/T04-113.1

Guenette, S., Araujo, J. N., and Bundy, A. (2014). Exploring the potential effects of climate change on the Western Scotian Shelf ecosystem, Canada. *J. Mar. Syst.* 134, 89–100. doi: 10.1016/j.jmarsys.2014.03.001

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'agrosa, C., et al. (2008). A global map of human impact on marine ecosystems. *Science* 319, 948–952. doi: 10.1126/science.1149345

Hastie, T. J., and Tibshirani, R. J. (1990). *Generalized Additive Models*. Boca Raton, FL: Chapman Hall/CRC, doi: 10.1002/sim.4780110717

Hermida, M., and Delgado, J. (2016). High trophic level and low diversity: would madeira benefit from fishing down? *Mar. Policy* 73, 130–137. doi: 10.1016/j.marpol.2016.07.013

Hoegh-Guldberg, O., and Bruno, J. F. (2010). The impact of climate change on the World's marine ecosystems. *Science* 328, 1523–1528. doi: 10.1126/science.1189930

Jennings, S. (2005). Indicator to support an ecosystem approach to fisheries. *Fish Fish.* 6, 212–232. doi: 10.1111/j.1467-2979.2005.00189.x

Jennings, S., and Kaiser, M. J. (1998). The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* 34, 201–352. doi: 10.1016/S0065-2881(08)60212-6

Jin, X. S. (2003). Fishery biodiversity and community structure in the Yellow and Bohai Seas. *Am. Fish. Soc. Symp.* 38, 643–650.

Jørgensen, S. E., Nielsen, S. N., and Fath, B. D. (2016). Recent progress in systems ecology. *Ecol. Model.* 319, 112–118. doi: 10.1016/j.ecolmodel.2015.08.007

Kadin, M., Blenckner, T., Casini, M., Gårdmark, A., Torres, M. A., and Otto, S. A. (2019). Trophic interactions, management trade-offs and climate change: the need for adaptive thresholds to operationalize ecosystem indicators. *Front. Mar. Sci.* 6:249. doi: 10.3389/fmars.2019.00249

Kidwell, A., Han, L., Jo, Y. H., and Yan, X. H. (2017). Decadal Western Pacific warm pool variability: a centroid and heat content study. *Sci. Rep.U. K.* 7:13141. doi: 10.1038/s41598-017-13351-x

Kirkman, S. P., Yemane, D., Atkinson, L. J., Kathena, J., Nsiangango, S., Singh, L., et al. (2015). Regime shifts in demersal assemblages of the Benguela current large marine ecosystem: a comparative assessment. *Fish. Oceanogr.* 24, 15–30. doi: 10.1111/fog.12053

Large, S. I., Fay, G., Friedland, K. D., and Link, J. S. (2013). Defining trends and thresholds in responses of ecological indicators to fishing and environmental pressures. *ICES J. Mar. Sci.* 70, 755–767. doi: 10.1093/icesjms/fst067

Large, S. I., Fay, G., Friedland, K. D., and Link, J. S. (2015). Critical points in ecosystem responses to fishing and environmental pressures. *Mar. Ecol. Prog. Ser.* 521, 1–17. doi: 10.3354/meps11165

Legendre, P., and Legendre, L. (1998). *Numerical Ecology*, 2nd Edn. Amsterdam: Elsevier Science B.V.

Levin, P. S., Fogarty, M. J., Murawski, S. A., and Fluharty, D. (2009). Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. *PLoS Biol.* 7:e14. doi: 10.1371/journal.pbio.1000014

Liang, C., Xian, W., and Pauly, D. (2018). Impacts of ocean warming on China's fisheries catches: an application of "mean temperature of the catcH′′. *Concept. Front. Mar. Sci.* 5:26. doi: 10.3389/fmars.2018.00026

Liang, C., Xian, W., and Pauly, D. (2020). Assessments of 15 Exploited Fish Stocks in Chinese, South Korean and Japanese Waters Using the CMSY and BSM Methods. *Front. Mar. Sci.* 7:623. doi: 10.3389/fmars.2020.00623

Lin, Q., Jin, X., and Zhang, B. (2013). Trophic interactions, ecosystem structure and function in the southern Yellow Sea. *Chin. J. Oceanol. Limnol.* 31, 46–58. doi: 10.1007/s00343-013-2013-6

Link, J. S. (2005). Translating ecosystem indicators into decision criteria. *ICES J. Mar. Sci.* 62, 569–576. doi: 10.1016/j.icesjms.2004.12.015

Link, J. S., Brodziak, J. K. T., Edwards, S. F., Overholtz, W. J., Mountain, D., Jossi, J. W., et al. (2002). Marine ecosystem assessment in a fisheries management context. *Can. J. Fish. Aquat. Sci.* 59, 1429–1440. doi: 10.1139/f02-115

Link, J. S., Stockhausen, W. T., Skaret, G., Overholtz, W., Megrey, B. A., Gjøster, H., et al. (2009). A comparison of biological trends from four marine ecosystems: Synchronies, differences, and commonalities. *Prog. Oceanogr.* 81, 29–46. doi: 10.1016/j.pocean.2009.04.004

Litzow, M. A., and Ciannelli, L. (2007). Oscillating trophic control induces community reorganization in a marine ecosystem. *Ecol. Lett.* 10, 1124–1134. doi: 10.1111/j.1461-0248.2007.01111.x

Litzow, M. A., Mueter, F. J., and Hobday, A. J. (2014). Reassessing regime shifts in the North Pacific: incremental climate change and commercial fishing are necessary for explaining decadal-scale biological variability. *Glob. Chang. Biol.* 20, 38–50. doi: 10.1111/gcb.12373

Ma, S., Cheng, J., Li, J., Liu, Y., Wan, R., and Tian, Y. (2018). Interannual to decadal variability in the catches of small pelagic fishes from China Seas and its responses to climatic regime shifts. *Deep Sea Res. Part II* 159, 112–129. doi: 10.1016/j.dsr2.2018.10.005

Ma, S., Liu, Y., Li, J., Fu, C., Ye, Z., Sun, P., et al. (2019). Climate-induced long-term variations in ecosystem structure and atmosphere-ocean-ecosystem processes in the Yellow Sea and East China Sea. *Prog. Oceanogr.* 175, 183–197. doi: 10.1016/j.pocean.2019.04.008

Martins, E. G., Hinch, S. G., Patterson, D. A., Hague, M. J., Cooke, S. J., Miller, K. M., et al. (2012). High river temperature reduces survival of sockeye salmon (*Oncorhynchus nerka*) approaching spawning grounds and exacerbates female mortality. *Can. J. Fish. Aquat. Sci.* 69, 330–342. doi: 10.1139/f2011-154

Merino, G., Barange, M., and Mullon, C. (2010). Climate variability and change scenarios for a marine commodity: modelling small pelagic fish, fisheries and fishmeal in a globalized market. *J. Mar. Syst.* 81, 196–205. doi: 10.1016/j.jmarsys.2009.12.010

Möllmann, C., and Diekmann, R. (2012). Marine ecosystem regime shifts induced by climate and overfishing: a review for the Northern Hemisphere. *Adv. Ecol. Res.* 47, 303–347. doi: 10.1016/B978-0-12-398315-2.00004-1

Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. (2009). Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. *Glob. Chang. Biol.* 15, 1377–1393. doi: 10.1111/j.1365-2486.2008.01814.x

Mu, Y., Yu, H., Chen, J., and Zhu, Y. (2007). A qualitative appraisal of China's efforts in fishing capacity management. *J. Ocean Univ. China* 6, 1–11. doi: 10.1007/s11802-007-0001-1

Munyandorero, J. (2012). A recruitment-mortality model in the precautionary management toolkit of African tropical inland, single-species fisheries. *Fish. Res.* 127, 26–33. doi: 10.1016/j.fishres.2012.04.017

Myers, R. A., and Worm, B. (2005). Extinction, survival or recovery of large predatory fishes. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 360, 13–20. doi: 10.1098/rstb.2004.1573

Newman, S. J., Wakefield, C. B., Williams, A. J., O'Malley, J. M., Nicol, S. J., DeMartini, E. E., et al. (2015). International workshop on methodological evolution to improve estimates of life history parameters and fisheries management of data-poor deep-water snappers and groupers. *Mar. Policy* 60, 182–185. doi: 10.1016/j.marpol.2015.06.020

Newman, S. J., Williams, A. J., Wakefield, C. B., Nicol, S. J., Taylor, B. M., and O'Malley, J. M. (2016). Review of the life history characteristics, ecology and fisheries for deep-water tropical demersal fish in the Indo-Pacific region. *Rev. Fish Biol. Fish.* 26, 537–562. doi: 10.1007/s11160-016-9442-1

Nurani, T. W., Wahyuningrum, P. I., Wisudo, S. H., Arhatin, R. E., and Komarudin, D. (2015). Catch of tuna fish on trolling fishing in Indian Ocean Waters, Southern Coast of East Java related to sea surface temperature variability. *Malays. Appl. Biol.* 44, 25–28.

Ochoa-Hueso, R. (2016). Nonlinear disruption of ecological interactions in response to nitrogen deposition. *Ecology* 87, 2802–2814. doi: 10.1002/ecy.1521

O'Gorman, E. J., Ólafsson, ÓP., Demars, B. O. L., Friberg, N., Guðbergsson, G., Hannesdóttir, E. R., et al. (2016). Temperature effects on fish production across a natural thermal gradient. *Glob. Chang. Biol.* 22, 3206–3220. doi: 10.1111/gcb.13233

Östman, Ö, Lingman, A., Bergström, L., and Olsson, J. (2017). Temporal development and spatial scale of coastal fish indicators in reference ecosystems: hydroclimate and anthropogenic drivers. *J. Appl. Ecol.* 54, 557–566. doi: 10.1111/1365-2664.12719

Ottersen, G., Olsen, E., van der Meeren, G. I., Dommasnes, A., and Loeng, H. (2011). The Norwegian plan for integrated ecosystem-based management of the marine environment in the Norwegian Sea. *Mar. Policy* 35, 389–398. doi: 10.1016/j.marpol.2010.10.017

Otto, S. A., Kadin, M., Casini, M., Torres, M. A., and Blenckner, T. (2018a). A quantitative framework for selecting and validating food web indicators. *Ecol. Indic.* 84, 619–631. doi: 10.1016/j.ecolind.2017.05.045

Otto, S. A., Niiranen, S., Blenckner, T., Tomczak, M. T., Müller-Karulis, B., Rubene, G., et al. (2020). Life cycle dynamics of a key marine species under multiple stressors. *Front. Mar. Sci.* 7:296. doi: 10.3389/fmars.2020.00296

Otto, S. A., Plonus, R., Funk, S., and Keth, A. (2018b). *INDperform: Evaluation of Indicator Performances for Assessing Ecosystem States. R Package Version 0.1.1.*

Palomera, I., Olivar, M. P., Salat, J., Sabatés, A., Coll, M., and García, A. (2007). Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Prog. Oceanogr.* 74, 377–396. doi: 10.1016/j.pocean.2007.04.012

Pang, Y., Tian, Y., Fu, C., Wang, B., Li, J., Ren, Y., et al. (2018). Variability of coastal cephalopods in overexploited China Seas under climate change with implications on fisheries management. *Fish. Res.* 208, 22–33. doi: 10.1016/j.fishres.2018.07.004

Park, K. A., Lee, E. Y., Chang, E., and Hong, S. (2015). Spatial and temporal variability of sea surface temperature and warming trends in the Yellow Sea. *J. Marine Syst.* 143, 24–38. doi: 10.1016/j.jmarsys.2014.10.013

Pauly, D., and Zeller, D. (2016). *Catch Reconstruction: Concepts, Methods, and Data Sources: Sea Around Us*. Vancouver: University of British Columbia.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science* 308, 1912–1915. doi: 10.1126/science.1111322

Petersen, J. K., Hansen, J. W., Laursen, M. B., Clausen, P., Carstensen, J., and Conley, D. J. (2008). Regime shift in a coastal marine ecosystem. *Ecol. Appl.* 18, 497–510. doi: 10.1890/07-0752.1

Pikitch, E. K., Santora, C., Babcock, E. A., Bonfil, R., Conover, D. O., Dayton, P., et al. (2004). Ecosystem-based fishery management. *Science* 305, 346–347. doi: 10.1126/science.109822210.1126/science.1098222

R Core Team (2019). R: A Language and Environment for Statistical Computing. Vienna, Australia.

Ransom, M., and Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283. doi: 10.1038/nature01610

Rochet, M.-J., and Trenkel, V. (2009). Why and how could indicators be used in an ecosystem approach to fisheries management? *Fish Fish. Ser.* 31, 209–226.

Rodionov, S., and Overland, J. E. (2005). Application of a sequential regime shift detection method to the Bering Sea ecosystem. *ICES J. Mar. Sci.* 62, 328–332.

Rodionov, S. N. (2004). A sequential algorithm for testing climate regime shifts. *Geophys. Res. Lett.* 31, 111–142. doi: 10.1029/2004GL019448

Rossberg, A. G., Uusitalo, L., Berg, T., Zaiko, A., Chenuil, A., Uyarra, M. C., et al. (2017). Quantitative criteria for choosing targets and indicators for sustainable use of ecosystems. *Ecol. Indic.* 72, 215–224. doi: 10.1016/j.ecolind.2016.08.005

Sainsbury, K. J., Punt, A. E., and Smith, A. D. M. (2000). Design of operational management strategies for achieving fishery ecosystem objectives. *ICES J. Mar. Sci.* 57, 731–741. doi: 10.1006/jmsc.2000.0737

Samhouri, J. F., Levin, P. S., and Ainsworth, C. H. (2010). Identifying thresholds for ecosystem-based management. *PLoS One* 5:e8907. doi: 10.1371/journal.pone.0008907

Shan, X. J., Jin, X. S., Zhou, Z. P., and Dai, F. Q. (2012). Stock dynamics of Cleisthenes herzensteini in the central and southern Yellow Sea. *Acta Ecol. Sin.* 32, 244–252. doi: 10.1016/j.chnaes.2012.07.010

Shannon, L. J., Coll, M., and Neira, S. (2009). Exploring the dynamics of ecological indicators using food web models fitted to time series of abundance and catch data. *Ecol. Indic.* 9, 1078–1095. doi: 10.1016/j.ecolind.2008.12.007

Sherman, K., Sissenwine, M., Christensen, V., Duda, A., Hempel, G., Ibe, C., et al. (2005). A global movement toward an ecosystem approach to management of marine resources. *Mar. Ecol. Prog. Ser.* 300, 241–296. doi: 10.3354/meps300275

Shin, Y. J., Bundy, A., Shannon, L. J., Simier, M., Coll, M., Fulton, E. A., et al. (2010). Can simple be useful and reliable? Using ecological indicators to represent and compare the states of marine ecosystems. *ICES J. Mar. Sci.* 67, 717–731. doi: 10.1093/icesjms/fsp287

Shin, Y. J., Houle, J. E., Akoglu, E., Blanchard, J. L., Bundy, A., Coll, M., et al. (2018). The specificity of marine ecological indicators to fishing in the face of environmental change: a multi-model evaluation. *Ecol. Indic.* 89, 317–326. doi: 10.1016/j.ecolind.2018.01.010

Simpson, S. D., Jennings, S., Johnson, M. P., Blanchard, J. L., Schön, P. J., Sims, D. W., et al. (2011). Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Curr. Biol.* 21, 1565–1570. doi: 10.1016/j.cub.2011.08.016

Solanki, H. U., Bhatpuria, D., and Chauhan, P. (2015). Signature analysis of satellite derived SSHa, SST and chlorophyll concentration and their linkage with marine fishery resources. *J. Mar. Syst.* 150, 12–21. doi: 10.1016/j.jmarsys.2015.05.004

Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES J. Mar. Sci.* 57, 476–494. doi: 10.1006/jmsc.2000.0724

Swenson, N. (2014). *Functional and Phylogenetic Ecology in R*. New York, NY: Springer-Verlag.

Tang, Q. (2009). "Changing states of the yellow sea large marine ecosystem: anthropogenic forcing and climate impacts," in *Sustaining the Worlds Large Marine Ecosystems*, eds K. Sherman, M. C. Aquarone, and S. Adams (Gland: IUCN).

Tang, Q. S., Ying, Y. P., and Wu, Q. (2016). The biomass yields and management challenges for the Yellow sea large marine ecosystem. *Environ. Dev.* 17, 175–181. doi: 10.1016/j.envdev.2015.06.012

Tian, Y., Akamine, T., and Suda, M. (2004). Modeling the influence of oceanic-climatic changes on the dynamics of Pacific saury in the northwestern Pacific using a life cycle model. *Fish. Oceanogr.* 13, 125–137. doi: 10.1111/j.1365-2419.2004.00314.x

Tian, Y., Kidokoro, H., and Fujino, T. (2011). Interannual-decadal variability of demersal fish assemblages in the Tsushima Warm Current region of the Japan Sea: Impacts of climate regime shifts and trawl fisheries with implications for ecosystem-based management. *Fish. Res.* 112, 140–153. doi: 10.1016/j.fishres.2011.01.034

Tian, Y., Kidokoro, H., and Watanabe, T. (2006). Long-term changes in the fish community structure from the Tsushima warm current region of the Japan/East Sea with an emphasis on the impacts of fishing and climate regime shift over the last four decades. *Prog. Oceanogr.* 68, 217–237. doi: 10.1016/j.pocean.2006.02.009

Tian, Y., Kidokoro, H., Watanabe, T., and Iguchi, N. (2008). The late 1980s regime shift in the ecosystem of Tsushima warm current in the Japan/East Sea: evidence from historical data and possible mechanisms. *Prog. Oceanogr.* 77, 127–145. doi: 10.1016/j.pocean.2008.03.007

Tian, Y., Uchikawa, K., Ueda, Y., and Cheng, J. (2013). Comparison of fluctuations in fish communities and trophic structures of ecosystems from three currents around Japan: synchronies and differences. *ICES J. Mar. Sci.* 71, 19–34. doi: 10.1093/icesjms/fst169

Toms, J. D., and Villard, M. A. (2015). Threshold detection: matching statistical methodology to ecological questions and conservation planning objectives. *Avian Conserv. Ecol.* 10:2. doi: 10.5751/ACE-00715-100102

Trenkel, V. M., and Rochet, M. J. (2009). Intersection-union tests for characterising recent changes in smoothed indicator time series. *Ecol. Indic.* 9, 732–739. doi: 10.1016/j.ecolind.2008.09.005

Tsikliras, A. C., Dinouli, A., Tsiros, V. Z., and Tsalkou, E. (2015). The Mediterranean and Black Sea fisheries at risk from overexploitation. *PLoS One* 10:e0121188. doi: 10.1371/journal.pone.0121188

Tsikliras, A. C., and Stergiou, K. I. (2014). Mean temperature of the catch increases quickly in the Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 515, 281–284. doi: 10.3354/meps11005

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science* 348, 571–573. doi: 10.1126/science.aaa4984

Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., et al. (2010). Global threats to human water security and river biodiversity. *Nature* 467, 555–561. doi: 10.1038/nature09440

Wei, H., Yuan, C., Lu, Y., Zhang, Z., and Luo, X. (2013). Forcing mechanisms of heat content variations in the Yellow Sea. *J. Geophys. Res. Oceans* 118, 4504–4513. doi: 10.1002/jgrc.20326

Weiskopf, S. R., Rubenstein, M. A., Crozier, L. G., Gaichas, S., Griffis, R., Halofsky, J. E., et al. (2020). Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. *Sci. Total Environ.* 733, 137782. doi: 10.1016/j.scitotenv.2020.137782

Wilhm, J. L. (1968). Use of biomass units in Shannon's formula. *Ecology* 49, 153–156. doi: 10.2307/1933573

Xu, B. D., and Jin, X. S. (2005). Variations in fish community structure during winter in the southern Yellow Sea over the period 1985–2002. *Fish. Res.* 71, 79–91. doi: 10.1016/j.fishres.2004.07.011

Zhang, B., Tang, Q., and Xu, J. (2007). Decadal-scale variations of trophic levels at high trophic levels in the Yellow Sea and the Bohai Sea ecosystem. *J. Mar. Syst.* 67, 304–311. doi: 10.1016/j.jmarsys.2006.04.015

Zhang, K., Guo, J. Z., Xu, Y. W., Jiang, Y., Fan, J. T., Xu, S. N., et al. (2020). Long-term variations in fish community structure under multiple stressors in a semi-closed marine ecosystem in the South China Sea. *Sci. Total Environ.* 745:140892. doi: 10.1016/j.scitotenv.2020.140892

Zhao, X., Cui, L., Liu, X., Situ, J., and Chen, E. (2015). *Chinese Fishery Statistics*. Beijing: China Agriculture Press.

Zheng, C., Pan, J., Tan, Y., Gao, Z., Rui, Z., and Chen, C. (2015). The seasonal variations in the significant wave height and sea surface wind speed of the China's seas. *Acta. Oceanol. Sin.* 34, 58–64. doi: 10.1007/s13131-015-0738-0

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.

frontiers
in Marine Science

REVIEW
published: 07 July 2021
doi: 10.3389/fmars.2021.567266

Toward Improved Model Capacities for Assessment of Climate Impacts on Coastal Bentho-Pelagic Food Webs and Ecosystem Services

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Edited by:
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Dalhousie University, Canada
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Specialty section:
This article was submitted to Marine Fisheries, Aquaculture and Living Resources, a section of the journal Frontiers in Marine Science

Received: *29 May 2020*
Accepted: *07 June 2021*
Published: *07 July 2021*

Citation:
Horn S, Meunier CL, Fofonova V, Wiltshire KH, Sarker S, Pogoda B and Asmus H (2021) Toward Improved Model Capacities for Assessment of Climate Impacts on Coastal Bentho-Pelagic Food Webs and Ecosystem Services. Front. Mar. Sci. 8:567266. doi: 10.3389/fmars.2021.567266

Global climate change is a key driver of change in coastal waters with clear effects on biological communities and marine ecosystems. Human activities in combination with climate change exert a tremendous pressure on marine ecosystems and threaten their integrity, structure, and functioning. The protection of these ecosystems is a major target of the 14th United Nations sustainable development goal "Conserve and sustainably use the oceans, seas and marine resources for sustainable development." However, due to the complexity of processes and interactions of stressors, the status assessment of ecosystems remains a challenge. Holistic food web models, including biological and environmental data, could provide a suitable basis to assess ecosystem health. Here, we review climate change impacts on different trophic levels of coastal ecosystems ranging from plankton to ecologically and economically important fish and shellfish species. Furthermore, we show different food web model approaches, their advantages and limitations. To effectively manage coastal ecosystems, we need both a detailed knowledge base of each trophic level and a holistic modeling approach for assessment and prediction of future scenarios on food web-scales. A new model approach with a seamless coupling of physical ocean models and food web models could provide a future tool for guiding ecosystem-based management.

Keywords: global warming, ecosystem effects, species interactions, marine, food webs, ecosystem models

INTRODUCTION

The complexity of the direct and indirect effects of global climate change on marine ecosystems and the immense diversity of scales call for novel multifaceted views and the combination of different types of analyses via models. Without this we will not be able to make management decisions and protect ecosystem services in a meaningful and sustainable manner.

Global climate change is a key driver of change in coastal marine ecosystems (Gissi et al., 2020). It is caused by increasing anthropogenic greenhouse gas emissions and is responsible for the rapid alteration of abiotic environmental factors in marine systems, such as water temperature, pH, hydrography, and salinity. These changes manifest with clear effects on biological communities and the structure and function of marine ecosystems (IPCC, 2014). Temperature has been suggested to be one of the most important physical drivers of aquatic environments and biological community structure (Richardson, 2008; IPCC, 2014). Rising temperatures are globally significant and result in reduced sea-ice in the Arctic and Antarctic. Glacier runoff and precipitation patterns have changed considerably with resultant redistribution of annual river discharge rates. Such shifts result in more evident changes in pelagic salinity and particulate matter loadings in coastal areas (IPCC, 2014). Climate change also alters ocean evaporation and current flows, which are likely to result in changes in the ocean circulation (Toggweiler and Russell, 2008; Greene et al., 2013; IPCC, 2014) with as yet unquantifiable and largely unknown effects for marine life and biodiversity.

Ocean waters take up CO_2 from the atmosphere (Sabine et al., 2004). Since the beginning of the industrial era, ocean waters have absorbed about 30% of the atmospheric CO_2 (IPCC, 2014). The resulting acidification alters the physical environment, the carbon cycle and it impacts marine communities, for instance by affecting larval development and calcification processes of ecologically and economically important shellfish species (Waldbusser and Salisbury, 2014; Wallace et al., 2014) or calcifying plankton (Riebesell, 2004). Also, the increasing trend of extreme weather events associated with climate change (IPCC, 2014) affects marine communities. Extreme hot summers, more frequently occurring hypoxia events and harmful algal blooms can lead to a higher mortality rate in fish stocks and shellfish populations (Rijnsdorp et al., 2009; Wendling and Wegner, 2013).

In addition to the effects of global climate change, marine ecosystems are also affected by local anthropogenic pressures, such as eutrophication (e.g., van Beusekom, 2005), fishing (e.g., Lindeboom and De Groot, 1998) or seabed degradation (e.g., Airoldi et al., 2008). The exploitation and the destruction of marine, inshore and catchment habitats strongly impact coastal ecosystems, in their complex buffer-like position between land and ocean (He and Silliman, 2019). The scales of impact are highly variable, ranging from the impact of stressors on a global to a local geographic scale. For instance, ocean warming and acidification are global phenomena with large-scale impacts on the entire marine environment, but these can also induce further local effects, such as hypoxia events or melting sea-ice (IPCC, 2014). In addition, stressors interact with each other resulting in potentially unpredictable changes and immensely complex impacts on the marine environment (He and Silliman, 2019; Gissi et al., 2020).

In short, direct human activities in combination with climate change exert a tremendous pressure on marine ecosystems and threaten their integrity, structure and functioning. The human population heavily relies on healthy coastal ecosystems, and the negative feedback on ecosystem services (ES) from anthropogenic pressures reduces the chance for sustainable resource use. Coasts provide a wide range of ES from which humans benefit directly or indirectly (Barbier et al., 2011; Liquete et al., 2013). ES are classified as supporting, provisioning, regulating or cultural services (Millennium Assessment Board, 2005) which include, for instance, the increase of water quality by filtration (regulating ES) or the provision of food (provisioning ES). Global and local stressors impact different trophic levels of coastal food webs, such as plankton, fish and shellfish, and thus, jeopardize the provision of ES (Poloczanska et al., 2013; He and Silliman, 2019).

Given the magnitude of the pressures exerted on coastal environments, their protection is a major target of the 14th United Nations sustainable development goal "Conserve and sustainably use the oceans, seas and marine resources for sustainable development". Several guidelines, such as the European Marine Strategy Framework Directive (MSFD) (European Commission, 2008), have been established to achieve a "good environmental status" in coastal waters (Pogoda et al., 2020). However, due to the complexity of processes and interactions of stressors, the status assessment of ecosystems remains a challenge. Holistic food web models, including biological and environmental data, could provide a suitable basis to assess ecosystem health (de la Vega et al., 2018; Fath et al., 2019; Safi et al., 2019). These model approaches have significantly improved over the last decade (Coll et al., 2015; Geary et al., 2020), but their capacities to evaluate multiple-stressor impacts on different trophic levels are still limited (Coll et al., 2015).

Here, we focus on the following aims: (1) summarize current knowledge on climate change impact on different trophic levels of coastal food webs and their ES, (2) review current food web model approaches and their limitations, and (3) discuss a novel suggestion for a future high-resolution food web model approach, to assess climate change impacts in a holistic approach.

IMPACT OF GLOBAL CLIMATE CHANGE ON COASTAL FOOD WEBS AND CONSEQUENCES FOR ES

Climate change alters organisms' abundance, distribution, physiology and phenology (IPCC, 2014). These changes are not restricted to one trophic level or one local region, but affect the entire ecosystem on a global scale. This highlights the challenge of assessing ecosystem status and climate change impacts to guide conservation and management.

Coastal waters are highly productive areas and supply approximately 80% of the global wild-captured seafood (Capuzzo et al., 2018). This production relies on planktonic organisms at the basis of coastal food webs. Plankton supports ecologically and economically important species, which structure and stabilize pelagic and benthic communities (e.g., in their role as key predators) and provide habitats (e.g., as ecosystem engineers). Based on their importance for food web functioning and the provision of ES (Atkins et al., 2015; Turner et al., 2015), we focus on climate induced changes of plankton communities, and of ecologically and economically important fish and shellfish species and their trophic interactions.

Phytoplankton

Phytoplankton provide half of the global net primary production despite their comparably low biomass (Field et al., 1998). Biogeochemical cycles, such as the carbon or nitrogen cycles (Falkowski, 1994), and energy transfer to higher trophic levels depend on phytoplankton diversity and community composition. Phytoplankton affect fluxes of elements in the ecosystem by the uptake and storage of nutrients (Falkowski et al., 1998). Phytoplankton can also serve as a major source of trace gases, such as dimethyl sulfide, which can in turn also affect atmospheric chemistry and thus influence climate (Charlson et al., 1987; Andreae and Crutzen, 1997). Phytoplankton can photosynthetically fix atmospheric CO_2 into organic matter (Sunda, 2012), which is sequestered in the deep ocean through the biological pump (Tedesco and Thunell, 2003; Muller-Karger et al., 2005). Climate change induced alterations of the phytoplankton community are therefore likely to affect the regulating ES of marine phytoplankton.

Trends in phytoplankton responses to changing environmental conditions strongly vary across regional and temporal scales. Thus, very long and well understood database are required to link climate-related shifts to phytoplankton productivity. In addition, the fundamental controlling factors of plankton growth should be determined based on multi-decadal data (Wiltshire et al., 2015). For example, the continuous plankton recorder (CPR) operating in the North Atlantic and the North Sea provides one of the longest time series of plankton species composition and density in the world (Reid, 1975; Richardson et al., 2006). The CPR methodology was expanded to the North Pacific in 2000 with sister surveys in Narragansett, United States and Tasmania, Australia (Reid et al., 2003). Furthermore, several local but long-term plankton monitoring stations were established, for instance the German Helgoland Roads Time Series (HRTS) (Wiltshire et al., 2010), Hawaii Ocean Time series (HOT) (Bingham and Lukas, 1996), and Bermuda Atlantic Time Series (BATS) (Steinberg et al., 2001). The long-term data sets enable us to study multi-decadal patterns, and provide a unique basis to evaluate the influence of climate change on plankton.

Planktonic communities are affected at different scales by climate change (**Figure 1**). Analyses of CPR and HRTS data revealed warming induced changes in phytoplankton abundance (Richardson and Schoeman, 2004; Wiltshire et al., 2010). Richardson and Schoeman (2004) also showed a phytoplankton increase in cooler regions and a decrease in warmer regions. Declines in phytoplankton abundance and biomass are often linked to a nutrient depletion in surface waters since higher water temperatures generally lead to more stable and stratified water conditions resulting in less nutrient supply from deeper waters (Richardson, 2008; Gittings et al., 2018). For instance, this was shown for phytoplankton communities in the northern Red Sea (Gittings et al., 2018). Moreover, warming also alters the phenology of phytoplankton, such as growth and blooming behavior (Winder and Sommer, 2012; Wiltshire et al., 2015; Gittings et al., 2018; Scharfe and Wiltshire, 2019). Long-term studies of the phytoplankton community in the North Sea revealed that increasing temperatures change the timing of growth in more than half of the studied phytoplankton species (Scharfe and Wiltshire, 2019). Such phenological shifts can cause severe alterations in the food web if phytoplankton blooms are decoupled from zooplankton growth periods (Wiltshire et al., 2010; Winder and Sommer, 2012). A mismatch in times of peaking phytoplankton biomass and growth periods of their consumers can decrease the survival of those herbivores due to reduced food supply (Wiltshire and Manly, 2004; Richardson, 2008; Wiltshire et al., 2008). Because phytoplankton biomass appears to be one of the key drivers of zooplankton communities (Wiltshire et al., 2008; Capuzzo et al., 2018), changes at phytoplankton level are likely to propagate through the food web to higher trophic levels.

Under climate change, numerical models predict a severe decline of phytoplankton production due to rising CO_2 (Bopp et al., 2004, 2005). Furthermore, numerical simulations and observations suggested that increasing temperatures reduce plankton biomass, change the turnover time and break the stable coexistence of phytoplankton and zooplankton (Sarker et al., 2018, 2020). Sekerci and Petrovskii (2015) found that warming-induced oxygen depletion could cause plankton species extinction. Their model outputs also suggested that warming-induced stratification in tropical marine systems will reduce surface nutrient concentrations, and favor smaller phytoplankton cells at the expense of larger diatoms. An additional effect of warming is the melting of ice, which could impact planktonic communities. Reduced sea-ice cover results in an earlier attenuation of light limitation and induces a stabilization of stratification causing an earlier spring bloom in the Arctic and high-latitude Southern Ocean (Henson et al., 2018). While these models already predict climate change impacts on the phytoplankton level, they do not consider any propagations to higher trophic levels or feedback loops.

Zooplankton

Zooplankton are a key component of coastal food webs, which link the energy generated by primary production to higher trophic levels. Zooplankton are poikilothermic organisms and may express changes in physiological responses to higher temperatures, including higher ingestion and respiration rates (Dam and Peterson, 1988; Vaquer-Sunyer et al., 2010; Chen et al., 2012) as well as faster reproductive development (Heinle, 1969; Weydmann et al., 2018). This affects primary production via increased grazing pressure and can lead to shifts in phytoplankton size and species structure (Bergquist et al., 1985; Granéli et al., 1993). Furthermore, climate change impacts the community structure of zooplankton when environmental conditions exceed the tolerance limits of certain species. Richardson and Schoeman (2004) found a shift of various herbivorous and carnivorous zooplankton species of the North Sea and Atlantic toward cooler regions based on CPR data. Changes in the environment can also allow the invasion of new organisms. For instance, species such as *Penilia* spp. and

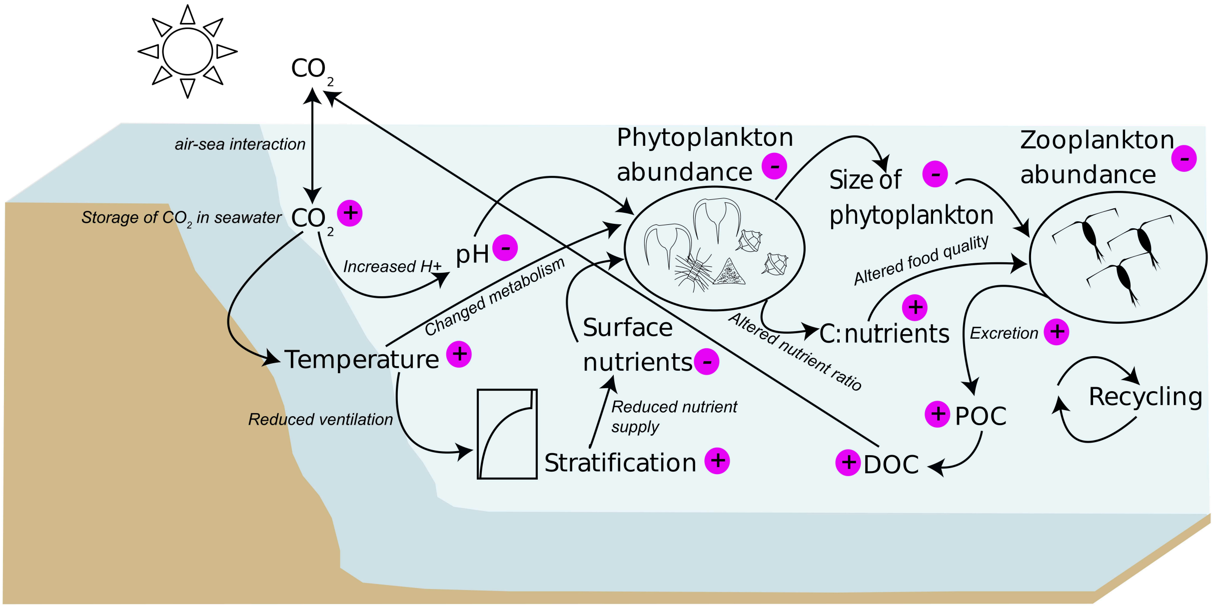

FIGURE 1 | Graphical summary of climate change impacts on planktonic communities. Positive signs indicate an increase and negative signs indicate a decrease. Information are based on literature cited in the text.

the introduced species *Mnemiopsis leidyi* have become more abundant in the southern North Sea due to warmer water temperatures (Johns et al., 2005; Boersma et al., 2007; Jaspers et al., 2018). Similarly, investigations of zooplankton in the Bering Sea revealed that warmer temperatures lead to changes in community structure with negative impacts on large, lipid-rich zooplankton and higher abundances of small zooplankton species in warm years (Eisner et al., 2014). In coral reefs, acidification results in changes in the zooplankton community structure and leads to an overall decrease of zooplankton abundance (Smith et al., 2016). Absorbed carbon from the atmosphere might also decrease the food quality for zooplankton by changing the carbon to nutrient ratio of the water (Van de Waal et al., 2010; Meunier et al., 2016) and thus the nutrient composition of planktonic primary producers (Sterner and Elser, 2002; Meunier et al., 2014). Consumers need to find a way to get rid of the surplus carbon, for instance by excreting carbon as dissolved organic carbon (DOC), which is potentially available for microbes and bacteria and can therefore influence the entire food web (Schoo et al., 2013).

To understand the impact of climate change on zooplankton communities, a significant number of model-based studies have been conducted. These studies include statistical models, small scale numerical simulations and large-scale numerical simulations. For example, Carter et al. (2017) used a statistical multivariate autoregressive model to reveal that warming was the dominant driver of change in the zooplankton community in an Alaskan lake from 1963 to 2009. Warming-induced oxygen depletion also caused a zooplankton biomass decrease in non-linear mathematical models (Sekerci and Ozarslan, 2020). Coupled population and hydrodynamic models were used to understand the impact of climate change on critical copepod life-history processes (Speirs et al., 2005). Wakelin et al. (2015) investigated the impact of climate change along with anthropogenic drivers on the zooplankton communities using a coupled hydrodynamic-ecosystem model. Their findings suggested that climate change has a negative impact on the zooplankton community. Model simulations in higher latitudes revealed that melting sea ice decreases the salinity of the surface layer causing an alteration in the timing of spring increase in copepod abundance (Ding et al., 2019). These models already successfully predict changes in zooplankton community structure and biomass related to climate change, but they do not provide effects on higher trophic levels or feedback loops to phytoplankton.

Meroplankton

During their early life stages, larvae of fish and shellfish are part of the zooplankton community (meroplankton). Elevated temperatures influence the timing of gametogenesis, gonad and embryonic development, spawning and hence, the abundance of these larvae (Birchenough et al., 2015; Bayne, 2017). Shifts in spawning time in relation to climate change have already been described by Cushing (1969) who suggested the risk of a potential de-coupling between fish larvae and the production cycle of their prey. As pelagic fish larvae mainly feed on zooplankton (Daan et al., 1990), the climate change associated shifts in phytoplankton and zooplankton can result in a decrease of food quality and quantity for these higher trophic levels. Beaugrand et al. (2003) found a decline in cod recruitment from the mid-1980s onward due to a mismatch between the prey size and appearance of cod larvae. Zooplankton of the genus *Calanus* belong to the most important prey of larvae and juveniles of cod in the North Sea. The replacement of *C. finmarchicus* by *C. helgolandicus* due to higher water temperatures had a direct effect on cod recruitment survival because *C. finmarchicus* peaks in spring while *C. helgolandicus* peaks in late summer/autumn resulting in insufficient prey supply for cod recruitment (Beaugrand et al., 2003). Similarly, there has been an entire regime shift in the Central Baltic Sea in the late 1980s presumably due to a change in atmospheric forcing causing a sudden increase in temperature (Möllmann et al., 2009). However, effects of increased temperature are not negative *per se*. In Lake Aleknagkik, Alaska, increasing temperatures led to an earlier ice breakup in spring with positive effects on sockeye salmon (*Oncorhynchus nerka*) larvae due to increased zooplankton growth (Schindler et al., 2005).

Shellfish larvae pass through critical life-stages while depending on phytoplankton as an exclusive food source. Specific phytoplankton compositions within narrow time windows induce successful development of long-adapted populations and affect total recruitment by allowing or by impeding metamorphosis and settlement (Birchenough et al., 2015; Bayne, 2017). Furthermore, increased predation pressures, caused by reduced winter migration of predators in warming waters, raise mortality rates of early larval populations in spring (Beukema and Dekker, 2005). Kirby et al. (2008) showed a climate-induced decrease of bivalve larvae, but it is still unknown how reduced abundances of larvae affect adult populations (Birchenough et al., 2015). On community level, mismatch effects of primary consumers are suggested to induce trophic cascades and major changes in coastal ecosystems, confirming the role of benthic shellfish as central components regulating functioning of both pelagic and benthic systems (Jochum et al., 2012; Lindegren et al., 2012).

Shellfish

Shellfish are well known for their provisional ES. Global annual capture production of mollusk groups and crustaceans, as well as aquaculture production, sum up to over 45 million tons. Negative trends in bivalve fisheries are related to an increasing aquaculture production, but in some areas also to pollution and the degradation of marine environments (FAO, 2018; Wijsman et al., 2019). In addition, bivalves regulate the water quality of coastal waters by their filtration capacity (e.g., Cranford, 2019). Most shellfish species are less mobile or even sessile and are thus limited in their ability to actively move to other areas if habitat conditions decrease due to climate change.

Among crustaceans, pandalid shrimps occupy a central position in the food web because they prey upon zooplankton and are the main food of different fish species. In the Gulf of Alaska, different species of pandalid shrimps declined sharply in relation to increasing water temperatures with critical impacts on the fishing sector (Anderson, 2000). Pandalids also have been shown to react with phenological changes to temperature alterations. In the Gulf of Maine, the northern shrimp *Pandalus borealis* exhibited an earlier hatch initiation with a later hatching completion in relation to increasing temperature (Richards, 2012). Furthermore, temperature affects larval dispersal (Le Corre et al., 2020) and recruitment survival (Ouellet et al., 2017) of *P. borealis*.

Other shellfish taxa, such as bivalves, are commonly classified as ecosystem engineers, as their numerical abundance creates significant effects in benthic communities and they often provide a relevant structuring component for their habitat by creating biogenic reefs (Birchenough et al., 2015; Bayne, 2017). Bivalves are filter-feeding primary consumers and depend on phytoplankton availability in quantity, quality and time. Climate change induced shifts in phytoplankton availability affects growth and reproductive output of bivalves (Birchenough et al., 2015). Declines in bivalve abundance result in reduced filtration capacity, which allows for increased phytoplankton blooms, hypoxia events at the benthic-pelagic interface, sediment instability and reduced marine vegetation (Schulte et al., 2009; Cranford, 2019). The ecosystem is forced from benthic to pelagic production and recruitment and reproductive output of the benthic community will decrease (Birchenough et al., 2015; Bayne, 2017). Furthermore, shellfish are often exposed to climate related range and virulence extension of parasites and pathogens. Rowley et al. (2014) reviewed the influence of climate change on shellfish diseases in the Irish Sea and related an increase of the range and prevalence of different parasite and pathogen groups (e.g., *Vibrio* populations) to elevated summer and winter temperatures. However, due to a lack of knowledge on pathogen dispersal conclusions remain fragmentary. Also, ocean acidification affects species depending on calcification, such as bivalves (Gazeau et al., 2007) with unknown long-term effects for species survival and benthic communities.

A recent integrated model approach addressed the evaluation of climate change impact on fish and shellfish in Alaska, primarily considering the potential consequences for socio-ecological interactions under different fishing scenarios (Hollowed et al., 2020). Guyondet et al. (2015) used a coupled hydrodynamic-biogeochemical model to study the effects of warming and nutrient loads on mussel aquaculture. They found a production increase in mussels as long as the mussels can sustain summer temperatures. Nevertheless, model predictions for shellfish distribution, fitness and respective ecosystem service provision under climate change are scarce.

Finfish

Fish play an important role in global nutrition (FAO, 2018) and sustaining healthy fish populations in a changing world is one of the key roles of global and local management strategies (ICSU, 2017). Fish are highly mobile and rising water temperatures cause a general poleward shift in distribution of tropical, temperate and subpolar fish species (Schindler et al., 2005). On a local scale, fishes also move to cooler water depths to avoid high water temperatures (Dulvy et al., 2008). The distribution of each species is constrained by its thermal tolerance (Rijnsdorp et al., 2009; Pörtner and Peck, 2010) and the shifting trend could affect especially those species which currently have a more poleward distribution since the suitable habitat decreases (Kleisner et al., 2017). Preferences for and dependencies on a specific habitat can complicate range adaptation to thermal changes for some fish species. In the North Sea, sandeel populations (e.g., *Ammodytes marinus*) are identified as highly threatened by climate change. Sandeels are ecological key species as they link primary and secondary (zooplankton) production to top predators (seabirds, fish, marine mammals) (Heath et al., 2012). But they are also of significant economic importance, supporting a large fishery in the North Sea (ICES, 2014). Sandeels are exclusively associated to coarse sediments and therefore indicate only limited potential for extending their distribution to the north (Heath et al., 2012). Similarly, the cape anchovy (*Engraulis capensis*) is unable to shift poleward lacking a refugium (Grant and Bowen, 2006). Most anchovy stocks are coastal and the cape anchovy habitat in the Benguela Current System is bounded by two warm currents: the Angola Current to the north and the Agulhas Current to the east. The cape anchovy off South Africa is unusually vulnerable to ocean warming (Checkley et al., 2017) and at the same time highly important for local fisheries. In addition to geographical range shifts, changing abiotic conditions can alter the annual migration of fishes to their feeding and spawning grounds (Rijnsdorp et al., 2009). A relationship between water temperatures and migration patterns have already been shown for fish species, such as flounders *Platichthys flesus* (Sims et al., 2004). However, alterations in fish migration with respect to climate change still require further investigations (Lennox et al., 2019).

Several model studies focus on the impact of climate change on fish stocks, especially due to their importance for fisheries and human nutrition. The model approach of Kleisner et al. (2017) supported the observed poleward shift of thermal fish habitats. This was also shown in the ensemble model study of Bryndum-Buchholz et al. (2020) with a fish biomass increase in Arctic regions and a decrease in tropical regions. The fish collapse in the Northwest Atlantic was explored with statistical models, which revealed that the reason was a mixture of fishing and environmental impacts (Dempsey et al., 2018). However, while these model approaches successfully represent potential responses to climate change, interactions with prey organisms are often not included.

What Needs to Be Included in Ecosystem Models to Assess and Project Climate Change Impacts?

The complex interactions within coastal food webs and the interactive effects of anthropogenic stressors such as fisheries and climate change make it difficult to assess changes on ecosystem scale (Gissi et al., 2020). However, this assessment and the projection of future changes are essential to provide the relevant knowledge to guide sustainable management of coastal ecosystems supporting the robust provision of ES, such as marine food supplies. Without such assessments, the regulation of ES becomes almost impossible, with particular regard to optimal spawning and recruitment conditions for stable populations of relevant key species. To effectively manage coastal ecosystems, both a detailed knowledge base of each trophic level and a holistic modeling approach for assessment and prediction of future scenarios on food web-scales are needed (Howell et al., 2021).

In order to achieve a realistic future simulation, such models should be able to simulate the different effects and drivers of climate change across trophic levels and on different scales. On the abiotic scale, models need to be able to predict future conditions under different climate change scenarios with a high temporal and spatial resolution. The predicted changes in the abiotic environment will then drive the identified biological changes in distribution, physiology and phenology of the different trophic levels and changes in food web interactions.

EXISTING FOOD WEB MODEL APPROACHES

A plethora of different models are available to test different scenarios and hypotheses on different trophic levels and food web-scales (Plagányi, 2007; Jørgensen, 2008; Fulton, 2010; Tittensor et al., 2018). A detailed comparison of all available model approaches is beyond the scope of this manuscript. In contrast, we focus on those models representing trophic interactions from low trophic levels to high trophic levels in relation to climate change. These models are potential tools to guide sustainable actions because they provide a holistic representation of the ecosystem.

NPZD-Based Models

Many trophic models use the dispersion of nutrients as a basis for food web interactions (Fulton, 2010). On a basic scale, this includes the interaction between nutrients (N), phytoplankton (P), zooplankton (Z) and detritus (D), represented in NPZ(D) models (Wroblewski et al., 1988; Dadou et al., 1996). These models can be three-dimensional and have the ability to describe ecosystem structure and functions in detail. Thus, they are useful tools to address questions focusing on plankton dynamics and physical oceanography (Franks and Chen, 2001; Aumont et al., 2015; Leles et al., 2016). NPZD models allow the combination of species into functional groups (Fasham, 1993), and therefore, these models can be used to investigate the impact of climate change on these functional groups. Through advanced modeling approaches complexity of ecosystems can be added in NPZD models by splitting nutrients, phytoplankton and zooplankton into subgroups (Allen et al., 2001).

In the context of climate change, Aumont et al. (2003) considered four plankton functional groups under nutrient co-limitation of phytoplankton growth as a function of N, P, Si and Fe in NPZD models. Werner et al. (2007) and Aita et al. (2007) performed simulations using NPZD models to understand food web dynamics. Furthermore, there are approaches toward ecosystem models by coupling NPZD models with hydrodynamic modules, in order to assess the impact of environmental changes (Chen et al., 2006; Schrum et al., 2006a,b; Aumont et al., 2015). In proceeding attempts, components representing fish and macrofauna have been added to these NPZD-hydrodynamic models providing a model solution from nutrients to higher trophic levels, such as NEMURO.FISH (Megrey et al., 2007; Rose et al., 2008) or ECOSMO E2E (Daewel et al., 2008, 2019).

NPZD-based models provide a detailed representation of plankton dynamics in relation to changes in the nutrient supply. However, even advanced approaches focus on specific system components and do not integrate the entire food web (**Table 1**).

TABLE 1 | Overview of common trophodynamic model approaches and their major limitations.

Model	Model base	Spatially explicit	Temporal-dynamic	Inclusion of physical environment	Provision of management indicators	Major limitation
NPZD	Nutrients	x	x	x		Limited representation of higher trophic levels
ECOSMO E2E	Nutrients	x	x	x		Incomplete representation of higher trophic levels
Atlantis	Nutrients	x	x	x	x	Offline coupling with physical parameters, coarse spatial resolution
EwE	Biomass	x	x		x	Inclusion of biotic and abiotic changes is difficult, only few model parameters can be changed by environmental drivers
ENA	Biomass				x	Static model, no temporal or spatial resolution, inclusion of biotic and abiotic changes is difficult

Atlantis

One of the most advanced marine trophic models with a biogeochemical fundament is the hybrid model Atlantis, which includes all ecosystem trophic levels and their interactions (Fulton et al., 2004). In Atlantis, the nutrient flow through the different biological groups is modeled, including non-living detritus components. In addition to the biogeochemical module, Atlantis includes a hydrographic submodel representing physical processes, a fisheries submodel and a management submodel, allowing for the test of different future scenarios (Fulton et al., 2004).

Atlantis has been applied to different coastal ecosystems worldwide (Fulton, 2010; Hansen et al., 2019), including studies on climate change effects. Ortega-Cisneros et al. (2016) used Atlantis in the Benguela upwelling system to assess impacts of climate change and fishing. They found that warming had the largest effects on species' biomass, with mainly negative impacts. Furthermore, Atlantis was used to predict future changes in coral reef ecosystems (Weijerman et al., 2015). The study showed that climate change will have severe impacts on coral reefs in the near future, especially by interactions and cumulative effects with other stressors, such as fishing and pollution. Thus, first studies using Atlantis related to climate change appear promising.

The Atlantis framework includes all system components, changes in the abiotic environment and anthropogenic impacts, such as fisheries. These models could even provide suitable indicators for assessing the ecosystem health (Fulton et al., 2005). The management module allows for simulations of different strategies. Thus, the Atlantis framework provides advanced tools for exploring, e.g., climate change impacts on food web scales. However, there are also some limitations. Atlantis does not use the same grid coordinates as hydrodynamic models, but rather irregular polygons (Fulton et al., 2005, 2007) with relatively coarse resolution, which seems to represent a compromise between the complexity and computational costs. Physical parameters are coupled offline as time series data. They are taken from observations or from ocean model simulations. This means that important processes like vertical mixing or intertidal processes are largely parametrized rather than resolved. Parametrization leads to an averaging in space and time of the impact of different dynamic processes, which sometimes cannot be done in a consistent manner especially for relatively large areas. For example, vertical mixing depends on buoyancy and vertical shear stress, these terms are highly dynamic in coastal areas in time and space due to the presence of regions of the freshwater influence, shallowness of the area and the large role of tides in coastal dynamics. Therefore, biogeochemical and ecosystem processes become largely de-coupled to the physical processes. Additionally, an exchange between physical and biological modules assumes interpolation due to different physical and ecosystem grid geometries (ocean model grid/observation tracks versus polygons). Accordingly, the resolution of early life history stages including pelagic dispersal phases of organisms linked to coastal areas with complex dynamics is rather coarse in Atlantis-based models (Itoh et al., 2018).

EwE and ENA

In contrast to Atlantis and similar nutrient-based model approaches, trophodynamic models can also be based on species biomass data. Common biomass-based food web methodologies are network models analyzed with Ecological Network Analysis (ENA) (Kay et al., 1989; Ulanowicz, 2004) or the widely used framework Ecopath with Ecosim and Ecospace (EwE) (Christensen and Walters, 2004). Both approaches are based on a similarly structured *snap-shot* model, representing the studied trophodynamic system. ENA and Ecopath are based on the biomass of system components, their energetic requirements and the diet spectra. However, while ENA is a static model, representing an averaged ecosystem during a specific time, Ecopath also includes a temporal-dynamic component (Ecosim) and a spatial-temporal-dynamic component (Ecospace).

Both approaches, ENA and EwE, have been used in a variety of studies to describe the structure and functioning of coastal food webs (e.g., Baird et al., 2004; Scharler and Baird, 2005; Coll et al., 2011; Horn et al., 2019; Vilas et al., 2020), but few studies focus on climate change. ENA has been applied in shallow coastal areas of the south-eastern North Sea, the Wadden Sea, to investigate the impact of increasing temperatures on the food web (Baird et al., 2019). In this system, an increase in ambient water temperature resulted in a higher detritivory and recycling in the food web whereas the degree of organization, diversity of flows and specialization of the food web structure decreased. Furthermore, climate change caused alterations in the Wadden

Sea food web due to long-term shifts in the species composition according to ENA results (Schückel et al., 2015). Range shifts of species are supposed to be a major driver in future food web changes. A dynamic EwE modeling approach of the food web in the Barents Sea focused on the impact of poleward migrating fish species due to warmer water temperatures (Kortsch et al., 2015). The study suggests a shift from the more modular, specialized Arctic food web toward a system with increased connectivity driven by boreal fish generalists. Further changes of the Barents Sea food web due to warming were studied in Bentley et al. (2017) who suggested a gradual shift toward a system dominated by pelagic species and a reduction in boreal species. On a multi-stressor level, the combined effects of eutrophication and overfishing (Vasas et al., 2007) as well as eutrophication and increased temperature (Binzer et al., 2016) have been studied using EwE implying unexpected interactions between the pressures. For the Baltic Sea, Niiranen et al. (2013) tested the influence of management strategies for fisheries and nutrient input under different IPCC climate change scenarios until the end of this century with EwE. Results ranged from a cod dominated food web with reduced nutrient levels and phytoplankton biomass close to today in the best case, to a sprat dominated, severely eutrophicated system in the worst case highlighting the importance of management strategies with regard to climate change.

Field data are included as model input (e.g., biomass data) in ENA and EwE models. Thus, trends of the system components are directly incorporated, if the models are based on regular monitoring data. In terms of EwE, additional long-term data can be used to parametrize the model over time. ENA and EwE are particularly interesting for management purposes because both methodologies provide a set of global system indices following the theory of Ulanowicz (1986). Some of these indices are potential candidate indicators for the MSFD to assess the health status of coastal food webs (Fath et al., 2019; Safi et al., 2019). However, changes of the candidate indicators provided by ENA and EwE models in relation to climate change impacts are largely unknown. The complexity of processes and a lack of data on trophodynamic relationships and feedback are reflected in model limitations. However, this fundamental gap can be attributed to all ecosystem models with advanced representation of the food web. Furthermore, dynamic shifts in the abiotic environment are difficult to represent in EwE and ENA. In ENA, the static model behavior permits a dynamic response over space and time. In EwE, abiotic changes are usually used to alter specific model parameters, such as primary production, consumption rates or fish egg production (Niiranen et al., 2013; de Mutsert et al., 2016; Serpetti et al., 2017), but not the entire food web (**Table 1**).

OCEAN MODELS IN RELATION TO CLIMATE CHANGE PRESSURE

The evaluation of climate change impacts on coastal ecosystems requires a deep understanding of the abiotic parameters based on precise data (Wiltshire and Manly, 2004; Wiltshire et al., 2010). Shelf zones are characterized by a complex morphology and hydrography resulting from interactions of coastal currents and currents formed in the deep ocean, riverine input, tidal and atmospheric forcing (Gowen et al., 1995; Tett and Walne, 1995; Schrum, 1997; Orvik et al., 2001; Sundby and Drinkwater, 2007; Scharfe, 2013; Fofonova et al., 2019). Physical ocean models are powerful tools for prediction and assessment of climate change impacts on abiotic parameters. There is a rich diversity of models available to conduct climate change projections in coastal areas, such as GETM, FESOM-C, SCHISM/SELFE, NEMO, DELFT3D, ROMS, FVCOM, and others (Burchard and Bolding, 2002; Shchepetkin and McWilliams, 2005; Chen et al., 2006; Zhang and Baptista, 2008; Zhang et al., 2016; Madec et al., 2017; Androsov et al., 2019). The role of the physical models can be divided into four pieces: (1) predictions of the abiotic parameters' distribution in space and time to supply the biogeochemical and food-web models (Hofmeister et al., 2017; Kerimoglu et al., 2017; Lemmen et al., 2018), (2) prediction of pathways of water parcels, passive and active tracers (van der Molen et al., 2018; Ricker and Stanev, 2020; Sprong et al., 2020), (3) predictions of the future "hot-spots" in a sense of largest changes in the abiotic parameters' behavior (sensitivity studies) (Delworth et al., 2012; Yin, 2012; Schrum et al., 2016), and (4) evaluation of the representativeness of long-term observational stations for larger areas.

Making progress on identified roles requires an accurate representation of the physical environment in a coupled estuaries-shelf sea-deep ocean modeling system. The coupling of regional and large-scale models presents a challenging task since dynamics resolved by different models involve different temporal and spatial scales, and the simulations use grids of different types. Therefore, for example, upwelling events on the shelf, are not well reproduced based on one numerical solution. However, with increased computer power the larger range of process scales can be dealt within one modeling platform. Indeed, currently there are attempts to organize a seamless ocean modeling system based on available deep ocean and coastal solutions, for example, in frame of Earth System Modeling (ESM)[1] or NEMO[2] modeling frameworks.

Current physical ocean models extensively represent the abiotic changes and dynamics of the pelagic system and are useful for forecasting future abiotic scenarios. In contrast, food web models focus on the biological interactions in an ecosystem and possible effects of multiple stressors and management strategies. A dynamic coupling between both model types appears to be a challenging but essential step in order to achieve the realistic combination of abiotic dynamics with biotic interactions (**Figure 2**). The consideration of ecosystems dynamically related to the physical and biogeochemical processes requires seamless considerations of processes in a wide range of temporal and spatial scales and fundamental understanding of the dynamic response of ecosystems to the abiotic conditions. At the current stage, an ambitious goal such as the seamless dynamic coupling between food web models and physical and biogeochemical models becomes more feasible.

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[1] https://www.esm-project.net/

[2] https://www.nemo-ocean.eu/

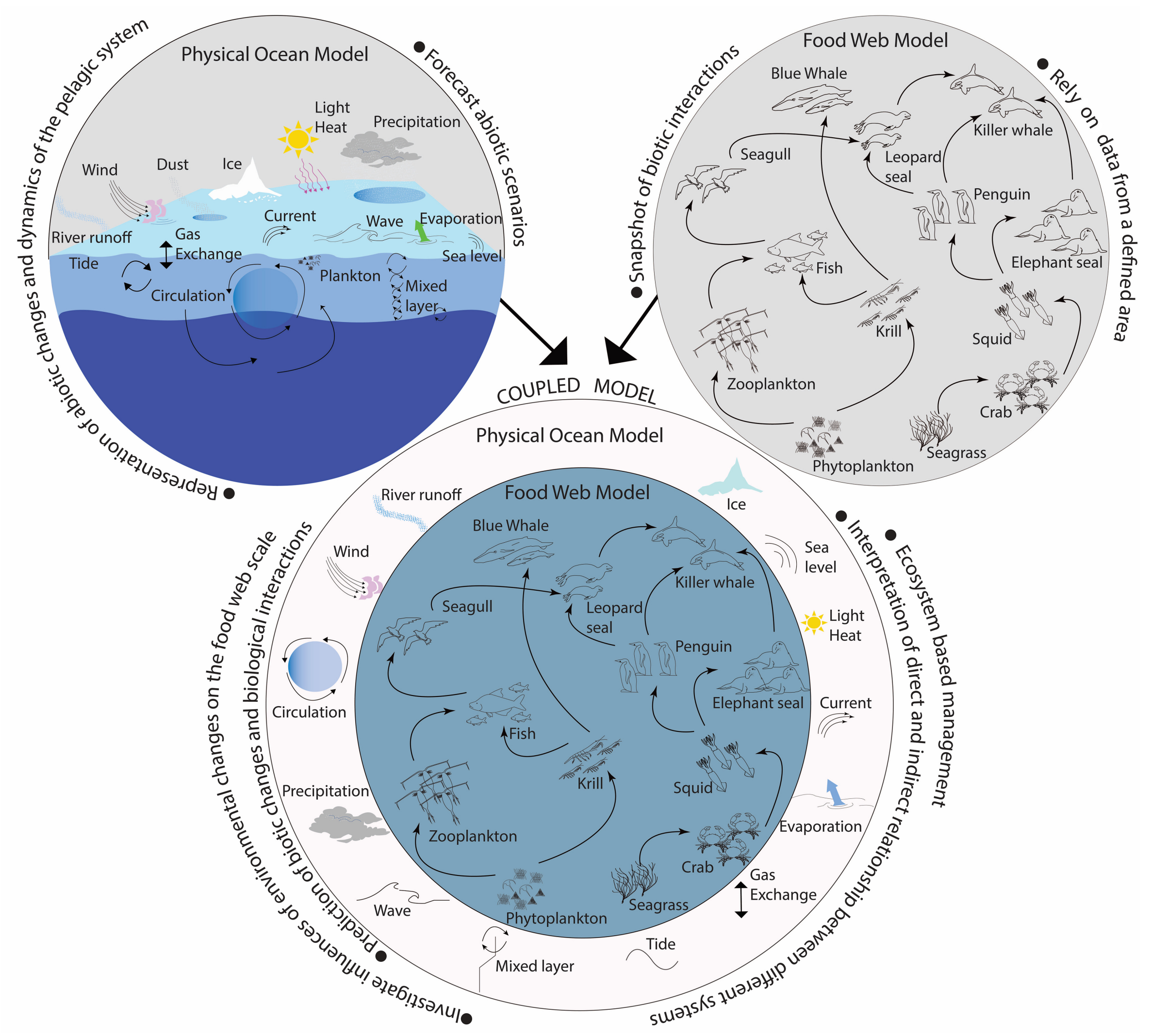

FIGURE 2 | Illustration of the coupled ocean-food-web-model. The ocean model contains the physical drivers while the food web model represents biological interactions. The figure was inspired by https://www.gfdl.noaa.gov/ocean-mixing/ and https://intl.siyavula.com/read/science/grade-8/interactions-and-interdependence-within-the-environment/02-interactions-and-interdependence-within-the-environment?id=toc-id-9.

One of the main social motivations for such a coupling is deriving high quality predictions of coastal ecosystem stage and of indicators for sustainable ES management.

DISCUSSION

Toward Seamless Coupling Between Food Web and Physical Ocean Models

Holistic food web model studies focusing on the impacts of climate change on the system's structure and functioning are still scarce. Our predictive capacities for a reliable future assessment using food web models are restricted because they consider the changes in the abiotic conditions only in a limited way. However, available model approaches trying to overcome this challenge have progressed significantly over the last decade. For example, Atlantis and EwE were used to explore possible management strategies under multi-stressor scenarios (e.g., Niiranen et al., 2013; Ortega-Cisneros et al., 2016). However, both frameworks have their limitations considered in section "Existing Food Web Model Approaches" (**Table 1**). These limitations underline the necessity of a seamless coupling between ocean physical and biological food web models in the future.

A major challenge is the great variability of temporal and spatial scales, considering the multi-scale nature of ecosystem dynamics as a simulated system, exacerbated by the additional involvement of multi-scale physical processes, which should be reproduced by a physical model. The *simulated* ecosystem and physical processes should be in agreement. This problem is relevant to both numeric and fundamental aspects and to the general understanding of the processes.

One example to highlight the challenge is the consideration of population connectivity in coastal areas with intertidal zones. Population connectivity is intricately linked to habitat heterogeneity and trophic interactions, which are biologically rich and complex in coastal areas compared to the open ocean. In the ocean numerical solutions, the vertical and spatial resolutions, the parametrization of vertical dynamics and reproduction of intertidal dynamics (wetting/drying option) are crucial to solve the connectivity task. The grid cell size is essential due to the large role of non-linear processes (e.g., bottom friction and advection of momentum) in coastal and shelf-sea dynamics. With a reduction in grid cell size, the model output can result in a completely different local circulation pattern. Concomitantly, different possible connections may be predicted between the considered positions (Sprong et al., 2020). Obviously, there is no universal answer for the optimal horizontal and vertical resolutions across all water bodies and coastal realms. The numerical consideration of relatively large areas requires an unstructured grid approach to maintain computational costs, gain geometrical flexibility and provide seamless modeling across the scales. In the case of structured grid approaches the necessity of higher resolution in some sub-areas requires nesting. However, the quality of the solution depends not only on the resolution itself but also on numerical filling of the model. For example, if the ocean model solution does not resolve the intertidal dynamics (wetting/drying option), the dynamics of higher tidal harmonics are presented incorrectly. This leads to significant errors in the simulation of transport and mixing (Stanev et al., 2016; Fofonova et al., 2019), which can play a major role in a realistic solving of connectivity tasks and in simulating ecosystem dynamics in general.

A further coupling between a chosen food web model and a physical ocean model with an irregular grid is challenging and reveals several gaps. We suggest using biomass-based food web models, such as ENA or EwE because of the empirical model input of all trophic levels. In a first step, the biomass-based food web model needs to be transferred into the unstructured grid-resolution of the ocean models. Although it is hardly possible to provide empirical data of biological components for each grid cell, approaches with the spatial-dynamic routine Ecospace have been promising and provide a suitable base for further coupling with ocean models. Additional tracer equations organize the passive exchange of materials (e.g., detritus, plankton) between the cells considering the hydrodynamics of the studied system. The inclusion of active tracers, such as fish or shrimps, remains challenging. The determination of these components in the studied area requires a formalization of their behavior (e.g., dispersal toward the best forage site) depending on different abiotic conditions. At this level, we identified a fundamental gap that requires further studies.

The next step is the representation of abiotic dynamics over a specified time and space influencing the biological components. As discussed, changes in the abiotic environment are not directly usable in most food web models but need a translation into biological responses (e.g., changes in physiology). Usually, physiological parameters are represented in the master equations (1) and (2) after Crisp (1971):

$$\text{Gross primary production} = \text{Net primary production} + \text{Respiration} \tag{1}$$

in autotrophs and

$$\text{Consumption} = \text{Production} + \text{Respiration} + \text{Egestion/Excretion} \tag{2}$$

in heterotrophs. These master equations provide a crucial link to abiotic dynamics (**Figure 3**). Species' physiologies are dependent on abiotic drivers such as temperature or salinity represented in physical ocean models. There are diverse studies of changes in species physiology in relation to abiotic parameters (Heinle, 1969; Pörtner and Knust, 2007; Marinov et al., 2010). One of the key challenges here is developing a theory that explicitly incorporates the separate components of climate change and their potential interactions. Some steps in this direction have been done, for example, Taherzadeh et al. (2019) proved an ability to explain when impacts become additive or non-additive based on a new size-based plankton model resolving major dependencies of plankton growth and interaction rates. Thus, each physiological parameter (i.e., production, respiration, consumption, egestion) can be represented as a function of abiotic conditions which can be implemented as a driver in coupled food web and physical ocean models. This requires combined work of ecologists, physiologists and mathematicians. Studies based on Atlantis and EwE have already achieved important steps in this direction, by altering specific parameters, such fish egg production, consumption or primary production in relation to abiotic changes. However, as discussed, climate change impacts all these parameters simultaneously. In the suggested coupled model, all physiological parameters can potentially be represented dependent on the abiotic environment.

In the last step, additional information can be added to the coupled model. For instance, the resolution of lower trophic level dynamics can be improved by a coupling with biogeochemical models. This was already successfully done for EwE with the ECOTRAN model (Steele and Ruzicka, 2011; Ruzicka et al., 2016). With this, the information of nutrient dispersion can be included in the new approach. Furthermore, temporal-dynamic predator prey interactions need to be formalized and included to provide a realistic simulation of food web changes over space and time.

With snap-shot models, we can simulate scenarios by constructing additional setups with altered data reflecting the particular stress factor or driver. Like a film that represents a dynamic sequence of different fixed-images, the new type of coupled models should be a sequence of different holistic model scenarios to show trends and developments within total ecosystems. Multi-stressor scenarios should be the leading topic that determines the direction of the "film" and may lead to new possibilities of interpretations of ecosystem functions and services under stress. Thus, the coupled model would address the identified climate change effects on physiology and phenology of the different trophic levels. A high temporal resolution could even

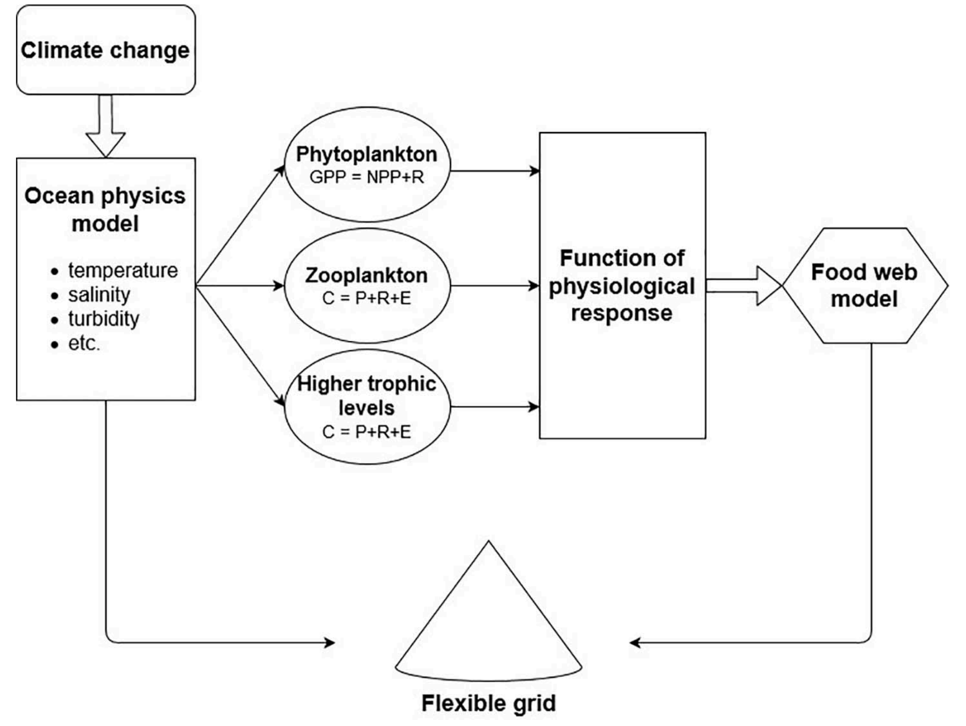

FIGURE 3 | Schematic coupling approach between ocean models driven by climate change and food web models via functions of physiological responses.

represent de-coupled shifts in prey availability and predator requirements, and changes of migration patterns. Furthermore, the spatial component allows for the inclusion of range shifts if environmental factors exceed tolerance limits of specific system components.

The large variety of approaches to study the ecosystem dynamics stresses the complexity of the task to investigate the impact of climate change on marine coastal ecosystems. At this stage, the synergy between approaches is intriguing, but the next step in this direction requires intensive work on cross-roads of science, large computer power and it brings numerical and fundamental challenges, as briefly discussed above. However, this step promises a more holistic and solid view on the ecosystem dynamics.

Relevance for Ecosystem Management

The protection of coastal ecosystems is a major target of politics and management to sustain ES. Against the background of biodiversity loss, habitat degradation, decreasing ES and climate change mitigation, there is a clear demand for precise and efficient management tools to reverse these negative trends in marine ecosystems. To achieve ecological and economical goals, ecosystem-based management (EBM) is the most relevant approach. EBM is supposed to consider all trophic levels and ES to sustain healthy and resilient ecosystems (O'Higgins et al., 2020). This becomes increasingly challenging given the multiple stressors impacting ecosystems and our limited knowledge of stressor interaction (Gissi et al., 2020). While climate change has already impacted coastal and shelf-sea ecosystems in diverse ways, local stressors add another dimension to the problem. For instance, commercial fisheries exert a constant pressure on the entire fish community and on benthic communities (Lindeboom and De Groot, 1998; Daan et al., 2005), including severe destructive effects on biogenic habitats, such as shellfish reefs (Pogoda, 2019). Effects of fishing, pollution and climate change are likely to interact with each other (Gissi et al., 2020). Accordingly, we need additional studies of stressor interactions and potential cumulative effects for a better representation in model studies.

To support EBM decisions, holistic, fine-scale and high-resolution ecosystem models, which are able to address multiple stressor effects on the entire food web are highly relevant. The suggested coupling between biomass-based food web models and physical ocean models with an unstructured grid will provide such a tool. However, while we have highlighted some technical challenges of the coupling, we also found several research gaps, which need to be addressed, such as the incorporation of active tracer behavior in models or defining the physiological responses of species to the environmental changes. In addition, a regular monitoring of the relevant ecosystem components is required to provide a solid model base. Indeed, every model we construct is just as good as the available data base. The more we know, the better we can include the information into models. Thus, detailed knowledge on climate change impacts on each trophic level, and advanced model approaches incorporating available information to provide a holistic representation are required.

AUTHOR CONTRIBUTIONS

SH, CM, and KW conceptualized and drafted the work. SS designed **Figures 1**, **2**. All authors wrote and revised the manuscript and contributed expertise to their research area.

FUNDING

SH was partly supported by the project MERCES of the European Union's Horizon 2020 research program (grant agreement no. 689518). CM was supported by the German Federal Ministry of Education and Research (BMBF grant no. 01LN1702A). BP was supported by the projects RESTORE and PROCEED of the German Federal Agency for Nature Conservation with funds from the German Federal Ministry for the Environment, Conservation and Nuclear Safety (FKZ 3520892013 and FKZ 3517685013).

ACKNOWLEDGMENTS

We would like to thank the European Union's Horizon 2020 research program (project MERCES, grant agreement number 689518), the German Federal Ministry of Education and Research (BMBF grant number 01LN1702A), and the German Federal Agency for Nature Conservation (grants 3520892013 and 3517685013) for supporting this work. Furthermore, we warmly thank our reviewers for their constructive comments, which helped to improve the manuscript substantially.

REFERENCES

Airoldi, L., Balata, D., and Beck, M. W. (2008). The gray zone: relationships between habitat loss and marine diversity and their applications in conservation. *J. Exp. Mar. Biol. Ecol.* 366, 8–15. doi: 10.1016/j.jembe.2008.07.034

Aita, M. N., Yamanaka, Y., and Kishi, M. J. (2007). Interdecadal variation of the lower trophic ecosystem in the northern Pacific between 1948 and 2002, in a 3-D implementation of the NEMURO model. *Ecol. Model.* 202, 81–94. doi: 10.1016/j.ecolmodel.2006.07.045

Allen, J. I., Blackford, J., Holt, J., Proctor, R., Ashworth, M., and Siddorn, J. (2001). A highly spatially resolved ecosystem model for the North West European Continental Shelf. *Sarsia* 86, 423–440. doi: 10.1080/00364827.2001.10420484

Anderson, P. J. (2000). Pandalid shrimp as indicators of ecosystem regime shift. *J. Northw. Atlant. Fish. Sci.* 27, 1–10. doi: 10.2960/j.v27.a1

Andreae, M. O., and Crutzen, P. J. (1997). Atmospheric aerosols: biogeochemical sources and role in atmospheric chemistry. *Science* 276, 1052–1058. doi: 10.1126/science.276.5315.1052

Androsov, A., Fofonova, V., Kuznetsov, I., Danilov, S., Rakowsky, N., Harig, S., et al. (2019). FESOM-C v. 2: coastal dynamics on hybrid unstructured meshes. *Geosci. Model Dev.* 12, 1009–1028. doi: 10.5194/gmd-12-1009-2019

Atkins, J. P., Burdon, D., and Elliott, M. (2015). "Identification of a practicable set of ecosystem indicators for coastal and marine ecosystem services," in *Coastal Zones Ecosystem Services*, eds R. K. Turner and M. Schaafsma (Berlin: Springer), 79–102. doi: 10.1007/978-3-319-17214-9_5

Aumont, O., Éthé, C., Tagliabue, A., Bopp, L., and Gehlen, M. (2015). PISCES-v2: an ocean biogeochemical model for carbon and ecosystem studies. *Geosci. Model Dev. Discuss.* 8, 2465–2513. doi: 10.5194/gmd-8-2465-2015

Aumont, O., Maier-Reimer, E., Blain, S., and Monfray, P. (2003). An ecosystem model of the global ocean including Fe, Si, P colimitations. *Glob. Biogeochem. Cycles* 17:GB001745.

Baird, D., Asmus, H., and Asmus, R. (2004). Energy flow of a boreal intertidal ecosystem, the sylt-rømø bight. *Mar. Ecol. Prog. Ser.* 279, 45–61. doi: 10.3354/meps279045

Baird, D., Asmus, H., Asmus, R., Horn, S., and de la Vega, C. (2019). Ecosystem response to increasing ambient water temperatures due to climate warming in the Sylt-Rømø Bight, northern Wadden Sea, Germany. *Estuar. Coast. Shelf Sci.* 228:106322. doi: 10.1016/j.ecss.2019.106322

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., and Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* 81, 169–193.

Bayne, B. (2017). Oysters and the ecosystem. *Dev. Aquac. Fish. Sci.* 41, 703–834. doi: 10.1016/b978-0-12-803472-9.00010-8

Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature* 426, 661–664. doi: 10.1038/nature02164

Bentley, J. W., Serpetti, N., and Heymans, J. J. (2017). Investigating the potential impacts of ocean warming on the Norwegian and Barents Seas ecosystem using a time-dynamic food-web model. *Ecol. Model.* 360, 94–107. doi: 10.1016/j.ecolmodel.2017.07.002

Bergquist, A. M., Carpenter, S. R., and Latino, J. C. (1985). Shifts in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages 1. *Limnol. Oceanogr.* 30, 1037–1045. doi: 10.4319/lo.1985.30.5.1037

Beukema, J., and Dekker, R. (2005). Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. *Mar. Ecol. Prog. Ser.* 287, 149–167. doi: 10.3354/meps287149

Bingham, F. M., and Lukas, R. (1996). Seasonal cycles of temperature, salinity and dissolved oxygen observed in the Hawaii Ocean Time-series. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 43, 199–213. doi: 10.1016/0967-0645(95)00090-9

Binzer, A., Guill, C., Rall, B. C., and Brose, U. (2016). Interactive effects of warming, eutrophication and size structure: impacts on biodiversity and food-web structure. *Glob. Change Biol.* 22, 220–227. doi: 10.1111/gcb.13086

Birchenough, S. N., Reiss, H., Degraer, S., Mieszkowska, N., Borja, Á, Buhl-Mortensen, L., et al. (2015). Climate change and marine benthos: a review of existing research and future directions in the North Atlantic. *Wiley Interdiscip. Rev. Clim. Change* 6, 203–223. doi: 10.1002/wcc.330

Boersma, M., Malzahn, A. M., Greve, W., and Javidpour, J. (2007). The first occurrence of the ctenophore Mnemiopsis leidyi in the North Sea. *Helgoland Mar. Res.* 61, 153–155. doi: 10.1007/s10152-006-0055-2

Bopp, L., Aumont, O., Cadule, P., Alvain, S., and Gehlen, M. (2005). Response of diatoms distribution to global warming and potential implications: a global model study. *Geophys. Res. Lett.* 32:GL023653.

Bopp, L., Boucher, O., Aumont, O., Belviso, S., Dufresne, J.-L., Pham, M., et al. (2004). Will marine dimethylsulfide emissions amplify or alleviate global warming? A model study. *Can. J. Fish. Aquat. Sci.* 61, 826–835. doi: 10.1139/f04-045

Bryndum-Buchholz, A., Boyce, D. G., Tittensor, D. P., Christensen, V., Bianchi, D., and Lotze, H. K. (2020). Climate-change impacts and fisheries management challenges in the North Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 648, 1–17. doi: 10.3354/meps13438

Burchard, H., and Bolding, K. (2002). *GETM–a General Estuarine Transport Model.* Scientific documentation, no EUR 20253. Brussels: European Commission.

Capuzzo, E., Lynam, C. P., Barry, J., Stephens, D., Forster, R. M., Greenwood, N., et al. (2018). A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. *Glob. Change Biol.* 24, e352–e364.

Carter, J. L., Schindler, D. E., and Francis, T. B. (2017). Effects of climate change on zooplankton community interactions in an Alaskan lake. *Clim. Change Responses* 4, 1–12.

Charlson, R. J., Lovelock, J. E., Andreae, M. O., and Warren, S. G. (1987). Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature* 326, 655–661. doi: 10.1038/326655a0

Checkley, D. M. Jr., Asch, R. G., and Rykaczewski, R. R. (2017). Climate, anchovy, and sardine. *Annu. Rev. Mar. Sci.* 9, 469–493. doi: 10.1146/annurev-marine-122414-033819

Chen, B., Landry, M. R., Huang, B., and Liu, H. (2012). Does warming enhance the effect of microzooplankton grazing on marine phytoplankton in the ocean? *Limnol. Oceanogr.* 57, 519–526. doi: 10.4319/lo.2012.57.2.0519

Chen, C., Beardsley, R., and Cowles, G. (2006). An unstructured grid, finite-volume coastal ocean model (FVCOM) system. *Oceanography* 19, 78–89. doi: 10.5670/oceanog.2006.92

Christensen, V., and Walters, C. J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model.* 172, 109–139. doi: 10.1016/j.ecolmodel.2003.09.003

Coll, M., Akoglu, E., Arreguin-Sanchez, F., Fulton, E., Gascuel, D., Heymans, J., et al. (2015). Modelling dynamic ecosystems: venturing beyond boundaries with the Ecopath approach. *Rev. Fish Biol. Fish.* 25, 413–424. doi: 10.1007/s11160-015-9386-x

Coll, M., Schmidt, A., Romanuk, T., and Lotze, H. K. (2011). Food-web structure of seagrass communities across different spatial scales and human impacts. *PLoS One* 6:e22591. doi: 10.1371/journal.pone.0022591

Cranford, P. J. (2019). "Magnitude and extent of water clarification services provided by bivalve suspension feeding," in *Goods and Services of Marine Bivalves*, eds Ø Strand, J. G. Ferreira, and J. K. Petersen (Cham: Springer), 119–141. doi: 10.1007/978-3-319-96776-9_8

Crisp, D. (1971). "Energy flow measurements," in *Methods for the study of marine benthos*, ed. A. Eleftheriou (Hoboken, NJ: Wiley).

Cushing, D. (1969). The regularity of the spawning season of some fishes. *ICES J. Mar. Sci.* 33, 81–92. doi: 10.1093/icesjms/33.1.81

Daan, N., Bromley, P., Hislop, J., and Nielsen, N. (1990). Ecology of North sea fish. *Netherlands J. Sea Res.* 26, 343–386. doi: 10.1016/0077-7579(90)90096-y

Daan, N., Gislason, H., Pope, J. G., and Rice, J. C. (2005). Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES J. Mar. Sci.* 62, 177–188. doi: 10.1016/j.icesjms.2004.08.020

Dadou, I., Garçon, V., Andersen, V., Flierl, G., and Davis, C. (1996). Impact of the North Equatorial Current meandering on a pelagic ecosystem: a modeling approach. *J. Mar. Res.* 54, 311–342. doi: 10.1357/0022240963213411

Daewel, U., Peck, M. A., Kuehn, W., John, M. A. S. T., Alekseeva, I., and Schrum, C. (2008). Coupling ecosystem and individual-based models to simulate the influence of environmental variability on potential growth and survival of larval sprat (*Sprattus sprattus* L.) in the North Sea. *Fish. Oceanogr.* 17, 333–351. doi: 10.1111/j.1365-2419.2008.00482.x

Daewel, U., Schrum, C., and Macdonald, J. I. (2019). Towards end-to-end (E2E) modelling in a consistent NPZD-F modelling framework (ECOSMO E2E_v1.0): application to the North Sea and Baltic Sea. *Geosci. Model Dev.* 12, 1765–1789. doi: 10.5194/gmd-12-1765-2019

Dam, H. G., and Peterson, W. T. (1988). The effect of temperature on the gut clearance rate constant of planktonic copepods. *J. Exp. Mar. Biol. Ecol.* 123, 1–14. doi: 10.1016/0022-0981(88)90105-0

de la Vega, C., Schückel, U., Horn, S., Kröncke, I., Asmus, R., and Asmus, H. (2018). How to include ecological network analysis results in management? A case study of three tidal basins of the Wadden Sea, south-eastern North Sea. *Ocean Coast. Manag.* 163, 401–416. doi: 10.1016/j.ocecoaman.2018.07.019

de Mutsert, K., Steenbeek, J., Lewis, K., Buszowski, J., Cowan, J. H. Jr., and Christensen, V. (2016). Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model. *Ecol. Model.* 331, 142–150. doi: 10.1016/j.ecolmodel.2015.10.013

Delworth, T. L., Rosati, A., Anderson, W., Adcroft, A. J., Balaji, V., Benson, R., et al. (2012). Simulated climate and climate change in the GFDL CM2. 5 high-resolution coupled climate model. *J. Clim.* 25, 2755–2781. doi: 10.1175/jcli-d-11-00316.1

Dempsey, D. P., Gentleman, W. C., Pepin, P., and Koen-Alonso, M. (2018). Explanatory power of human and environmental pressures on the fish community of the grand bank before and after the biomass collapse. *Front. Mar. Sci.* 5:37. doi: 10.3389/fmars.2018.00037

Ding, Q., Schweiger, A., L'Heureux, M., Steig, E. J., Battisti, D. S., Johnson, N. C., et al. (2019). Fingerprints of internal drivers of Arctic sea ice loss in observations and model simulations. *Nat. Geosci.* 12, 28–33. doi: 10.1038/s41561-018-0256-8

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., and Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J. Appl. Ecol.* 45, 1029–1039. doi: 10.1111/j.1365-2664.2008.01488.x

Eisner, L. B., Napp, J. M., Mier, K. L., Pinchuk, A. I., and Andrews, A. G. III (2014). Climate-mediated changes in zooplankton community structure for the eastern Bering Sea. *Deep Sea Res. II Top. Stud. Oceanogr.* 109, 157–171. doi: 10.1016/j.dsr2.2014.03.004

European Commission (2008). Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). *Off. J. Eur. Union* 164, 19–40.

Falkowski, P. G. (1994). The role of phytoplankton photosynthesis in global biogeochemical cycles. *Photosyn. Res.* 39, 235–258. doi: 10.1007/bf00014586

Falkowski, P. G., Barber, R. T., and Smetacek, V. (1998). Biogeochemical controls and feedbacks on ocean primary production. *Science* 281, 200–206. doi: 10.1126/science.281.5374.200

FAO (2018). *The State of World Fisheries and Aquaculture 2018–Meeting the Sustainable Development Goals*. Rome: FAO.

Fasham, M. J. (1993). "Modelling the marine biota," in *The Global Carbon Cycle*, ed. M. Heimann (Berlin: Springer), 457–504. doi: 10.1007/978-3-642-84608-3_19

Fath, B. D., Asmus, H., Asmus, R., Baird, D., Borrett, S. R., de Jonge, V. N., et al. (2019). Ecological network analysis metrics: the need for an entire ecosystem approach in management and policy. *Ocean Coast. Manag.* 174, 1–14. doi: 10.1016/j.ocecoaman.2019.03.007

Field, C. B., Behrenfeld, M. J., Randerson, J. T., and Falkowski, P. (1998). Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281, 237–240. doi: 10.1126/science.281.5374.237

Fofonova, V., Androsov, A., Sander, L., Kuznetsov, I., Amorim, F., Hass, H. C., et al. (2019). Non-linear aspects of the tidal dynamics in the Sylt-Rømø Bight, south-eastern North Sea. *Ocean Sci.* 15, 1761–1782. doi: 10.5194/os-15-1761-2019

Franks, P., and Chen, C. (2001). A 3-D prognostic model study of the ecosystem over Georges Bank and adjacent coastal regions. Part II: coupled biological and physical model. *Deep Sea Res.* 48, 457–482. doi: 10.1016/s0967-0645(00)00125-9

Fulton, E., Smith, A. D., and Smith, D. C. (2007). *Alternative Management Strategies For Southeast Australian Commonwealth Fisheries: stage 2: Quantitative Management Strategy Evaluation*. Hobart: Commonwealth Scientific and Industrial Research Organisation (CSIRO).

Fulton, E. A. (2010). Approaches to end-to-end ecosystem models. *J. Mar. Syst.* 81, 171–183. doi: 10.1016/j.jmarsys.2009.12.012

Fulton, E. A., Fuller, M., Smith, A., and Punt, A. (2004). *Ecological Indicators of the Ecosystem Effects of Fishing*. Hobart: Commonwealth Scientific and Industrial Research Organisation (CSIRO).

Fulton, E. A., Smith, A. D., and Punt, A. E. (2005). Which ecological indicators can robustly detect effects of fishing? *ICES J. Mar. Sci.* 62, 540–551. doi: 10.1016/j.icesjms.2004.12.012

Gazeau, F., Quiblier, C., Jansen, J. M., Gattuso, J. P., Middelburg, J. J., and Heip, C. H. (2007). Impact of elevated CO2 on shellfish calcification. *Geophys. Res. Lett.* 34:GL028554.

Geary, W. L., Bode, M., Doherty, T. S., Fulton, E. A., Nimmo, D. G., Tulloch, A. I., et al. (2020). A guide to ecosystem models and their environmental applications. *Nat. Ecol. Evol.* 4, 1459–1471.

Gissi, E., Manea, E., Mazaris, A. D., Fraschetti, S., Almpanidou, V., Bevilacqua, S., et al. (2020). A review of the combined effects of climate change and other local human stressors on the marine environment. *Sci. Total Environ.* 2020:142564. doi: 10.1016/j.scitotenv.2020.142564

Gittings, J. A., Raitsos, D. E., Krokos, G., and Hoteit, I. (2018). Impacts of warming on phytoplankton abundance and phenology in a typical tropical marine ecosystem. *Sci. Rep.* 8, 1–12.

Gowen, R., Stewart, B., Mills, D., and Elliott, P. (1995). Regional differences in stratification and its effect on phytoplankton production and biomass in the northwestern Irish Sea. *J. Plankton Res.* 17, 753–769. doi: 10.1093/plankt/17.4.753

Granéli, E., Granéli, W., Rabbani, M. M., Daugbjerg, N., Fransz, G., Roudy, J. C., et al. (1993). The influence of copepod and krill grazing on the species composition of phytoplankton communities from the Scotia Weddell sea. *Polar Biol.* 13, 201–213. doi: 10.1007/bf00238930

Grant, W. S., and Bowen, B. W. (2006). Living in a tilted world: climate change and geography limit speciation in Old World anchovies (Engraulis; Engraulidae). *Biol. J. Linn. Soc.* 88, 673–689. doi: 10.1111/j.1095-8312.2006.00651.x

Greene, C. H., Meyer-Gutbrod, E., Monger, B. C., McGarry, L. P., Pershing, A. J. I, Belkin, M., et al. (2013). Remote climate forcing of decadal-scale regime shifts in Northwest Atlantic shelf ecosystems. *Limnol. Oceanogr.* 58, 803–816. doi: 10.4319/lo.2013.58.3.0803

Guyondet, T., Comeau, L., Bacher, C., Grant, J., Rosland, R., Sonier, R., et al. (2015). Climate change influences carrying capacity in a coastal embayment dedicated to shellfish aquaculture. *Estua. Coasts* 38, 1593–1618. doi: 10.1007/s12237-014-9899-x

Hansen, C., Drinkwater, K. F., Jähkel, A., Fulton, E. A., Gorton, R., and Skern-Mauritzen, M. (2019). Sensitivity of the Norwegian and Barents Sea Atlantis end-to-end ecosystem model to parameter perturbations of key species. *PLoS One* 14:e0210419. doi: 10.1371/journal.pone.0210419

He, Q., and Silliman, B. R. (2019). Climate change, human impacts, and coastal ecosystems in the Anthropocene. *Curr. Biol.* 29, R1021–R1035.

Heath, M. R., Neat, F. C., Pinnegar, J. K., Reid, D. G., Sims, D. W., and Wright, P. J. (2012). Review of climate change impacts on marine fish and shellfish around the UK and Ireland. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 22, 337–367. doi: 10.1002/aqc.2244

Heinle, D. R. (1969). Temperature and zooplankton. *Chesapeake Sci.* 10, 186–209. doi: 10.2307/1350456

Henson, S. A., Cole, H. S., Hopkins, J., Martin, A. P., and Yool, A. (2018). Detection of climate change-driven trends in phytoplankton phenology. *Glob. Change Biol.* 24, e101–e111.

Hofmeister, R., Flöser, G., and Schartau, M. (2017). Estuary-type circulation as a factor sustaining horizontal nutrient gradients in freshwater-influenced coastal systems. *Geo Mar. Lett.* 37, 179–192. doi: 10.1007/s00367-016-0469-z

Hollowed, A. B., Holsman, K. K., Haynie, A. C., Hermann, A. J., Punt, A. E., Aydin, K., et al. (2020). Integrated modeling to evaluate climate change impacts on coupled social-ecological systems in Alaska. *Front. Mar. Sci.* 6:775. doi: 10.3389/fmars.2019.00775

Horn, S., de la Vega, C., Asmus, R., Schwemmer, P., Enners, L., Garthe, S., et al. (2019). Impact of birds on intertidal food webs assessed with ecological network analysis. *Estua. Coast. Shelf Sci.* 219, 107–119. doi: 10.1016/j.ecss.2019.01.023

Howell, D., Schueller, A. M., Bentley, J. W., Buchheister, A., Chagaris, D., Cieri, M., et al. (2021). Combining ecosystem and single-species modeling to provide ecosystem-based fisheries management advice within current management systems. *Front. Mar. Sci.* 7:1163. doi: 10.3389/fmars.2020.607831

ICES (2014). *Annex 12 Stock Sandeel in IV. Quality Handbook Annex SAN-NSEA Stock-Specific Documentation of Standard Assessment Procedures*. Copenhagen: ICES.

ICSU (2017). *Guide To SDG Interactions: From Science to implementation*. Paris: International Council for Science.

IPCC (2014). *Climate Change 2014 Synthesis Report*. Geneva: IPCC.

Itoh, S., Takeshige, A., Kasai, A., and Kimura, S. (2018). Modeling the coastal ecosystem complex: present situation and challenges. *Fish. Sci.* 84, 293–307. doi: 10.1007/s12562-018-1181-x

Jaspers, C., Huwer, B., Antajan, E., Hosia, A., Hinrichsen, H. H., Biastoch, A., et al. (2018). Ocean current connectivity propelling the secondary spread of a marine invasive comb jelly across western Eurasia. *Glob. Ecol. Biogeogr.* 27, 814–827. doi: 10.1111/geb.12742

Jochum, M., Schneider, F. D., Crowe, T. P., Brose, U., and O'Gorman, E. J. (2012). Climate-induced changes in bottom-up and top-down processes independently alter a marine ecosystem. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 2962–2970. doi: 10.1098/rstb.2012.0237

Johns, D., Edwards, M., Greve, W., and Sjohn, A. (2005). Increasing prevalence of the marine cladoceran *Penilia avirostris* (Dana, 1852) in the North Sea. *Helgoland Mar. Res.* 59, 214–218. doi: 10.1007/s10152-005-0221-y

Jørgensen, S. E. (2008). Overview of the model types available for development of ecological models. *Ecol. Model.* 215, 3–9. doi: 10.1016/j.ecolmodel.2008.02.041

Kay, J. J., Graham, L. A., and Ulanowicz, R. E. (1989). "A detailed guide to network analysis," in *Network Analysis in Marine Ecology*, eds F. Wulff and J. G. Field (Berlin: Springer), 15–61. doi: 10.1007/978-3-642-75017-5_2

Kerimoglu, O., Hofmeister, R., Maerz, J., Riethmüller, R., and Wirtz, K. W. (2017). The acclimative biogeochemical model of the southern North Sea. *Biogeosciences* 14, 4499–4531. doi: 10.5194/bg-14-4499-2017

Kirby, R. R., Beaugrand, G., and Lindley, J. A. (2008). Climate-induced effects on the meroplankton and the benthic-pelagic ecology of the North Sea. *Limnol. Oceanogr.* 53, 1805–1815. doi: 10.4319/lo.2008.53.5.1805

Kleisner, K. M., Fogarty, M. J., McGee, S., Hare, J. A., Moret, S., Perretti, C. T., et al. (2017). Marine species distribution shifts on the US Northeast Continental Shelf under continued ocean warming. *Prog. Oceanogr.* 153, 24–36. doi: 10.1016/j.pocean.2017.04.001

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., and Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proc. R. Soc. B Biol. Sci.* 282:20151546. doi: 10.1098/rspb.2015.1546

Le Corre, N., Pepin, P., Burmeister, A., Walkusz, W., Skanes, K., Wang, Z., et al. (2020). Larval connectivity of Northern Shrimp (Pandalus borealis) in the northwest Atlantic. *Can. J. Fish. Aquat. Sci.* [Epub ahead of print].

Leles, S. G., Valentin, J. L., and Figueiredo, G. M. (2016). Evaluation of the complexity and performance of marine planktonic trophic models. *Anais da Acad. Brasil. Ciências* 88, 1971–1991. doi: 10.1590/0001-3765201620150588

Lemmen, C., Hofmeister, R., Klingbeil, K., Nasermoaddeli, M. H., Kerimoglu, O., Burchard, H., et al. (2018). Modular System for Shelves and Coasts (MOSSCO v1. 0)–a flexible and multi-component framework for coupled coastal ocean ecosystem modelling. *Geosci. Model Dev.* 11, 915–935. doi: 10.5194/gmd-11-915-2018

Lennox, R. J., Paukert, C. P., Aarestrup, K., Auger-Méthé, M., Baumgartner, L., Birnie-Gauvin, K., et al. (2019). One hundred pressing questions on the future of global fish migration science, conservation, and policy. *Front. Ecol. Evol.* 7:286. doi: 10.3389/fevo.2019.00286

Lindeboom, H., and De Groot, S. (1998). *IMPACT-II: The Effects of Different Types of Fisheries on the North Sea and Irish Sea Benthic Ecosystems*. The Hague: Netherlands Institute for Fisheries Research.

Lindegren, M., Blenckner, T., and Stenseth, N. C. (2012). Nutrient reduction and climate change cause a potential shift from pelagic to benthic pathways in a eutrophic marine ecosystem. *Glob. Change Biol.* 18, 3491–3503. doi: 10.1111/j.1365-2486.2012.02799.x

Liquete, C., Piroddi, C., Drakou, E. G., Gurney, L., Katsanevakis, S., Charef, A., et al. (2013). Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. *PLoS One* 8:e67737. doi: 10.1371/journal.pone.0067737

Madec, G., Bourdallé-Badie, R., Bouttier, P., Bricaud, C., Bruciaferri, D., Calvert, D., et al. (2017). *NEMO Ocean Engine (Version v3. 6)*. Zenodo: Du Pôle De Modélisation De L'institut Pierre-simon Laplace (IPSL).

Marinov, I., Doney, S., and Lima, I. (2010). Response of ocean phytoplankton community structure to climate change over the 21st century: partitioning the effects of nutrients, temperature and light. *Biogeosciences* 7:3941. doi: 10.5194/bg-7-3941-2010

Megrey, B. A., Rose, K. A., Klumb, R. A., Hay, D. E., Werner, F. E., Eslinger, D. L., et al. (2007). A bioenergetics-based population dynamics model of Pacific herring (*Clupea harengus* pallasi) coupled to a lower trophic level nutrient–phytoplankton–zooplankton model: description, calibration, and sensitivity analysis. *Ecol. Model.* 202, 144–164. doi: 10.1016/j.ecolmodel.2006.08.020

Meunier, C. L., Boersma, M., Wiltshire, K. H., and Malzahn, A. M. (2016). Zooplankton eat what they need: copepod selective feeding and potential consequences for marine systems. *Oikos* 125, 50–58. doi: 10.1111/oik.02072

Meunier, C. L., Malzahn, A. M., and Boersma, M. (2014). A new approach to homeostatic regulation: towards a unified view of physiological and ecological concepts. *PLoS One* 9:e107737. doi: 10.1371/journal.pone.0107737

Millennium Assessment Board (2005). *Millennium Ecosystem Assessment*. Washington, DC: Millennium Assessment Board.

Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. (2009). Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. *Glob. Change Biol.* 15, 1377–1393. doi: 10.1111/j.1365-2486.2008.01814.x

Muller-Karger, F. E., Varela, R., Thunell, R., Luerssen, R., Hu, C., and Walsh, J. J. (2005). The importance of continental margins in the global carbon cycle. *Geophys. Res. Lett.* 32:GL021346.

Niiranen, S., Yletyinen, J., Tomczak, M. T., Blenckner, T., Hjerne, O., MacKenzie, B. R., et al. (2013). Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. *Glob. Change Biol.* 19, 3327–3342.

O'Higgins, T. G., Lago, M., and DeWitt, T. H. (2020). *Ecosystem-Based Management, Ecosystem Services and Aquatic Biodiversity: Theory, Tools and Applications*. Cham: Springer.

Ortega-Cisneros, K., Scharler, U., and Whitfield, A. (2016). Carbon and nitrogen system dynamics in three small South African estuaries, with particular emphasis on the influence of seasons, river flow and mouth state. *Mar. Ecol. Prog. Ser.* 557, 17–30. doi: 10.3354/meps11870

Orvik, K. A., Skagseth, Ø, and Mork, M. (2001). Atlantic inflow to the Nordic Seas: current structure and volume fluxes from moored current meters, VM-ADCP and SeaSoar-CTD observations, 1995–1999. *Deep Sea Res. Part I Oceanogr. Res. Pap.* 48, 937–957. doi: 10.1016/s0967-0637(00)00038-8

Ouellet, P., Chabot, D., Calosi, P., Orr, D., and Galbraith, P. S. (2017). Regional variations in early life stages response to a temperature gradient in the northern shrimp Pandalus borealis and vulnerability of the populations to ocean warming. *J. Exp. Mar. Biol. Ecol.* 497, 50–60. doi: 10.1016/j.jembe.2017.09.007

Plagányi, ÉE. (2007). *Models for An Ecosystem Approach to Fisheries*. Rome: Food & Agriculture Org.

Pogoda, B. (2019). Current status of European oyster decline and restoration in Germany. *Humanities* 8:9. doi: 10.3390/h8010009

Pogoda, B., Merk, V., Colsoul, B., Hausen, T., Peter, C., Pesch, R., et al. (2020). Site selection for biogenic reef restoration in offshore environments: the Natura 2000 area Borkum reef ground as a case study for native oyster restoration. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 30, 2163–2179. doi: 10.1002/aqc.3405

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., et al. (2013). Global imprint of climate change on marine life. *Nat. Clim. Change* 3, 919–925.

Pörtner, H. O., and Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315, 95–97. doi: 10.1126/science.1135471

Pörtner, H. O., and Peck, M. (2010). Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *J. Fish Biol.* 77, 1745–1779. doi: 10.1111/j.1095-8649.2010.02783.x

Reid, P., Colebrook, J., Matthews, J., Aiken, J., and Team, C. P. R. (2003). The continuous plankton recorder: concepts and history, from Plankton Indicator to undulating recorders. *Prog. Oceanogr.* 58, 117–173. doi: 10.1016/j.pocean.2003.08.002

Reid, P. C. (1975). Large scale changes in North Sea phytoplankton. *Nature* 257, 217–219. doi: 10.1038/257217a0

Richards, R. A. (2012). Phenological shifts in hatch timing of northern shrimp *Pandalus borealis*. *Mar. Ecol. Prog. Ser.* 456, 149–158. doi: 10.3354/meps09717

Richardson, A., Walne, A., John, A., Jonas, T., Lindley, J., Sims, D., et al. (2006). Using continuous plankton recorder data. *Prog. Oceanogr.* 68, 27–74. doi: 10.1016/j.pocean.2005.09.011

Richardson, A. J. (2008). In hot water: zooplankton and climate change. *ICES J. Mar. Sci.* 65, 279–295. doi: 10.1093/icesjms/fsn028

Richardson, A. J., and Schoeman, D. S. (2004). Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305, 1609–1612. doi: 10.1126/science.1100958

Ricker, M., and Stanev, E. V. (2020). Circulation of the European northwest shelf: a lagrangian perspective. *Ocean Science* 16, 637–655. doi: 10.5194/os-16-637-2020

Riebesell, U. (2004). Effects of CO 2 enrichment on marine phytoplankton. *J. Oceanogr.* 60, 719–729. doi: 10.1007/s10872-004-5764-z

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., and Pinnegar, J. K. (2009). Resolving the effect of climate change on fish populations. *ICES J. Mar. Sci.* 66, 1570–1583. doi: 10.1093/icesjms/fsp056

Rose, K. A., Megrey, B. A., Hay, D., Werner, F., and Schweigert, J. (2008). Climate regime effects on Pacific herring growth using coupled nutrient-phytoplankton-zooplankton and bioenergetics models. *Trans. Am. Fish. Soc.* 137, 278–297. doi: 10.1577/t05-152.1

Rowley, A. F., Cross, M. E., Culloty, S. C., Lynch, S. A., Mackenzie, C. L., Morgan, E., et al. (2014). The potential impact of climate change on the infectious diseases of commercially important shellfish populations in the Irish Sea—a review. *ICES J. Mar. Sci.* 71, 741–759. doi: 10.1093/icesjms/fst234

Ruzicka, J. J., Brink, K. H., Gifford, D. J., and Bahr, F. (2016). A physically coupled end-to-end model platform for coastal ecosystems: simulating the effects of climate change and changing upwelling characteristics on the Northern California Current ecosystem. *Ecol. Model.* 331, 86–99. doi: 10.1016/j.ecolmodel.2016.01.018

Sabine, C. L., Feely, R. A., Gruber, N., Key, R. M., Lee, K., Bullister, J. L., et al. (2004). The oceanic sink for anthropogenic CO2. *Science* 305, 367–371. doi: 10.1126/science.1097403

Safi, G., Giebels, D., Arroyo, N. L., Heymans, J. J., Preciado, I., Raoux, A., et al. (2019). Vitamine ENA: a framework for the development of ecosystem-based indicators for decision makers. *Ocean Coast. Manag.* 174, 116–130. doi: 10.1016/j.ocecoaman.2019.03.005

Sarker, S., Feudel, U., Meunier, C. L., Lemke, P., Dutta, P. S., and Wiltshire, K. H. (2018). To share or not to share? Phytoplankton species coexistence puzzle in a competition model incorporating multiple resource-limitation and synthesizing unit concepts. *Ecol. Model.* 383, 150–159. doi: 10.1016/j.ecolmodel.2018.05.021

Sarker, S., Yadav, A. K., Akter, M., Hossain, M. S., Chowdhury, S. R., Kabir, M. A., et al. (2020). Rising temperature and marine plankton community dynamics: Is warming bad? *Ecol. Complex.* 43:100857. doi: 10.1016/j.ecocom.2020.100857

Scharfe, M. (2013). *Analyse Biologischer Langzeitveränderungen auf Basis Hydroklimatischer Parameter in Der Südlichen Nordsee (Helgoland)*. Ph.D. thesis. Hamburg: Universität Hamburg.

Scharfe, M., and Wiltshire, K. H. (2019). Modeling of intra-annual abundance distributions: constancy and variation in the phenology of marine phytoplankton species over five decades at Helgoland Roads (North Sea). *Ecol. Model.* 404, 46–60. doi: 10.1016/j.ecolmodel.2019.01.001

Scharler, U. M., and Baird, D. (2005). A comparison of selected ecosystem attributes of three South African estuaries with different freshwater inflow regimes, using network analysis. *J. Mar. Syst.* 56, 283–308. doi: 10.1016/j.jmarsys.2004.12.003

Schindler, D. E., Rogers, D. E., Scheuerell, M. D., and Abrey, C. A. (2005). Effects of changing climate on zooplankton and juvenile sockeye salmon growth in southwestern Alaska. *Ecology* 86, 198–209. doi: 10.1890/03-0408

Schoo, K. L., Malzahn, A. M., Krause, E., and Boersma, M. (2013). Increased carbon dioxide availability alters phytoplankton stoichiometry and affects carbon cycling and growth of a marine planktonic herbivore. *Mar. Biol.* 160, 2145–2155. doi: 10.1007/s00227-012-2121-4

Schrum, C. (1997). Thermohaline stratification and instabilities at tidal mixing fronts: results of an eddy resolving model for the German Bight. *Continent. Shelf Res.* 17, 689–716. doi: 10.1016/s0278-4343(96)00051-9

Schrum, C., Alekseeva, I., and John, M. S. (2006a). Development of a coupled physical–biological ecosystem model ECOSMO: part I: model description and validation for the North Sea. *J. Mar. Syst.* 61, 79–99. doi: 10.1016/j.jmarsys.2006.01.005

Schrum, C., John, M. S., and Alekseeva, I. (2006b). ECOSMO, a coupled ecosystem model of the North Sea and Baltic Sea: part II. Spatial-seasonal characteristics in the North Sea as revealed by EOF analysis. *J. Mar. Syst.* 61, 100–113. doi: 10.1016/j.jmarsys.2006.01.004

Schrum, C., Lowe, J., Meier, H. M., Grabemann, I., Holt, J., Mathis, M., et al. (2016). "Projected change—North sea," in *North Sea Region Climate Change Assessment*, eds M. Quante and F. Colijn (Cham: Springer), 175–217. doi: 10.1007/978-3-319-39745-0_6

Schückel, U., Kröncke, I., and Baird, D. (2015). Linking long-term changes in trophic structure and function of an intertidal macrobenthic system to eutrophication and climate change using ecological network analysis. *Mar. Ecol. Prog. Ser.* 536, 25–38. doi: 10.3354/meps11391

Schulte, D. M., Burke, R. P., and Lipcius, R. N. (2009). Unprecedented restoration of a native oyster metapopulation. *Science* 325, 1124–1128. doi: 10.1126/science.1176516

Sekerci, Y., and Ozarslan, R. (2020). Oxygen-plankton model under the effect of global warming with nonsingular fractional order. *Chaos Solitons Fractals* 132:109532. doi: 10.1016/j.chaos.2019.109532

Sekerci, Y., and Petrovskii, S. (2015). Mathematical modelling of plankton–oxygen dynamics under the climate change. *Bull. Math. Biol.* 77, 2325–2353. doi: 10.1007/s11538-015-0126-0

Serpetti, N., Baudron, A. R., Burrows, M., Payne, B. L., Helaouet, P., Fernandes, P. G., et al. (2017). Impact of ocean warming on sustainable fisheries management informs the ecosystem approach to fisheries. *Sci. Rep.* 7, 1–15. doi: 10.1163/9789004242005_002

Shchepetkin, A. F., and McWilliams, J. C. (2005). The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Model.* 9, 347–404. doi: 10.1016/j.ocemod.2004.08.002

Sims, D. W., Wearmouth, V. J., Genner, M. J., Southward, A. J., and Hawkins, S. J. (2004). Low-temperature-driven early spawning migration of a temperate marine fish. *J. Anim. Ecol.* 73, 333–341. doi: 10.1111/j.0021-8790.2004.00810.x

Smith, J. N., De'ath, G., Richter, C., Cornils, A., Hall-Spencer, J. M., and Fabricius, K. E. (2016). Ocean acidification reduces demersal zooplankton that reside in tropical coral reefs. *Nat. Clim. Change* 6, 1124–1129. doi: 10.1038/nclimate3122

Speirs, D. C., Gurney, W. S., Heath, M. R., and Wood, S. N. (2005). Modelling the basin-scale demography of Calanus finmarchicus in the north-east Atlantic. *Fish. Oceanogr.* 14, 333–358. doi: 10.1111/j.1365-2419.2005.00339.x

Sprong, P., Fofonova, V., Wiltshire, K. H., Neuhaus, S., Ludwichowski, K.-U., Käse, L., et al. (2020). Spatial dynamics of eukaryotic microbial communities in the German Bight. *J. Sea Res.* 163:101914. doi: 10.1016/j.seares.2020.101914

Stanev, E. V., Schulz-Stellenfleth, J., Staneva, J., Grayek, S., Grashorn, S., Behrens, A., et al. (2016). Ocean forecasting for the German Bight: from regional to coastal scales. *Ocean Sci.* 12, 1105–1136. doi: 10.5194/os-12-1105-2016

Steele, J. H., and Ruzicka, J. J. (2011). Constructing end-to-end models using ECOPATH data. *J. Mar. Syst.* 87, 227–238. doi: 10.1016/j.jmarsys.2011.04.005

Steinberg, D. K., Carlson, C. A., Bates, N. R., Johnson, R. J., Michaels, A. F., and Knap, A. H. (2001). Overview of the US JGOFS Bermuda Atlantic Time-series Study (BATS): a decade-scale look at ocean biology and biogeochemistry. *Deep Sea Res. II Top. Stud. Oceanogr.* 48, 1405–1447. doi: 10.1016/s0967-0645(00)00148-x

Sterner, R. W., and Elser, J. J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton, NJ: Princeton university press.

Sunda, W. (2012). Feedback interactions between trace metal nutrients and phytoplankton in the ocean. *Front. Microbiol.* 3:204. doi: 10.3389/fmicb.2012.00204

Sundby, S., and Drinkwater, K. (2007). On the mechanisms behind salinity anomaly signals of the northern North Atlantic. *Prog. Oceanogr.* 73, 190–202. doi: 10.1016/j.pocean.2007.02.002

Taherzadeh, N., Bengfort, M., and Wirtz, K. W. (2019). A trait-based framework for explaining non-additive effects of multiple stressors on plankton communities. *Front. Mar. Sci.* 6:351. doi: 10.3389/fmars.2019.00351

Tedesco, K., and Thunell, R. (2003). High resolution tropical climate record for the last 6,000 years. *Geophys. Res. Lett.* 30:GL017959.

Tett, P., and Walne, A. (1995). Observations and simulations of hydrography, nutrients and plankton in the southern North Sea. *Ophelia* 42, 371–416. doi: 10.1080/00785326.1995.10431514

Tittensor, D. P., Eddy, T. D., Lotze, H. K., Galbraith, E. D., Cheung, W., Barange, M., et al. (2018). A protocol for the intercomparison of marine fishery and ecosystem models: fish-MIP v1. 0. *Geosci. Model Dev.* 11, 1421–1442.

Toggweiler, J. R., and Russell, J. (2008). Ocean circulation in a warming climate. *Nature* 451, 286–288. doi: 10.1038/nature06590

Turner, R., Schaafsma, M., Mee, L., Elliott, M., Burdon, D., Atkins, J. P., et al. (2015). "Conceptual framework," in *Coastal Zones Ecosystem Services*, eds R. Kerry Turner and M. Schaafsma (Berlin: Springer), 11–40.

Ulanowicz, R. E. (1986). *Growth and Development Ecosystems Phenomenology*. Berlin: Springer.

Ulanowicz, R. E. (2004). Quantitative methods for ecological network analysis. *Comput. Biol. Chem.* 28, 321–339. doi: 10.1016/j.compbiolchem.2004.09.001

van Beusekom, J. (2005). A historic perspective on Wadden Sea eutrophication. *Helgoland Mar. Res.* 59, 45–54. doi: 10.1007/s10152-004-0206-2

Van de Waal, D. B., Verschoor, A. M., Verspagen, J. M., van Donk, E., and Huisman, J. (2010). Climate-driven changes in the ecological stoichiometry of aquatic ecosystems. *Front. Ecol. Environ.* 8, 145–152. doi: 10.1890/080178

van der Molen, J., García-García, L. M., Whomersley, P., Callaway, A., Posen, P. E., and Hyder, K. (2018). Connectivity of larval stages of sedentary marine communities between hard substrates and offshore structures in the North Sea. *Sci. Rep.* 8, 1–14.

Vaquer-Sunyer, R., Duarte, C. M., Santiago, R., Wassmann, P., and Reigstad, M. (2010). Experimental evaluation of planktonic respiration response to warming in the European Arctic Sector. *Polar Biol.* 33, 1661–1671. doi: 10.1007/s00300-010-0788-x

Vasas, V., Lancelot, C., Rousseau, V., and Jordán, F. (2007). Eutrophication and overfishing in temperate nearshore pelagic food webs: a network perspective. *Mar. Ecol. Prog. Ser.* 336, 1–14. doi: 10.3354/meps336001

Vilas, D., Coll, M., Pedersen, T., Corrales, X., Filbee-Dexter, K., Pedersen, M. F., et al. (2020). Kelp-carbon uptake by Arctic deep-sea food webs plays a noticeable role in maintaining ecosystem structural and functional traits. *J. Mar. Syst.* 203:103268. doi: 10.1016/j.jmarsys.2019.103268

Wakelin, S. L., Artioli, Y., Butenschön, M., Allen, J. I., and Holt, J. T. (2015). Modelling the combined impacts of climate change and direct anthropogenic drivers on the ecosystem of the northwest European continental shelf. *J. Mar. Syst.* 152, 51–63. doi: 10.1016/j.jmarsys.2015.07.006

Waldbusser, G. G., and Salisbury, J. E. (2014). Ocean acidification in the coastal zone from an organism's perspective: multiple system parameters, frequency domains, and habitats. *Annu. Rev. Mar. Sci.* 6, 221–247. doi: 10.1146/annurev-marine-121211-172238

Wallace, R. B., Baumann, H., Grear, J. S., Aller, R. C., and Gobler, C. J. (2014). Coastal ocean acidification: the other eutrophication problem. *Estuarine Coast. Shelf Sci.* 148, 1–13. doi: 10.1016/j.ecss.2014.05.027

Weijerman, M., Fulton, E. A., Kaplan, I. C., Gorton, R., Leemans, R., Mooij, W. M., et al. (2015). An integrated coral reef ecosystem model to support resource management under a changing climate. *PLoS One* 10:e0144165. doi: 10.1371/journal.pone.0144165

Wendling, C. C., and Wegner, K. M. (2013). Relative contribution of reproductive investment, thermal stress and *Vibrio* infection to summer mortality phenomena in *Pacific oysters*. *Aquaculture* 412, 88–96. doi: 10.1016/j.aquaculture.2013.07.009

Werner, F. E., Ito, S.-I., Megrey, B. A., and Kishi, M. J. (2007). Synthesis of the NEMURO model studies and future directions of marine ecosystem modeling. *Ecol. Model.* 202, 211–223. doi: 10.1016/j.ecolmodel.2006.08.019

Weydmann, A., Walczowski, W., Carstensen, J., and Kwaśniewski, S. (2018). Warming of Subarctic waters accelerates development of a key marine zooplankton Calanus finmarchicus. *Glob. Change Biol.* 24, 172–183. doi: 10.1111/gcb.13864

Wijsman, J., Troost, K., Fang, J., and Roncarati, A. (2019). "Global production of marine bivalves. Trends and challenges," in *Goods and Services of Marine Bivalves*, ed. R. E. Ulanowicz (Cham: Springer), 7–26. doi: 10.1007/978-3-319-96776-9_2

Wiltshire, K. H., Boersma, M., Carstens, K., Kraberg, A. C., Peters, S., and Scharfe, M. (2015). Control of phytoplankton in a shelf sea: determination of the main drivers based on the helgoland roads time series. *J. Sea Res.* 105, 42–52. doi: 10.1016/j.seares.2015.06.022

Wiltshire, K. H., Kraberg, A., Bartsch, I., Boersma, M., Franke, H.-D., Freund, J., et al. (2010). Helgoland roads, North Sea: 45 years of change. *Estua. Coasts* 33, 295–310. doi: 10.1007/s12237-009-9228-y

Wiltshire, K. H., Malzahn, A. M., Wirtz, K., Greve, W., Janisch, S., Mangelsdorf, P., et al. (2008). Resilience of North Sea phytoplankton spring bloom dynamics: an analysis of long-term data at Helgoland Roads. *Limnol. Oceanogr.* 53, 1294–1302. doi: 10.4319/lo.2008.53.4.1294

Wiltshire, K. H., and Manly, B. F. (2004). The warming trend at Helgoland Roads, North Sea: phytoplankton response. *Helgoland Mar. Res.* 58, 269–273. doi: 10.1007/s10152-004-0196-0

Winder, M., and Sommer, U. (2012). Phytoplankton response to a changing climate. *Hydrobiologia* 698, 5–16. doi: 10.1007/978-94-007-5790-5_2

Wroblewski, J. S., Sarmiento, J. L., and Flierl, G. R. (1988). An Ocean Basin Scale Model of plankton dynamics in the North Atlantic:

1. Solutions For the climatological oceanographic conditions in May. *Glob. Biogeochem. Cycles* 2, 199–218. doi: 10.1029/gb002i003p00199

Yin, J. (2012). Century to multi-century sea level rise projections from CMIP5 models. *Geophys. Res. Lett.* 39:17709.

Zhang, Y., and Baptista, A. M. (2008). SELFE: a semi-implicit Eulerian–Lagrangian finite-element model for cross-scale ocean circulation. *Ocean Model.* 21, 71–96. doi: 10.1016/j.ocemod.2007.11.005

Zhang, Y. J., Ye, F., Stanev, E. V., and Grashorn, S. (2016). Seamless cross-scale modeling with SCHISM. *Ocean Model.* 102, 64–81. doi: 10.1016/j.ocemod.2016.05.002

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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in Marine Science

ORIGINAL RESEARCH
published: 23 August 2021
doi: 10.3389/fmars.2021.570354

Changes in Life History Traits of Small Pelagic Fish in the Western Mediterranean Sea

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Specialty section:
This article was submitted to
Marine Fisheries, Aquaculture
and Living Resources,
a section of the journal
Frontiers in Marine Science

Received: 07 June 2020
Accepted: 03 August 2021
Published: 23 August 2021

Citation:
Albo-Puigserver M, Pennino MG,
Bellido JM, Colmenero AI, Giráldez A,
Hidalgo M, Gabriel Ramírez J,
Steenbeek J, Torres P,
Cousido-Rocha M and Coll M (2021)
Changes in Life History Traits of Small
Pelagic Fish in the Western
Mediterranean Sea.
Front. Mar. Sci. 8:570354.
doi: 10.3389/fmars.2021.570354

Small pelagic fish (SPF) in the western Mediterranean Sea are key elements of the marine food web and are important in terms of biomass and fisheries catches. Significant declines in biomass, landings, and changes in the age/size structure of sardine *Sardina pilchardus* and anchovy *Engraulis encrasicolus* have been observed in recent decades, particularly in the northern area of the western Mediterranean Sea. To understand the different patterns observed in SPF populations, we analyzed key life history traits [total length at age, length at maturity, gonadosomatic index (GSI), and body condition (Kn)] of sardine and anchovy collected between 2003 and 2017, from different fishing harbors distributed along a latitudinal gradient from northern to southern Spain. We used Generalized Linear Models (GLM) to estimate the length at maturity and Generalized Additive Models (GAMs) to test the relationship with environmental variables (seawater temperature, water currents, and net primary productivity). The life history traits of both species presented seasonal, interannual and latitudinal differences with a clear decline in length at age, length at first maturity, and body condition, for both species in the northern part of the study area. In the southern part, on the contrary, life history traits did not present a clear temporal trend. The environmental conditions partially explained the long-term changes in life history traits, but the selected variables differed between areas, highlighting the importance of regional oceanographic conditions to understand the dynamics of small pelagic fish. The truncated length-at-age pattern for both species with the disappearance of the larger individuals of the population could have contributed to the poor condition of small pelagic fish populations in the northern part of the western Mediterranean Sea in recent years. In the south area, recent declines in body condition for sardine and anchovy were observed and could be a possible first sign for future population declines. This study highlights the importance of understanding the trade-off between the energy invested in reproduction, maintenance and growth at seasonal and interannual level to advance our knowledge on how environmental and human pressures influence population dynamics of small pelagic fish at local and regional scales.

Keywords: sardine, anchovy, length at age, maturity, reproduction, body condition

INTRODUCTION

Marine ecosystems are subjected to different global changes and anthropogenic disturbances. Strong pressures such as changes in the environmental conditions, fishing exploitation or pollution are impacting their functioning (Halpern et al., 2015; Ramírez et al., 2017). As a consequence, fluctuations in life history traits of marine fish affecting their population dynamics have been widely described (Rochet, 1998; De Roos et al., 2003). Changes in the reproductive period or the size at first maturity are usually related to changes in somatic growth and condition and ultimately affect natural mortality and recruitment success (Lloret et al., 2013; Stawitz and Essington, 2018). All of these changes are a consequence of the trade-off between the energy invested in growth, maintenance and reproduction (Stearns, 1989; McBride et al., 2015).

Because fishing is often the main cause of mortality for exploited species, it may induce phenotypic adaptive responses with changes in length and/or age at first maturity and declines in biomass (Nash et al., 2000; Ernande et al., 2004). Life history changes can be reversible if species exhibit phenotypic plasticity, while they can become irreversible if the species evolutionary adapt through selection (Stenseth and Rouyer, 2008). For example, size-selective mortality can trigger a selection for those individuals that have an early maturation (De Roos et al., 2006; Jørgensen et al., 2007). Fishing-induced truncation of size structure has been mostly found in species with protracted demography such as gadoids (Jørgensen et al., 2007), while evidence in species with short-life cycle, such as small pelagic fish, is scarce (but see Walsh et al., 2006; Enberg and Heino, 2007; Sharpe and Hendry, 2009; Dickey-Collas et al., 2010). Besides, populations that suffered from demographic erosion can become more sensitive to environmental fluctuations because of their increased dependence on young age classes and recruitment (Hsieh et al., 2006; Anderson et al., 2008; Planque et al., 2010), a process observed for various species in the western Mediterranean Sea, such as European hake (*Merluccius merluccius*) (Hidalgo et al., 2011, 2012).

Small pelagic fish have relatively short life-cycles, with fast growth, high mobility and plankton-base feeding. Therefore, they are highly sensitive to fluctuations in environmental conditions, including those related to human-induced climate change, and fishing (Agostini and Bakun, 2002; Checkley et al., 2009). Collapses of small pelagic fish have been observed in different ecosystems, such as the Pacific sardine (*Sardinops sagax*) in the California current and in the Benguela upwelling region, the *Peruvian anchoveta* (*Engraulis ringens*) in southeast Pacific Ocean or more recently the European anchovy (*Engraulis encrasicolus*) in the Bay of Biscay (Checkley et al., 2009; Taboada and Anadón, 2016). The collapse of these populations has been mainly attributed to a combination of fishing pressure and environmental-dependent recruitment success processes. However, the underlying processes driving population changes are not well understood, with varying environmental conditions, density-dependence processes and fishing pressure put forth as potential candidates of small pelagic fish population dynamics and changes (Silva et al., 2006; Peck et al., 2013; Mangano et al., 2020; Véron et al., 2020a).

Due to their large biomass, fast growth and key trophic position, the fluctuations in small pelagic fish populations can have ultimate ecological and socio-economic consequences. This is the case in the Mediterranean Sea, where sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) have a long fishing history and account for almost 40% of the total catch (FAO, 2018). Moreover, both species are key components of the functioning of Mediterranean ecosystems (Palomera et al., 2007; Coll et al., 2008). However, in the last decades, declines in landings and stock biomass of sardine and anchovy have been observed in the northwestern Mediterranean Sea, accompanied by noticeable changes in life history traits, such as declines in body condition and in length at age and length at maturity observed in the Gulf of Lions (northwestern Mediterranean Sea) (Van Beveren et al., 2014; Brosset et al., 2016b, Brosset et al., 2017; Quattrocchi and Maynou, 2017). The main hypothesis proposed for the Gulf of Lions was that these changes could be explained by bottom-up control mechanisms due to a change in plankton (Saraux et al., 2019). Similarly, in other areas of the western Mediterranean Sea, the stock assessment showed that both species are overexploited and a combination of environmental and fishing pressure could be important drivers to explain the depletion of the stocks (Coll and Bellido, 2019; Coll et al., 2019; GFCM, 2019). Interestingly, the reported changes in the life history traits of the northwestern Mediterranean populations have not been observed yet in the southwestern area (Brosset et al., 2017; GFCM, 2019), suggesting that potential regional differences in life history traits of sardine and anchovy may exist across a latitudinal gradient in the western Mediterranean Sea.

This study assesses the changes in life history traits of sardine and anchovy throughout different areas in the western Mediterranean Sea; a better understanding of the small pelagic fish population's resilience to fishing and climate change may lead to improved stock assessments and ecological analyses. Earlier studies have reported a decline in body condition for anchovy and sardine for the entire Mediterranean, with the exception of the northern Alboran Sea and Sicily channel (Brosset et al., 2017). However, general patterns to explain these changes in body condition were not found and were attributed to local environmental and anthropogenic pressure (Brosset et al., 2017).

Based on this previous study, and on the fact that the stocks of sardine and anchovy have not declined homogeneously in the western Mediterranean Sea (Pennino et al., 2020), we expected life history traits of sardine and anchovy to present different interannual patterns among areas. This prediction is based on the fact that environmental and oceanographic conditions in the southwest are different from the northwestern Mediterranean (Viñas et al., 2014; Coll and Bellido, 2019). Accordingly, our main research question was: do the life history traits of sardine and anchovy show different interannual patterns in different latitudinal areas? And if so, can this be explained by differences in the local environment? By using generalized linear and additive models (GLMs and GAMs) we investigated changes in length at age, length at first maturity, reproductive activity and body condition, and explored the synchrony of life history traits with local environmental conditions to identify potential local adaptations to exogenous drivers.

MATERIALS AND METHODS

Study Area and Data Collection

The study area is located in the western Mediterranean Sea, covering the Geographical Sub-Areas (GSAs) 01 and 06 (**Figure 1**). This area is characterized by a narrow continental shelf in the south that broadens to the north, reaching its maximum width in the Ebro delta continental shelf. We studied the area in three separated regions, that either function as different fishing grounds or with significant different potential habitat for sardine and anchovy.

The south area, GSA01 (the Alboran Sea, 36.6976° N – −3.4513° E/36.3358° N – −3.4656° E and 36.4039° N – −5.1904° E/36.2214° N – −5.3030 E) is a highly productive area, where the influx of Atlantic Oceanic waters that are rich in nutrients form important hydrographic mesoscale features. The area is delimitated in the east by the Almeria-Oran hydrographic front (Agostini and Bakun, 2002).

The central area is the Levantine region (GSA06; 38.7313° N – 0.2205° E/38.5590° N – 0.5594° E and 37.6550° N – −0.7066° E/37.4749° N – −0.2477° E), which is delineated by the Ibiza Channel (Ramírez-Amaro et al., 2018). This area is considered a more oligotrophic area (D'Ortenzio et al., 2009; Salgado-Hernanz et al., 2019), highly influenced by the dynamics of the Balearic channels (Ibiza and Mallorca channels) (Pinot et al., 2002; Balbín et al., 2014).

The north area, the Catalan coast (GSA06; 41.3492° N – 2.1875° E/41.1284° N – 2.3694° E and 40.2842° N – 0.3520° E/39,9671° N - 1.0044° E), is influenced by a southwestward current that follows the continental shelf and is considered a highly productive area due to the river run-off of the Ebro River with a marked seasonality in the primary production due to the late winter-early spring phytoplankton bloom (Salat et al., 2002; Bosc et al., 2004).

The North and South areas are both important spawning areas for sardine and anchovy in autumn-winter and spring-summer, respectively (García and Palomera, 1996; Agostini and Bakun, 2002; Palomera et al., 2007; Bellido et al., 2008). Monthly samples were obtained from commercial landings (purse seiners) in all three areas from 2003 to 2017 (see **Supplementary Table 1**). In the north samples were obtained from the harbor of Tarragona, and in the central area samples were from the harbor of Torrevieja. In the southern area samples were obtained from the harbors of Málaga and Fuengirola (**Figure 1**). Sardines were sampled in all three areas, whereas anchovies were only sampled in the northern and the southern areas, since fishing landings of anchovy in the central area were low and in consequence biological data was not collected in the period studied. Due to fishing closure and adverse weather conditions depending on the year, data in certain months were not available. Total length (cm), total weight (g), sex (male; female; indeterminate), maturity stage by visual examination [1, immature; 2, maturing; 3, mature; 4, spawning; 5, post-spawning; 6, resting; (ICES, 2008)] and gonad weight (g) were recorded for sardine and anchovy. To estimate the length at age, otoliths were collected. The number of samples for each year and area is reported in **Supplementary Table 1**.

Life History Parameters

Length at age, length at first maturity, gonadosomatic and body condition index were calculated from the data collected in the monthly biological sampling. The temporal variation of these parameters for each area was analyzed using different methodologies that are described below. In the case of length at age and length at first maturity, the relationship with environmental variables was not analyzed since changes in these traits are a consequence of long-term effects experienced by individuals throughout their life (Véron et al., 2020a) and are not driven by current environmental conditions. Instead, in the case of gonadosomatic index and body condition, the temporal relationship with environmental conditions was explored since these are two biological parameters that can respond rapidly to recent changes in environmental conditions (Lloret et al., 2013). The different areas were analyzed separately since each area presents differentiated oceanographic conditions as described above.

Length at Age and Length at First Maturity

Age-length data for sardine and anchovy were obtained from otoliths collected year-round in each area of study and thus, reflect the average status of the population all year-round. An average of 40 otoliths per month were read, covering the size range of each species sampled per month following the protocol of ICES (2017).

For each species and area, the mean length at maturity, defined as 50% of individuals reaching the sexual maturity (L_{50}), was estimated including females, males and indeterminate individuals together. Only maturity data corresponding to the reproduction period of each species was used in the determination of the L_{50} (October to March in the case of sardine, and April to September in the case of anchovy). Mature individuals were defined as those with maturity stages 2–6, and immature were defined as the individuals with maturity stage 1. Individuals at maturity stage 2 (maturing) of age 0, with otolith reading available, were considered immature, since they have not spawned previously. Generalized Linear Models (GLM) with

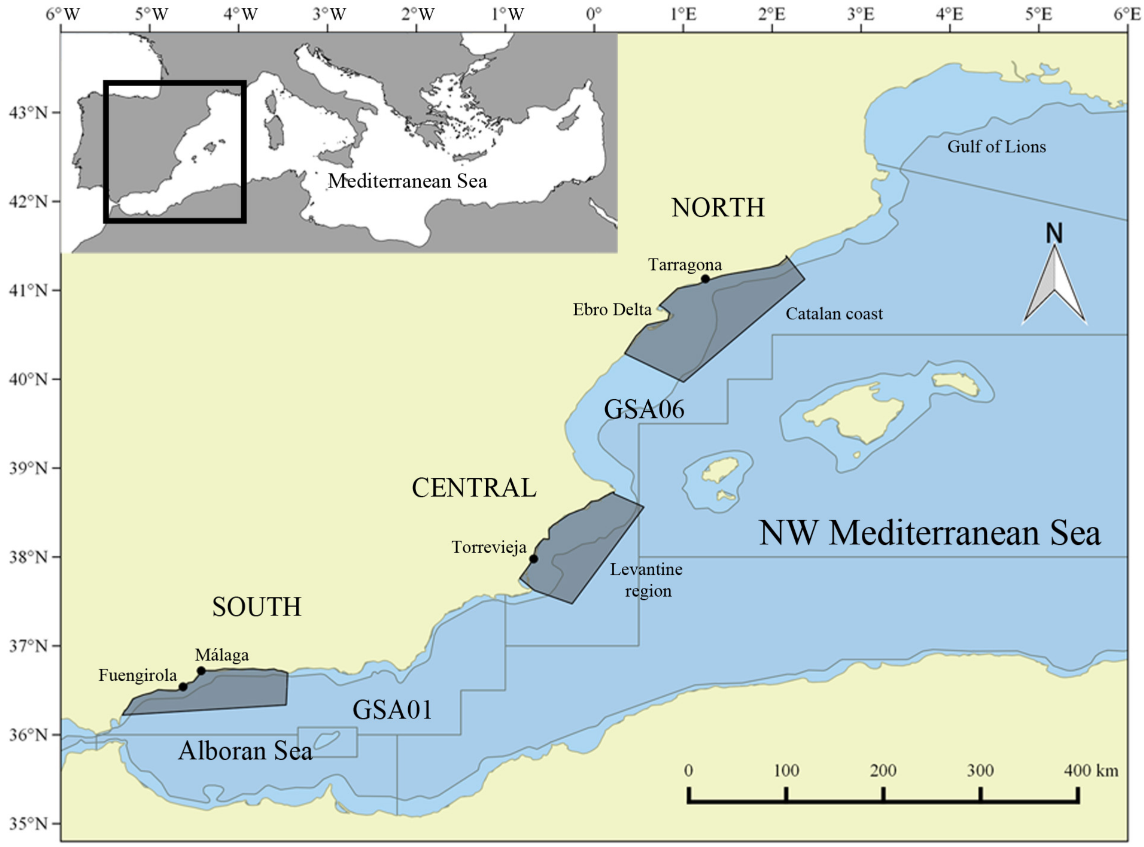

FIGURE 1 | Study area with the Geographical Sub Areas 06 and 01 delimitated. Sampling ports are indicated with a dot (Tarragona-North; Torrevieja-Central; Málaga, Fuengirola-South). The shaded polygon corresponds to the area from where the environmental data were extracted (north, central, and south). The bathymetric line corresponds to the 200 m depth.

a binomial error distribution and a logit link were used to estimate the length at first maturity (L_{50}) for each area and species by year. The proportion of mature fish and the length class at 0.5 cm were the dependent and independent variables, respectively. The lack of sufficient immature individuals did not allow us to calculate the L_{50} in certain years and further statistics to analyze the temporal variability were not applied (**Supplementary Table 1**).

Gonadosomatic Index and Body Condition

To determine the reproductive activity, only females were considered for the calculation of the gonadosomatic index (GSI), since the offspring production is frequently limited to a greater degree by egg than sperm production (Murua and Saborido-Rey, 2003). GSI was calculated as a proportion of the gonad weight to the total body weight minus the gonad weight [*%GSI = 100·Gonad weight/(Total weight − Gonad weight)*].

The analysis of temporal variability on somatic body condition was based on the calculation of the relative condition factor that has been widely used for small pelagic fish (Le Cren, 1951; Brosset et al., 2015a). The relative condition factor Kn was obtained as the ratio between the weight of the fish (expressed as total weight minus the gonad weight; W_{gutted}) and the predicted weight (Wp) for a fish of the same length (Le Cren, 1951) [$Kn = W_{gutted}/Wp$].

The Wp was estimated applying the linear length-weight relationship $\log(W_{gutted}) = \log(a) + b \times \log(TL)$ to all fish sampled in the three areas together, since we wanted to investigate differences between areas. TL is the total length, and a and b are the regression coefficients and n the sample size (sardine: $a = 0.00394$, $b = 3.2492$, $n = 35362$; anchovy: $a = 0.00398$, $b = 3.1795$, $n = 21591$). This relationship was used to calculate the somatic predicted weight ($Wp = a^{*}TL^{b}$). The selection of W_{gutted} instead of total weight was made to avoid changes related to reproduction and analyze exclusively changes in somatic body condition. By definition, values above 1 represent individuals in better condition than a standard individual, while values below 1 are individuals in worse condition than a standard individual of the studied population.

Environmental Variables

Satellite-derived environmental variables, obtained from models that assimilate satellite data, were used to model the interannual variability in gonadosomatic index and body condition. Four different variables were used: Sea Temperature (ST150 in°C) averaged over the first 150 m, mean Meridional (MC in m/s, current from south to north, positive northward) and Zonal Component of the water current field (ZC in m/s, current from west to east, positive eastward) and Net Primary

Productivity (NPP in mol/m^3/s) (**Supplementary Figure 1**). These variables were selected as they have been previously seen to influence sardine and anchovy biological processes (Giannoulaki et al., 2013; Quattrocchi et al., 2016; Pennino et al., 2020; Fernandez-Corredor et al., 2021). These variables are related to food availability and changes in temperature; the two main hypothesized drivers in previous studies to explain changes in Kn and GSI (Brosset et al., 2017; Véron et al., 2020a). Sea temperature averaged over the first 150 m was selected taking into account the bathymetric distribution of both species that can occur at depths of 100 and 200 m for sardine and anchovy, respectively (Palomera, 1992; Tugores et al., 2011). Both MC and ZC are involved in different processes of prey retention (Quattrocchi et al., 2016). The MC in the north and central area is controlled by the southwestward current that follows the continental slope, which would correspond to negative values of MC (Salat, 1996). In both areas, freshwater inputs from river discharge increase the ZC. However, the local mesoscale activity produced by local wind stress and vertical mixing can have a major influence on the circulation patterns (Salat, 1996; Agostini and Bakun, 2002). In the case of the south area, the dominance of the eastward Jet Atlantic current favor positive values of ZC (Ruiz et al., 2013). Monthly averages of oceanographic variables covering the entire study period (2003–2017) were extracted from the Copernicus Mediterranean Sea biogeochemistry reanalysis (Ref: MEDSEA_REANALYSIS_BIO_006_008; Date: 27/03/2020; Teruzzi et al., 2019; Bolzon et al., 2020) and the Copernicus Mediterranean physical reanalysis (Ref: MEDSEA_REANALYSIS_PHY_006_004; Date: 27/03/2020; Simoncelli et al., 2019).

Statistical Analysis

Temporal changes in length at age for each area were investigated by the mean of Generalized Additive Models (GAMs; Wood, 2006). Different models were tested following the procedure described in Véron et al. (2020a). First, length was modeled as a function of age class (introduced as categorical effect). Then a smooth function of the temporal co-variable year (defined as a continuous variable) was added to the previous model. Finally, the third model explored the partial effect of year in the length for each age, for that we used the "by" argument of the "gam()" function to fit a separate smooth function for each age group [i.e., s(year,by = age)], instead of one smooth function of year. In this way, we allowed the relationship between year and length to vary across age. As mentioned, age was included as a factor and year as a continuous variable through a plate regression spline. The number of knots was restricted to 4 to avoid over-fitting. GAMs were applied for the individual area, including the same predictors in each area. Each model was fitted using a Gaussian distribution validating on residuals the theoretical assumptions of normality, homoscedasticity and independence. The independence assumption of the residuals was checked plotting the residuals against the month time variable (**Supplementary Figure 4**), and no pattern suggesting lack of independence was identified. The partial autocorrelation at monthly scale was not used in this model since the response variable was a multiple time series, in the sense that, several observations were obtained at the same time. The best model was selected according to the lowest Akaike Information Criterion (AIC) and the highest adjusted R-square. The statistical analyses were performed using the *mgcv* (Wood, 2011) package, and graphs were plotted using *visreg* (Breheny and Burchett, 2017) *ggplot2* (Wickham, 2016) package of R 4.0.3 (R Core Team, 2020).

To investigate the potential environmental effects on long-term and seasonal changes in GSI and Kn, the time series of each area were decomposed in three components: (1) the trend component that was used to analyze the long-term interannual relationship between environmental variables and Kn and GSI trends, (2) the seasonal component that was used to compare the phenology of Kn and GSI in each area in relation to the seasonal behavior of the environmental variables and (3) the residual component that was not used further in the analysis. The function "decompose" (R Core Team, 2020) that uses the classical additive seasonal decomposition by moving averages (Kendall and Stuart, 1983), was implemented to decompose each response variable (GSI and Kn) and the environmental variables (NPP, ST150m, ZC, and MC) into Trend + Seasonality + Residuals. Since the time series of GSI and Kn had missing values in certain months of specific years (**Supplementary Table 1**), before performing the decomposition, the package *imputeTS* (Moritz and Bartz-Beielstein, 2017) was used to complete the time series applying Kalman smoother imputation method. After the decomposition, imputed values were removed from the time series for further analyses. Long-term de-seasonalized time series of environmental variables are presented in **Supplementary Figure 1**.

An exploratory analysis of seasonal pattern was carried out, while the de-seasonalized time series of GSI and Kn were modeled with GAMs for each species and area against the de-seasonalized environmental variables (ST150, NPP, MC, and ZC). Prior to performing the analyses, standard techniques were used to identify possible correlation and collinearity between the explanatory variables (Zuur et al., 2010). In particular, correlation among variables was checked by performing a Pearson's correlation test with the *corrplot* package (Wei and Simko, 2017). Collinearity was tested by computing the generalized variance-inflation factors (GVIF), which are the corrected VIF values by the number of degrees of freedom of a predictor variable (Fox and Weisberg, 2011). The GVIF was assessed using the "corvif" function in R software. Pairs of variables with high correlation values (Pearson's correlation above 0.7) and GVIF higher than 3, were identified. In the north area, the ZC and the MC presented high correlation and GVIF higher than 3. In the central area also ZC and MC presented high correlation and GVIF higher than 3, but also ST150 and NPP (**Supplementary Figure 5**). In those cases, only one of the variables within correlated pairs were included in the modeling process. In the GAMs, plate regression splines basis was used for explanatory variables, restricting the dimension of the basis (k) to 4, to allow a high degree of flexibility without overfitting problems. From the GAM including all the covariates, the explanatory variables included in the final model were selected with backward stepwise procedure based on Akaike Information Criterion (AIC) and adjusted R-square (R^2-*adj.*) (**Supplementary Tables 2, 5, 8**).

Considering the distribution of each response variable, GSI and Kn, a Gaussian distribution and identity link function were used. Temporal correlation in the residuals was also ultimately checked using the partial ACF (Wood, 2006). For each final GAM, a diagnosis of the model assumptions was carried out, among which the independence of the residuals was verified. In some cases, a clear temporal dependence in the residuals was detected. For solving the violation of the independence assumption the following two analyses were performed (**Table 1**). Firstly, a new temporal explanatory variable was included through a smooth function in the final GAM, such variable was defined as a sequence from 1 to the total number of observations of the response variable with step 1, representing the month in which observation was recorded. This variable, named "Time" (T), modeled the remaining time dependence of the response time series variable avoiding correlated residuals. If the diagnosis of the residuals of the previous model was corrected, a final model was achieved. In other cases, time series models could be useful to solve the temporal dependence in the residuals. More precisely, the best autoregressive–moving-average model (ARMA), see Brockwell and Davis (2002), according to the AIC criteria, must be identified for the residuals time series. The selection of the best ARMA model using AIC criteria was done through "auto.arima" function of *forecast* package (Hyndman and Khandakar, 2008; Hyndman et al., 2020). Once, the values of the optimal orders of the ARMA were identified, as described previously, the argument correlation of "gamm()" function of *mgcv* package (Wood, 2011) allowed to adjust both models simultaneously, the GAM model with ARMA terms, this approach has been widely used (Yang et al., 2012; Holmes et al., 2021). The best (and most parsimonious) model was finally chosen based on the compromise between low AIC values, high R^2-*adj.*, and significant predictors. The code used for the analysis carried out can be found in the GitHub repository[1].

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[1] https://github.com/MgraziaPennino/Changes-in-life-history-traits-of-small-pelagic-fish-in-the-western-Mediterranean-Sea

TABLE 1 | Comparison between the Generalized Additive Model selected (GAM) of GSI and Kn, the GAM combined with the temporal explanatory variable (time variable) (GAM + Time) and the GAM combined with an ARMA model (corARMA), for each species (sardine and anchovy), trait (GSI and Kn) and for each area.

	Area	Model type	Parameters included	R^2-*adj.*	AIC
Sardine GSI	North	GAM	MC + ST150 + NPP	0.526	23.1918
		GAM + Time	**MC + ST150 + NPP + T**	**0.675**	**−11.3313**
		GAM + Time + ARMA	ST150	0.343	−437.9223
	Central	GAM	ZC + NPP	0.496	−3.60679
		GAM + Time	**ZC + NPP + T**	**0.748**	**−49.31529**
		GAM + Time + ARMA	ZC	0.0735	−142.75485
	South	**GAM**	**ZC + ST150 + NPP**	**0.368**	**69.7838**
		GAM + Time	ZC + ST150 + NPP + T	0.398	73.7103
		GAM + ARMA	ZC	−0.108	−354.4148
Anchovy GSI	North	GAM	MC + ST150 + NPP	0.492	179.35468
		GAM + Time	**MC + ST150 + NPP + T**	**0.922**	**−44.81075**
		GAM + Time + ARMA	–	0.724	−307.31535
	South	**GAM**	**MC + ZC**	**0.388**	**87.00971**
		GAM + Time	MC + ZC + T	0.447	84.70779
		GAM + ARMA	MC + ZC	−0.419	−236.5413
Sardine Kn	North	GAM	MC + ST150 + NPP	0.397	−691.2924
		GAM + Time	**MC + ST150 + NPP + T**	**0.653**	**−765.8567**
		GAM + Time + ARMA	T	0.279	−1115.3969
	Central	GAM	MC + NPP	0.530	−665.8308
		GAM + Time	MC + NPP + T	0.691	−692.0069
		GAM + Time + ARMA	**MC + NPP + T**	**0.621**	**−881.1502**
	South	GAM	MC + ST150 + NPP	0.27	−619.5305
		GAM + Time	MC + ST150 + NPP + T	0.683	−717.0292
		GAM + Time + ARMA	**MC + ST150 + T**	**0.255**	**−1182.2717**
Anchovy Kn	North	GAM	ZC + ST150 + NPP	0.523	−763.9239
		GAM + Time	**ZC + ST150 + NPP + T**	**0.830**	**−847.8216**
		GAM + Time + ARMA	ZC + NPP	−0.0254	−1067.5924
	South	GAM	MC + ZC + ST150 + NPP	0.745	−715.4204
		GAM + Time	**MC + ZC + ST150 + NPP + T**	**0.816**	**−740.2001**
		GAM + Time + ARMA	MC + ST150	0.269	−1015.6587

The parameters that were statistical significant (p-value < 0.05) are reported. Statistics acronyms are: R^2-adj., coefficient of determination adjusted; AIC, Akaike Information Criterion. The model selected is highlighted in bold. The letters describing the parameters included in the model stands for: meridional current (MC), zonal currents (ZC), average sea temperature of 150 m (ST150), net primary production (NPP), and time (T).

RESULTS

Changes in Length at Age

Sardine

Sardine individuals of age classes from 0 to 8 were found, with few individuals belonging to the oldest categories (276 out of 23,269 individuals sampled, had an age of 6–8 years). Most of the older individuals were sampled in the south area (**Figure 2** and **Supplementary Figure 2**). In the north area, there was a sharp decline in length at age during the period 2012–2017 (**Figure 2** and **Supplementary Figure 2**). Moreover, individuals of older ages (4, 5, and 6) disappeared from the population in the north and central area.

Length modeled as a function of age and a partial effect of year for each age was the best model selected (**Supplementary Table 2**). The GAM fitted to the sardine length-at age showed no apparent violation of the normality of the residuals or of the homogeneity of variances. Overall, comparing the models in the three areas, length at age followed a latitudinal gradient with larger fish found in the south than in the central area and the smaller fish found in the north for all ages. GAM

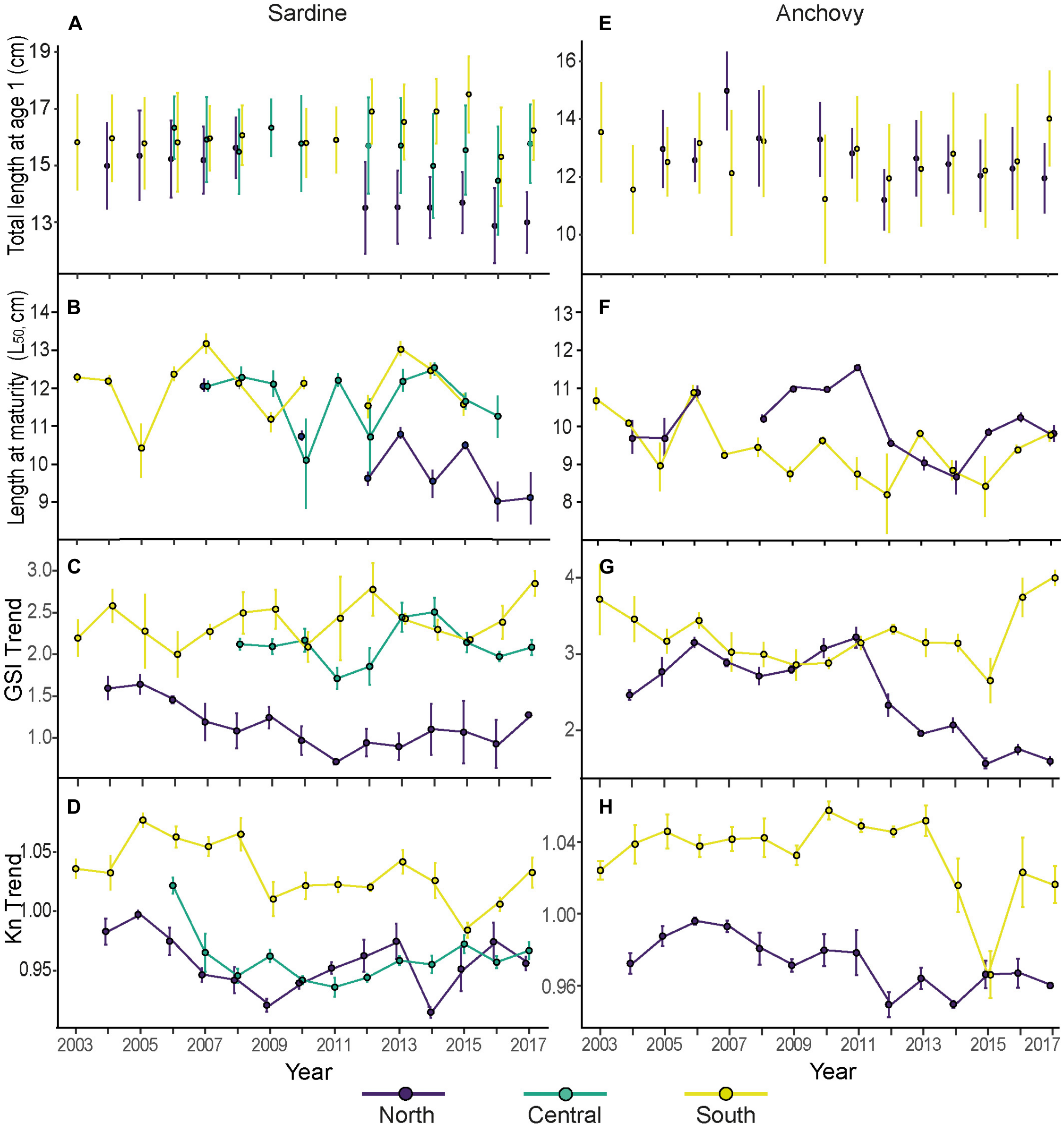

FIGURE 2 | Summary figure with annual mean and standard deviation values of total length of age 1 (see **Supplementary Figures 2, 3** for a plot of all ages) **(A,E)**, mean and standard error of length at maturity (L_{50}) **(B,F)**, mean and standard deviation values of the gonadosomatic index trend (values obtained after decomposition; GSI trend) **(C,G)** and trend of the relative condition factor (values obtained after decomposition; Kn trend) **(D,H)**. All values are reported by species, for sardine on the left and for anchovy on the right side. Each color represents an area (North, Central, and South).

of the north area showed that the decline in length at age was consistent through the age classes 0–4, and the model that include the covariates age and year had an adjusted R-square (R^2*-adj.*) of 0.653 (**Figure 3** and **Supplementary Table 2**). In the central area, an increase in length at age 0 was observed from 2013 until 2017, while in ages 1–4 there was a significant decline in length at age. The fitted model including age and year covariates had a R^2*-adj.* of 0.669. In the south area, a continuous increase of length at age for age 0 and an increase for ages 1–4 until 2014 were observed, with a latter decline in length at age for the period 2015–2017 for ages 1–4. In this case, the model had a R^2*-adj.* of 0.803 (**Figure 3** and **Supplementary Tables 2, 3**).

Anchovy

The ages of the majority of individuals of anchovy were comprised between 0 and 2 years of age and individuals of age 3 and 4 were only recorded before 2013 in the two areas sampled (**Figure 2** and **Supplementary Figure 3**). Opposite to sardine, in anchovy, latitudinal differences in length at age were not observed.

Length modeled as a function of age and a partial effect of year for each age was the best model selected (**Supplementary Table 2**). The GAM fitted to the anchovy length-at age showed no apparent violation of the normality of the residuals or of the homogeneity of variances. In the north area, the age class and the smooth function of year by age class had a R^2*-adj.* of 0.497, and a decline in length at age was observed in age 0 and 1. An increase in length at age 2 was observed from 2013 onward (**Figure 3** and **Supplementary Table 3**). In the south, the model had a R^2*-adj.* of 0.328. The dynamics in the south were different from the north area. Ages from 0 to 2 showed an increase in length at age. For age 3 a slight increase was observed followed by a decline after 2008 (**Figure 3**). In general, the fitted GAM models of anchovy had lower R^2*-adj.* values compared to sardine (**Supplementary Tables 2, 4**).

Changes in Length at First Maturity (L_{50})

Sardine

Different temporal patterns were observed in sardine L_{50} between areas (**Figure 2**). Although in the three areas there were yearly fluctuations in L_{50}, a clear temporal decline was only observed in the north area. Consequently, in the period 2012–2017 the north area presented lower L_{50} than the other two areas. The

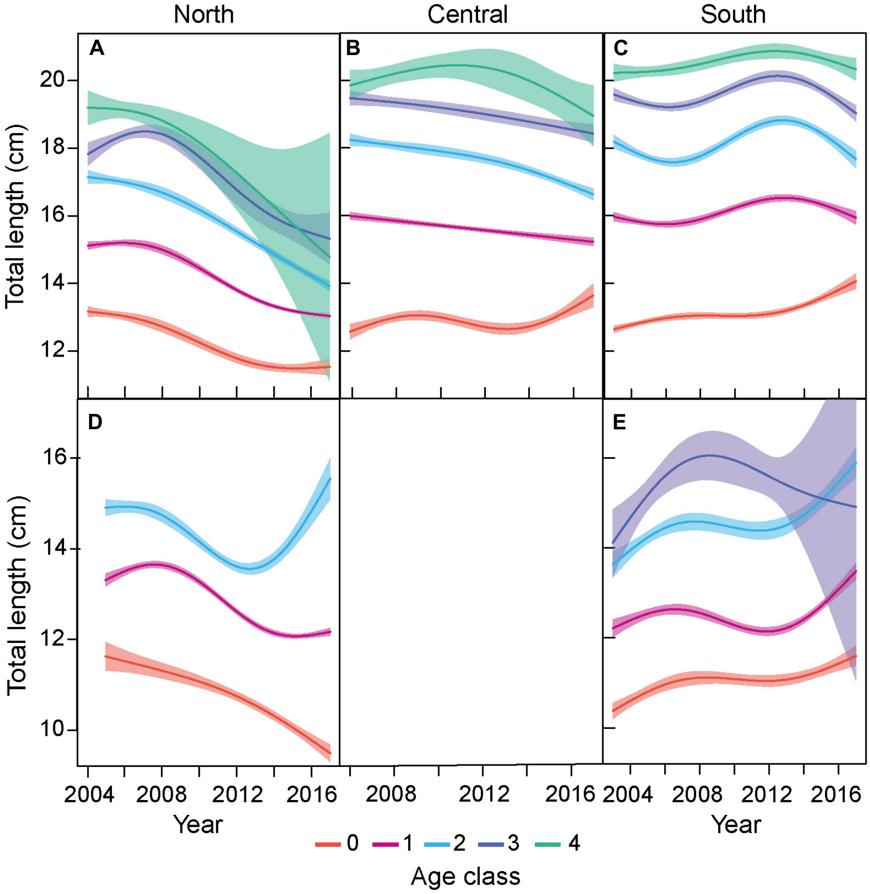

FIGURE 3 | Long-term changes in total body length at age for sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*). Partial effect of the GAMs model are represented for each species and area; sardine North **(A)**, Central **(B)**, South **(C)**; anchovy North **(D)**, south **(E)**. Lines correspond to the fit of the GAM model. The shaded areas indicate the 95% confidence interval. Only age classes with significant effects are represented.

average L_{50} in the north area in the period 2012–2017 was 10.45 ± 0.09 cm (mean ± standard error). Instead, the L_{50} in the central and southern areas showed larger L_{50} (12.41 ± 0.12 cm, and 12.39 ± 0.13 cm, respectively; **Figure 2**).

In the north area, for the period 2004–2011, it was only possible to calculate the L_{50} in 2007 and 2010, due to the lack of immature individuals in the other years. Despite the missing values, it was observed a progressive decline in L_{50} with the highest value of L_{50} observed in 2007 (12.58 ± 0.17 cm) and the lowest values observed in 2016 (9.51 ± 0.52 cm). In the central area, the L_{50} presented fluctuations with maximum L_{50} observed in 2014 (13.01 ± 0.18 cm) and minimum values in 2010 and 2012 (10.51 ± 1.19 cm and 11.22 ± 1.00 cm, respectively). Similar to the central area, the south also presented fluctuations in the L_{50}. The highest L_{50} values were observed in 2007 and 2013 (13.68 ± 0.26 cm and 13.55 ± 0.20 cm, respectively) and the lowest in 2005 (10.85 ± 0.71 cm).

Anchovy

Length at first maturity of anchovy estimated per year and area showed high interannual variability in both areas. In the period 2008–2011 the L_{50} in the north area was clearly higher than in the south. In the last period of this study (2012–2017), the average L_{50} was similar between both areas (9.56 ± 0.06 cm and 9.39 ± 0.1 cm, north and south areas, respectively).

In the north area, the maximum L_{50} values were observed in 2011 (11.56 ± 0.08 cm), followed by three consecutive years of L_{50} decrease. The minimum L_{50} was observed in 2014 (8.66 ± 0.44 cm). In the south area, the maximum L_{50} was observed in 2003 and 2006 (10.72 ± 0.30 and 10.92 ± 00.16 cm, respectively) and declined, with fluctuations, until 2012, when the lowest L_{50} value was observed (8.22 ± 1.06 cm) (**Figure 2**).

Changes in Gonadosomatic Index (GSI)

Sardine

The seasonal component of the decomposed gonadosomatic index (GSI) of sardine females showed maximum values from November to February in the three areas (**Figure 4A**). In the north the seasonal component had a lower amplitude, while the central area and the south presented similar seasonal patterns. Regarding interannual trends (**Figure 2C**), lower values of GSI were observed in the north compared to the central and south areas for 2004–2017. In the north area, the GSI was highest in 2005 and declined until 2011. Then, from 2011 to 2014, the GSI presented interannual fluctuations without a clear long-term trend. Instead, the other two areas, central and south area, showed fluctuations for the entire study period. The central area had a minimum value of GSI in 2011 coinciding with the minimum GSI of the north area and a maximum GSI value in 2014. In the south, the lowest GSI were observed in 2006 and 2010 and the highest in 2012 and 2017 (**Figure 2C**).

The interannual trend of NPP and ST150 in the central area, and MC and ZC in the north and central area, presented high correlation (Pearson's correlation above 0.7; **Supplementary Figure 5**), and hence only one of both explanatory variables, in particular MC variable in the north and ZC and NPP in the central area, was included in the GAM model. Therefore, all variables used in the models had a GVIF lower than 3. The environmental variables retained in the models, by the backward selection procedure, were MC, ST150, and NPP in the north and south area, and ZC and NPP in the central area (**Supplementary Table 5**). Results of the GAM analysis of the interannual trend of GSI showed marked differences between areas in the form of the partial effect of selected environmental variables. The GAM fitted to the sardine gonadosomatic index showed no apparent violation of the normality of the residuals or of the homogeneity of variances. Given the high autocorrelation of long-term trends time series, some partial autocorrelation at monthly scale once the seasonal cycles were removed, persisted in the residuals at the first and second order. Hence, as mentioned in section "Statistical Analysis," the temporal explanatory variable (month variable) was included in the model for avoiding correlated residuals. The resulting model showed that for the north and central area the R^2*-adj.*, AIC and partial autocorrelation function of the residuals improved (GAM + Time; **Table 1**). Despite this improvement, autocorrelation in the residuals was not removed completely (**Supplementary Figure 6**). Hence, we carried out the second analysis, described in section "Statistical Analysis," which models the dependence in the residuals through an ARMA model. The GAM combined with the ARMA model was able to remove the temporal dependency in the residuals and the obtained AIC was lower. However, the models were not meaningful and the R^2*-adj.* values were very low in the three areas (**Table 1**). Therefore, the selected models were the GAM including the temporal variable (month variable; GAM + Time) in the north and central area. In the south the selected model was the GAM, since the addition of a temporal variable had a small improvement of the R^2*-adj.* and the AIC increased (**Table 1**).

In the north area, the selected model had a R^2*-adj.* of 0.675 (**Supplementary Tables 5, 6**). The GSI displayed a negative relationship with NPP and a dome shaped relationship with MC. Maximum GSI values were observed when the meridional current was close to 0. The sea temperature positively affected the GSI at sea temperatures below 15.4°C. Above this value significant negative effects were found (**Figure 5A**). The final model of the central area had a R^2*-adj.* of 0.748 and included the ZC and NPP variables (**Supplementary Tables 5, 6**). The GSI of sardine had a positive relationship with ZC (eastward current) (**Figure 5B**). Unlike the north area, the GSI in the central area displayed a positive relationship with NPP. In the south area, the model selected had a R^2*-adj.* of 0.368 lower than in the other two areas, because the temporal variable was not included in this model (**Table 1** and **Supplementary Table 5**). In the south, GSI displayed a negative relationship with southward flowing current (corresponding to negative values of MC) and a positive relationship with northward flowing current (positive values of MC) (**Supplementary Table 6**). The ST150 and NPP had a positive effect on GSI of sardine (**Figure 5C**).

Anchovy

The seasonal component of the decomposed GSI of anchovy females showed high values from May to August in the north area and from April to August in the south area (**Figures 4B,E–H**). The south area presented higher maximum values than the north.

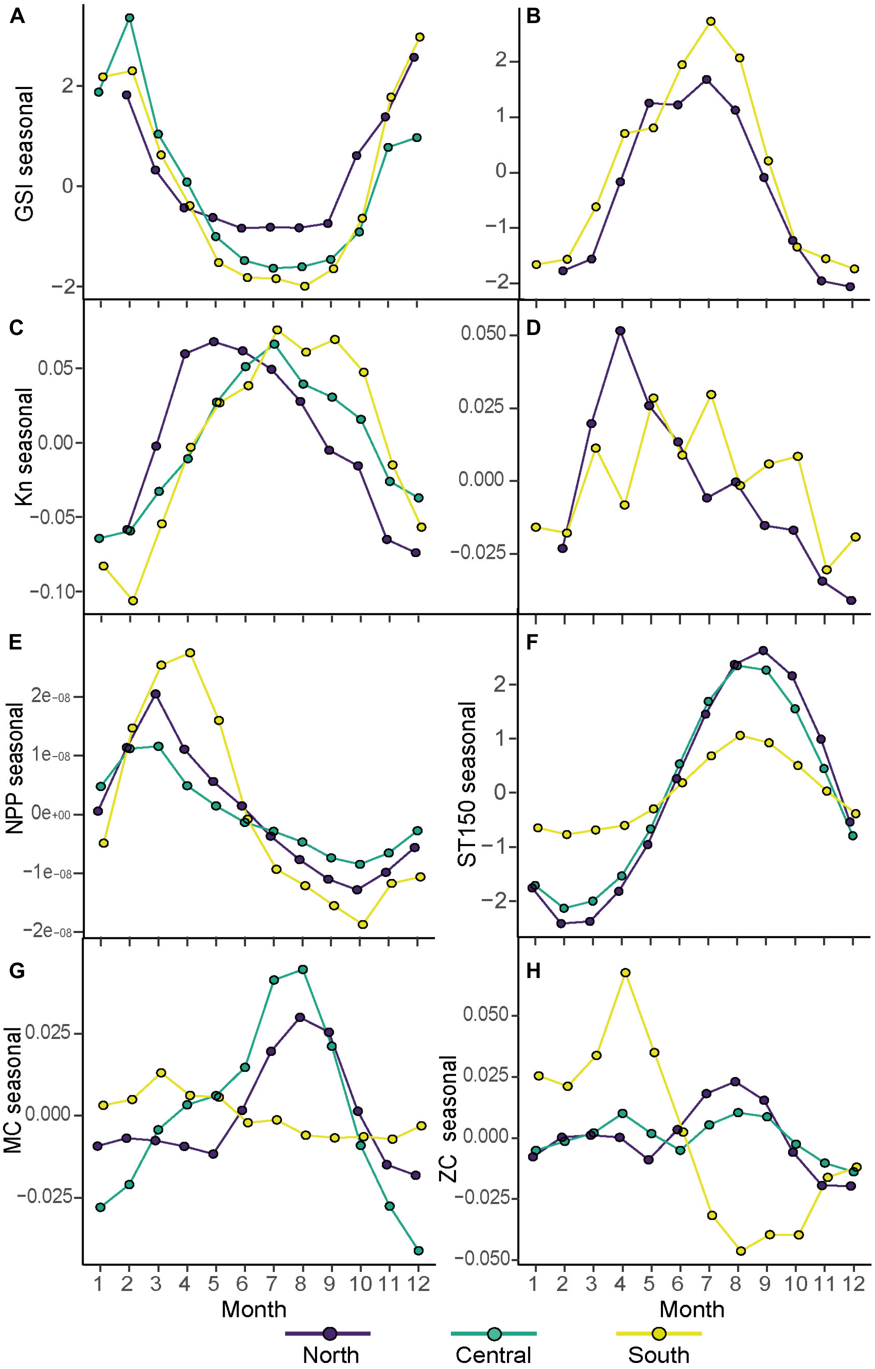

FIGURE 4 | Seasonal component of the detrended time series of the gonadosomatic index (GSI seasonal) and relative condition factor (Kn seasonal) for sardine **(A,C)** and for anchovy **(B,D)**. Environmental seasonal components for net primary production (NPP; **E**), Sea Temperature at 150 m (ST150m; **F**) and the zonal current (ZC; **G**) and meridional current (MC; **H**). Each color represents an Area (North, Central, and South).

The interannual trend in GSI (**Figure 2F**) showed similar values between areas in the period 2006–2011, after which a marked decline in the GSI of the north area was observed, while the GSI of the south was maintained. Consequently, the GSI values of the north were lower than the GSI values of the south in the period 2012–2017 (**Figure 2F**).

As mentioned above for sardine, MC and ZC in the north presented high correlation (Pearson's correlation above 0.7; **Supplementary Figure 5**), and hence only one of both explanatory variables, in particular MC variable, was included in the GAM model. Therefore, all variables used in the models had a GVIF lower than 3. The environmental variables retained

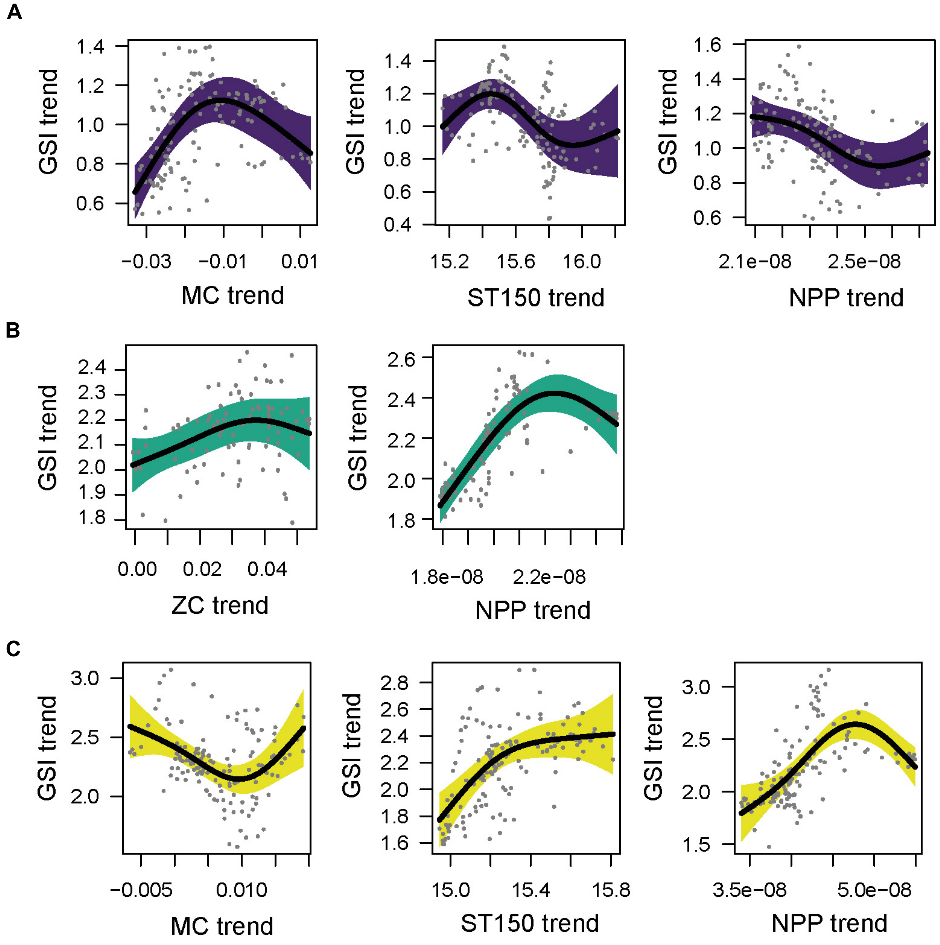

FIGURE 5 | Partial GAM plots for gonadosomatic index (GSI) of sardine females (*Sardina pilchardus*) for each area; **(A)** North (purple), **(B)** Central (green), **(C)** South (yellow). Significant partial effects of meridional current (MC), zonal currents (ZC), average sea temperature of 150 m (ST-150) and net primary production (NPP) are represented. The shaded areas indicate the 95% confidence interval.

in the models, by the backward selection procedure, were MC, ST150 and NPP in the north, and MC and ZC in the south (**Supplementary Table 5**). The GAM fitted to the anchovy gonadosomatic index, in the north and south area, showed no apparent violation of the normality of the residuals or of the homogeneity of variances. Similar to sardine and following the same procedure described in the previous section, partial autocorrelation at monthly scale once the seasonal cycles were removed, persisted in the residuals at the first and second order. In the north area, the GAM including the temporal variable (GAM + Time) was selected. In the south, the GAM without the temporal variable was maintained as the best model, since the slight improvement in terms of the R^2-*adj*. and the AIC criterion, when the temporal variable was included, did not compensate for the increase in the model complexity (**Table 1** and **Supplementary Figure 6**).

The final model of the north area had a R^2-*adj*. of 0.922 (**Supplementary Tables 5, 7**). High values of GSI in the north were related to MC close to 0 or positive (south to north current) and the ST150 had a positive effect. The NPP positively affected the GSI, but for high values of NPP the effect on GSI was negative (**Figure 6A**). The final model of the south area had a R^2-*adj*. of 0.368, this value was lower than in the north since the temporal variable was not included in the model (**Supplementary Table 7**). In the final model the two components of the current were selected. The MC, south to north current, had a positive effect with increasing GSI. The ZC also had a slight positive effect for low positive values, with maximum values of GSI between 0.4 and 0.6 m/s of the west to east current (**Figure 6B**).

Changes in Body Condition (Kn)

Sardine

The seasonal component of the decomposed body condition index (Kn) of sardine had different peaks between areas (**Figure 4C**). Maximum values of seasonal Kn in the north were observed from April to August, while in the central and south areas the maximum values of sardine seasonal Kn were observed from May to October. When looking at the interannual trend (**Figure 2D**), lower values of Kn were observed in the north and central area compared to south for the entire study period.

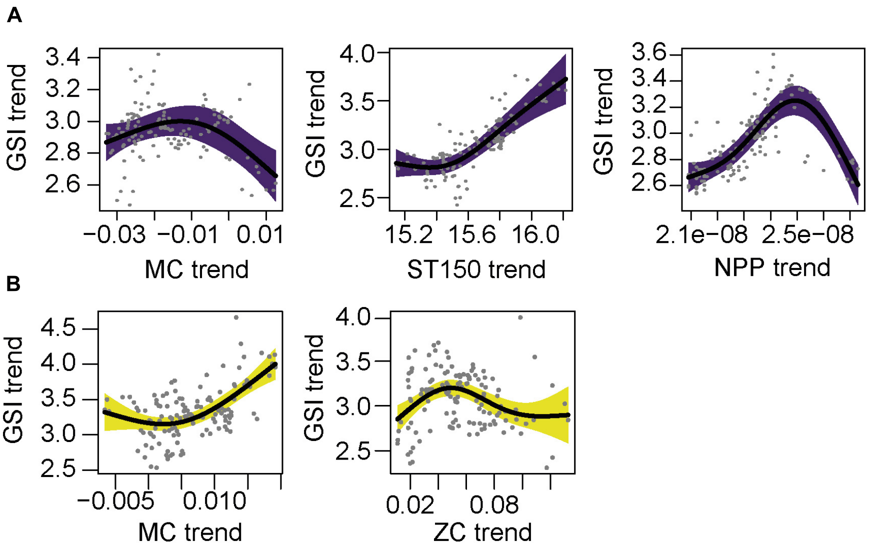

FIGURE 6 | Partial GAM plots for gonadosomatic index (GSI) of anchovy female (*Engraulis encrasicolus*) for each area; **(A)** North (purple) and **(B)** South (yellow). Significant partial effects of meridional current (MC), zonal currents (ZC), average sea temperature of 150 m (ST-150) and net primary production (NPP) are represented. The shaded areas indicate the 95% confidence interval.

In the north, the Kn interannual trend declined from 2006 to 2009, after which it increased from 2010 until 2013. Kn then sharply declined, followed by a recovery on the period 2015–2017. The central area showed Kn pattern similar to the north, with a decline of Kn from 2007 to 2011 and a moderate increase from 2012 to 2017 (**Figure 2D**). In the south area the maximum values of Kn were observed in the period 2005–2008, whereas the period with lower Kn values was from 2009 onward.

After the exploration of correlation between environmental variables explained in the section "Changes in Gonadosomatic Index (GSI)," the analysis of the relationship between interannual trend of sardine body condition and the environmental variables showed that the retained variables in the models differed between areas. In the north the environmental variables selected were MC, ST150 and NPP, in the central area MC and NPP and in the south MC and ST150 (**Supplementary Table 8**). The GAM fitted to the sardine body condition showed no apparent violation of the normality of the residuals or of the homogeneity of variances. Given the high autocorrelation of long-term trends time series some partial autocorrelation in the residuals persisted at the first and second order. Hence, as mentioned in sections "Statistical Analysis" and "Changes in Gonadosomatic Index (GSI)," two alternative models were applied to improve the temporal autocorrelation in the residuals. The best model attained in the north was the GAM model with the temporal variable (GAM + Time; **Table 1**) since the inclusion of an ARMA model on the residuals leads to a model where all environmental variables were not significant, and consequently to a substantial decrease in the R^2-*adj* value. In the central and south area the selected models were the GAM model combined with ARMA model on the residuals (GAM + Time + ARMA; **Table 1** and **Supplementary Figure 7**). This model was selected in the south area in spite of its lower R^2-*adj*. value since previous models showed a violation of the independence assumption on the residuals whereas the GAM + Time + ARMA attained a valid model removing such residuals pattern.

In the north area, from the correlated variables MC and ZC, only MC was included in the GAM model (**Supplementary Table 8**). The selected model had a R^2-*adj*. of 0.653 (**Supplementary Table 9**). The MC had a negative effect on Kn at negative values (negative values correspond to north to south current) and positive effect for low current (values close to 0). The ST150 and NPP had a positive effect on Kn (**Figure 7A**). In the central area from the pair correlated environmental variables, MC and NPP were included. The final GAM model combined with ARMA model had a R^2-*adj*. of 0.621 (**Supplementary Table 9**). Kn of sardine in the central area decreased with higher values of northward current (MC) and the NPP had a clear positive effect on Kn (**Figure 7B**). In the south area the final GAM with a ARMA model had a R^2-*adj*. of 0.255. The MC had a positive relationship with Kn, and the ST150 had a negative effect on Kn (**Figure 7C**).

Anchovy

When comparing the north and south area, the seasonal component of the decomposed body condition index (Kn) presented different seasonal pattern (**Figure 4D**). While in the north there was a clear peak in Kn of anchovy in April with a continued decline of Kn from May to December, in the south area the Kn of anchovy was maintained with similar Kn values from March until October and with monthly variability. When looking at the interannual trend of anchovy Kn (**Figure 2G**), lower values of Kn were observed in the north compared to the south area for the entire period studied (2004–2017), with the exception of 2015 that presented extremely low Kn values and was similar to the values observed in the north. The Kn in the north declined until

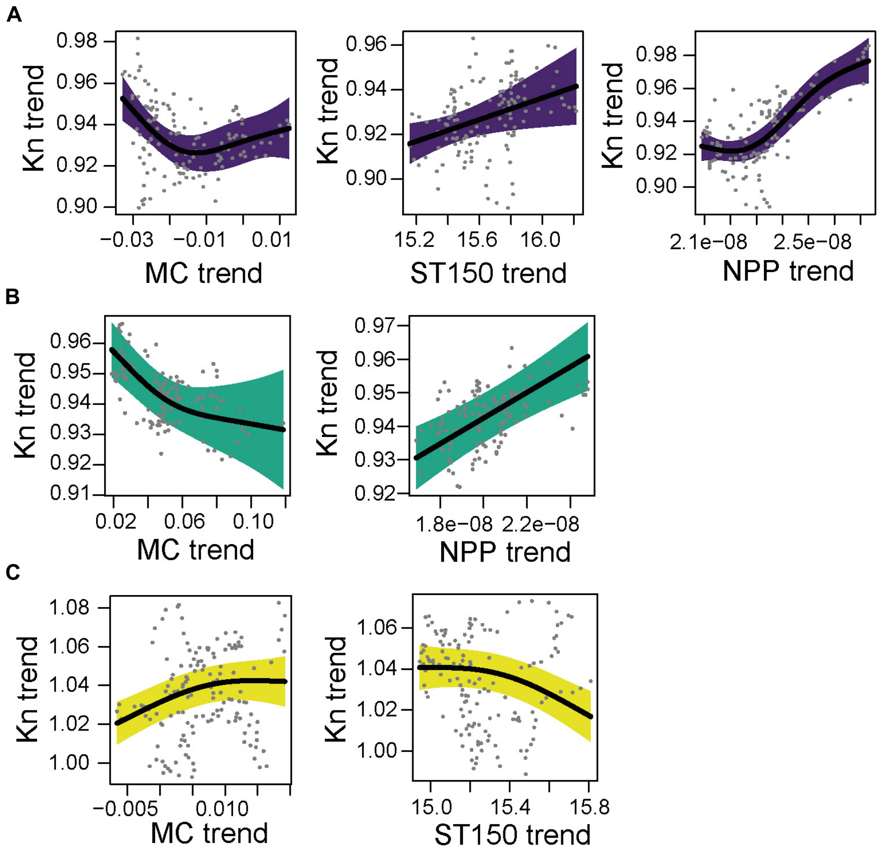

FIGURE 7 | Partial GAM plots for body condition index (Kn) of sardine (*Sardina pilchardus*) for each area; **(A)** North (purple), **(B)** Central (green), and **(C)** South (yellow). Significant partial effects of meridional current (MC), zonal currents (ZC), average sea temperature of 150 m (ST150) and net primary production (NPP), are represented. The shaded areas indicate the 95% confidence interval.

2012 and in the period 2012 to 2017 values of anchovy Kn in the north were lower than in the period 2004–2011.

In the interannual analysis of the Kn trends the four environmental variables were retained in the south and in the north since MC and ZC had a high correlation, only ZC was included in the GAM model. The GAMs fitted to the anchovy body condition, in the north and south areas, showed no apparent violation of the normality of the residuals or of the homogeneity of variances. Partial autocorrelation at monthly scale once the seasonal cycles were removed, persisted in the residuals at the first and second order. After adding to the GAM the explanatory month variable (GAM + Time), in the north and south area the R^2*-adj*., AIC and partial autocorrelation of the residuals improved (**Table 1** and **Supplementary Figure 7**). The GAM combined with the ARMA model was able to remove the temporal dependency in the residuals and the obtained AIC was lower. However, the models were not meaningful and the R^2*-adj*. values were very low in the two areas compared to the GAM and GAM + Time models (**Table 1**). Therefore, the selected models were the GAM including the temporal variable (GAM + Time) in both areas (**Table 1** and **Supplementary Tables 9, 10**).

The final GAM model of Kn for anchovy in the north had a R^2*-adj*. of 0.83 (**Supplementary Table 10**). The ZC had a positive effect at negative values of current (east to west current), and a negative effect at positive values of ZC (west to east current). The ST150 and NPP had a positive effect on Kn. In the case of sea temperature, the highest values of Kn of anchovy were observed between sea temperatures of 15.8 and 16.0°C (**Figure 8A**). In the south area, the final model of anchovy Kn in the south had a R^2*-adj*. of 0.816 (**Supplementary Table 10**). The MC had a positive effect until 0.010 m/s, above which the effect on Kn was negative. Similarly, the ZC had a positive effect on Kn for west to east currents up to 0.08 m/s. Both, ST150m and NPP had a clear positive effect on Kn of anchovy in the south (**Figure 8B**).

DISCUSSION

The overall aim of this study was to assess changes in life history traits of sardine and anchovy in three areas of the western Mediterranean Sea. Differentiated long-term patterns were observed between northern and southern areas in the traits studied in both species (i.e., length at age, length at maturity, GSI, and Kn) with major long-term declines observed in the north (**Table 2**). The environmental conditions partially explained the changes in GSI and Kn, but the selected variables

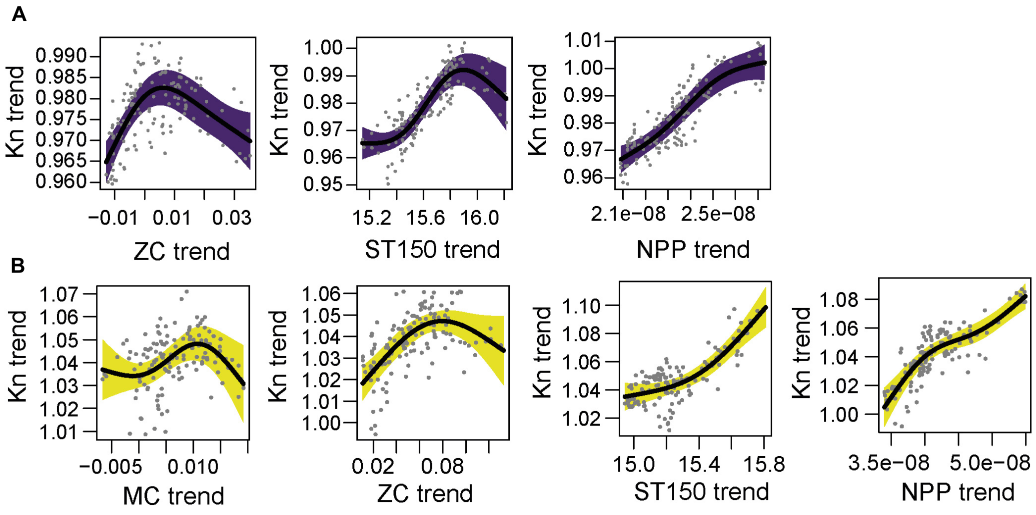

FIGURE 8 | Partial GAM plots for body condition index (Kn) of anchovy (*Engraulis encrasicolus*) for each area; **(A)** North (purple) and **(B)** South (yellow). Significant partial effects of meridional current (MC), zonal currents (ZC), average sea temperature of 150 m (ST-150) and net primary production (NPP), are represented. The shaded areas indicate the 95% confidence interval.

TABLE 2 | Summary table of the main trends observed for each life history trait studied; length at age, length at maturity (L_{50}), gonadosomatic index (GSI) and body condition index (Kn), for sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the western Mediterranean Sea.

Temporal/ Latitudinal	**Length at age**	**L_{50}**	**GSI**	**Kn**
Sardina pilchardus				
Latitudinal	N < C < S	N < C; S	N < C;S	N = C < S
North	Decreased all ages Disappearanced old ages	Decreased	Decreased 2004–2011 Increased 2011–2017	Decreased 2004–2009 Increased 2010–2017
Central	Increased Age 0 Decreased Ages 1–4	Fluctuations	Increased 2011–2014 Decreased 2015–2017	Decreased 2006–2011 Increased 2012–2017
South	Increased Age 0 Increased Age 1–4 until 2014 that decreased	Fluctuations	Fluctuations with Overall increased	Increased 2003–2008 Decreased 2009–2017
Engraulis encrasicolus				
Latitudinal	N < S	N = S	N < S	N < S
North	Decreased Ages 0–1 Decreased Age 2 until 2013 that increased	Decreased	Increased 2004–2011 Decreased 2012–2017	Decreased 2007–2017
South	Increased Ages 0–2 Increased Age 3 until 2008 that stabilized	Decreased	Decreased 2003–2015 Increased 2016–2017	Stable 2003–2013 Decreased 2014–2017

For each species, the latitudinal differences between north "N," central "C," and south "S" areas, and the temporal pattern for each area separately, are described. Decreasing trends are indicated with red and the combination of increasing and decreasing trends or fluctuations are indicated in yellow.

differed between areas, highlighting the importance of regional oceanographic conditions to understand the dynamics of small pelagic fish (**Table 3**). Although the overall seasonal phenology of the gonadosomatic index and body condition was similar to those described in previous studies for sardine and anchovy, monthly differences between areas were observed in both parameters, demonstrating that latitudinal differences exist at seasonal and interannual level. Thus, management plans of sardine and anchovy should take into consideration both large scale and regional dynamics.

Looking at the spatial differences in life history traits, the north and south area presented clear differences for both species, with higher GSI and Kn values in the south area and in the case of sardines, higher length at age and L_{50} as well. Spatial differences in L_{50} within the same species are common (Stahl and Kruse, 2008). For example, in the case of sardine, Silva et al. (2006) described lower size at first maturity in the Gulf of Cadiz than the northeastern Atlantic. Also, previous works described a higher growth for anchovy populations and a higher length at age for sardine in the Alboran Sea compared to the Ebro delta area (Alemany and Álvarez, 1993; Ventero et al., 2017). These differences between areas were linked to the existence of two genetically differentiated stocks that are separated by the Almeria-Oran front (Viñas et al., 2014;

Pascual et al., 2017; Coll and Bellido, 2019). In the northwestern Mediterranean larval dispersal between the Gulf of Lions and the Ebro Delta has been described for anchovy. The central area of our study has received less attention and studies on larval dispersion are not available, but certain connectivity between north and central area of study could be expected due to the effect of the Northern Current (Ospina-Alvarez et al., 2015). In other studies, better feeding conditions (quality and quantity) in anchovy and sardine larvae were proposed as the driver to explain the faster growth observed in the Alboran Sea compared to the northwestern Mediterranean Sea (García et al., 2003; Mercado et al., 2007; Quintanilla et al., 2015). As the south area presented higher net primary production levels than the central and north area, apart from genetic differences between populations, differences in length at age for adult stages of sardine and anchovy could be influenced by the early life stages growth and condition related to plankton dynamics. Similarly, the higher Kn and GSI values observed in the south could also be explained by the higher NPP observed in the south area.

Differences between areas in food (energy) availability or timing may influence the energy acquisition and allocation patterns and ultimately affect the trade-off between maintenance, reproduction and growth of sardine and anchovy. The seasonal cycles of life history traits play a key role in understanding these trade-offs. When exploring the relationship between seasonal patterns in GSI, body condition and environmental variables, we observed that for sardine and anchovy in the north, the body condition peaked and declined earlier than in the central and south area. Similar to our results, Giráldez and Abad (1995) also described different seasonal peaks of body condition in the south for anchovy. These differences in the seasonal pattern of body condition might play a key role in the dynamics of the reproduction of sardine, as this species accumulates energy during spring and summer for reproduction in autumn and winter (Albo-Puigserver et al., 2020). Low body condition before the start of the reproduction in October could have affected the quality of the spawning and ultimately the recruitment success in the northern area, as has been suggested for sardine off the coast of Portugal (Garrido et al., 2007). Instead, the delayed peak in body condition of the central area could explain the maintenance of higher GSI values. Surprisingly, the seasonal Kn pattern of anchovy was highly different between areas, with a clear decline of the body condition after the peak in April in the north. Anchovy reproduces in spring and summer and obtains energy from feeding that is directly used for reproduction (Ganias, 2009; Giráldez, 2009). Seasonal variability in the body condition of anchovy tends to be less marked than in sardine (Albo-Puigserver et al., 2020), but the marked seasonality of the body condition of anchovy observed in the north suggest potential food limitations and the use of reserves for reproduction. Seasonal environmental patterns could partially explain differences in the phenology of life history traits. In the north area NPP depends mainly on nutrients from river discharge and local wind stress (Lloret et al., 2004; Martín et al., 2008). In recent decades, the discharges of the main rivers, such as the Ebro River, in the western Mediterranean basin, have decreased which could have been a driver of the altered NPP and plankton dynamics in the north, reducing energy availability for higher trophic levels (Lloret et al., 2004; Ludwig et al., 2009). This could explain the lower body conditions observed in the north before the reproduction period in the case of sardine (Brosset et al., 2016b; Albo-Puigserver et al., 2020). In contrast, higher NPP values were observed in the south than in the north and central areas. Higher NPP could thus favor a more energetic and abundant zooplankton production, and in consequence, a higher accumulation of fat reserves in sardine and anchovy during spring that would allow maintaining better body conditions during summer (Dessier et al., 2018). These differences in seasonal environmental conditions, in combination with genetic differences, could explain different phenotypic adaptations in each area.

TABLE 3 | Summary table of the relationship of gonadosomatic index (GSI) and body condition index (Kn) of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) with environmental variables (NPP, net primary production; ST150, average sea temperature 150 m; MC, meridional current; ZC, zonal current).

Environmental	**MC**		**ZC**		**ST150**		**NPP**	
	GSI	**Kn**	**GSI**	**Kn**	**GSI**	**Kn**	**GSI**	**Kn**
Sardina pilchardus								
North	∩	∪			∩∪	+	−	+
Central		−	+				+	+
South	∪	+			+	−	∩	
Engraulis encrasicolus								
North	∩			∩	+	+	∩	+
South	+	∪∩	∩	+	+	+	+	+

Decrease or negative (−) relationship is indicated with red, increase or positive relationship (+) is indicated in green and (∩) dome shaped and (∪) U shaped relationships are indicated in yellow.

Temporal declines in the life history traits of sardine and anchovy were observed in the studied period. However, the declines were not homogenously observed in all the areas and a latitudinal gradient was apparent. In the north, there was a synchronized temporal decline in GSI and body condition for both species that was not observed in the south area. In the case of sardine, the decline in the north started in 2006, while in anchovy the major changes in GSI and Kn appeared in 2012 coinciding with the decline in L_{50}. Also, the decline in length at age was more pronounced in the north. In the case of sardine, older age classes disappeared and individuals of up to 7 and 8 years of age were only showed in the south in the entire study period. Previous studies showed that sardine of 7 and 8 years of age were present in the 1980's in the northwestern Mediterranean (Morales-Nin and Pertierra, 1990). Therefore, older age classes of sardine in the north must have disappeared before 2004. These changes in the population age structure may have impacted other life history parameters; for instance, reproduction output has been directly related to the age and size structure of the population (Barneche et al., 2018). In our study, the gonadosomatic index of sardine and anchovy in the north presented a temporal decline, probably linked to the absence of older age classes.

Similar to the decline in length at age in sardines from the north, a decline in length at maturity was also observed. While in 2007 the L_{50} of sardine was 12.58 cm, individuals of the period 2012–2017 presented a L_{50} more than 2 cm smaller than the L_{50} in the central and southernmost areas. The decline in L_{50} to levels below 10 cm and the disappearance of older individuals and the slower growth has also been reported in the Gulf of Lions (northwestern Mediterranean Sea) for sardine and anchovy (Van Beveren et al., 2014; Brosset et al., 2016b). A similar pattern was also apparent in the central area of our study but was less pronounced and without an important decline in L_{50}. Therefore, the Gulf of Lions (GSA07) and the northern area of our study (north-GSA06) presented more similar changes in L_{50} and length at age than the central area for sardine. Important observed declines in L_{50} are usually explained by unfavorable environmental conditions that reduce the growth or by a high fishing pressure (or a combination of both) as a mechanism to maximize the fitness (Basilone et al., 2017). These mechanisms have been previously reported in short-lived species with high plasticity, like small pelagic fish (Silva et al., 2006; Neuheimer and Grønkjær, 2012; Hunter et al., 2015; Brosset et al., 2016b). Somatic growth is a more plastic trait compared to maturation schedules, and then easily used to adapt L_{50}, particularly in heterogeneous environments (Hidalgo et al., 2014; Véron et al., 2020b). Fishing pressure has also been widely reported as a driver for the selection of larger individuals, with an effect resulting in spawners of smaller sizes that would affect the trade-offs in the energy allocation between reproduction and growth (Jørgensen et al., 2007; Hidalgo et al., 2011). In the western Mediterranean Sea, there is a long history of small pelagic fish exploitation (Pertierra and Lleonart, 1996; Van Beveren et al., 2016), and high fishing effort has been maintained during the last decades (Coll and Bellido, 2019). Moreover, the minimum landing size of 9 cm for anchovy and 11 cm for sardine were below the historical lengths at first maturity for both species (Palomera et al., 2007). In a recent study, the combination of climate impacts and fishing pressure on sardine and anchovy populations have been described to be more severe in the northwestern Mediterranean Sea (corresponding to the north area of our study and the Gulf of Lions; Ramírez et al., 2021) than to the central and southern areas of our study. It is thus plausible that the high fishing pressure in the north area has been an important driver behind the observed age structure truncation. This result is of high relevance as most of the previous studies mainly reported age-truncation in species with broad demography but there are few studies related to small pelagic fish (but see, Van Beveren et al., 2014; Brosset et al., 2016b).

When analyzing the overall long-term patterns with environmental variables, the net primary production (NPP) had a significant effect on the GSI and Kn for sardine and anchovy except for GSI of anchovy and Kn of sardine in the south. The positive effect of NPP with sardine Kn in the north and central area and anchovy in the north and south is probably related to higher food availability that could improve the energy reserves and the reproduction output. Specifically, for 2015 in the south, we observed that the lowest Kn values of the time series for sardine and anchovy coincided with an abrupt decline in NPP. Similar to our results, Basilone et al. (2006) found a positive relationship of Chl-a (as a proxy of primary production) with the body condition and GSI of anchovy in the Strait of Sicily, which was confirmed by a mechanistic energetic model (Mangano et al., 2020). Accordingly, previous studies highlighted that the lower quality or smaller food size could be driving the declines in sardine and anchovy in the northwestern Mediterranean Sea (Brosset et al., 2016a; Queiros et al., 2019; Feuilloley et al., 2020) and latitudinal trend in the diet of sardine and anchovy in the western Mediterranean Sea, with lower energetic prey present in the northern latitudes, have been recently reported (Bachiller et al., 2020). Surprisingly, in the north, the NPP had a negative effect on GSI of sardine that could be explained by more complex interactions, including time-lag effects, changes in quality of food or changes in the energy allocation. In the Gulf of Lions, already Brosset et al. (2016b) suggested that small pelagic fish under poor environmental conditions might modify the allocation trade-off between reproduction and maintenance.

In the case of sardine, sea surface temperature (SST) has been described as an important driver limiting the spawning activity (Ganias, 2009) and different authors have proposed the hypothesis that with the increase of SST the spawning window of sardine would be retracted (Palomera et al., 2007). At long-term, the effect of sea temperature of 150 m depth averaged (ST150) presented contrasting effects between areas and species. Since sardine spawns in winter, with a preference for colder waters (Palomera et al., 2007; Ramírez et al., 2021), we expected a negative relationship between ST150 and GSI or Kn. However, opposite to what we expected, for sardine in the north the ST150 did not present a strong negative effect on GSI, and had a positive effect on Kn of sardine. Warmer waters have been related to more stratified and less enriched waters while years with cooler sea temperatures can be indicative of other processes, such as wind mixing, river runoff and upwelling that could favor appropriate conditions for sardine and anchovy (Bellido et al., 2008; Quattrocchi et al., 2016; Fernandez-Corredor et al., 2021). Accordingly, we observed that the hydrological conditions of each area also had an effect in the GSI and Kn of both species. For anchovy, ST150 had a positive effect on GSI in the north, that could be related with an increasing number of days with optimal temperatures for their spawning, as previously described in the Bay of Biscay (Erauskin-Extramiana et al., 2019).

The meridional and zonal current are parameters involved in the prey retention and transport (Sabatés et al., 2007) and in the generation of mesoscale anticyclonic eddies that increase food availability (Bakun, 2006; Quattrocchi and Maynou, 2017). Depending on the species and trait the effect of the components of the current differed, probably due to the major complexity in the interactions between Kn and GSI and the eddy kinetic processes since the north and central area had local different process compared with the south area (Macías et al., 2014; Lorente et al., 2015). The Kn of sardine in the central area was negatively related to MC. Sardine in the central area had higher body conditions during periods with a north to south current, which could be related with increased inflow of main current in the Levantine area (Northern Current) that flows from north to south

(Font, 1990; Font et al., 1990), instead a positive relationship was observed for sardine landings per unit effort in the north (Quattrocchi and Maynou, 2017). In the south, the long-term change in GSI of anchovy was exclusively explained by the MC and ZC. The south area has highly differentiated oceanographic conditions from the other areas. In the south area, there is an enrichment processes where the Atlantic Jet current increases the kinetic energy in the area creating upwelling events with an increase in primary productivity during spring and summer (Ruiz et al., 2013; Macías et al., 2014). Accordingly, the meridional and zonal currents partially explain the variability in GSI and Kn of both sardine and anchovy in the south.

Future Directions and Implications for Management of Small Pelagic Fish

The life history traits of sardine and anchovy investigated here showed temporal and latitudinal differences within our study area. Overall, we observed that the changes in life history traits in the north, and to a lesser extent, in the central area were partially similar to the changes described for the same period and both species in the Gulf of Lions (Van Beveren et al., 2014; Brosset et al., 2015b, 2016b; Saraux et al., 2019). However, the patterns were different in the southernmost area, the Alboran Sea. Differences in life history traits in the south were expected since the Alboran Sea is a productive area with well-differentiated conditions from the central and north areas (Ruiz et al., 2013; García-Martínez et al., 2019). Although global change also affects the southern area, a plausible explanation could be the genetic differentiation between populations (Coll and Bellido, 2019) with a higher environmental heterogeneity and variability, and consequently more plastic traits in the south than in the north, as previously suggested by Viñas et al. (2014) for anchovy populations.

For sardine in the northern area of this study, the observed declines in length at age, length at first maturity and age structure are critical. The implications of the disappearance of older individuals and truncation of the age-structure, in terms of the capacity of populations to buffer environmental events and in the reproductive capacity, are mechanisms that have been well studied and defined in previous studies (Hsieh et al., 2006; Barneche et al., 2018). Therefore, there is an urgent need to manage this resource proactively and precautionary to promote the recovery of the age-structure of the sardine population in the north and the central areas of the Western Mediterranean Sea and ultimately increase the resilience of the population to environmental extreme events and further changes in environmental conditions. Interestingly, a recent study has identified regions within these areas as potential "future climate refugees" for sardine and anchovy (Pennino et al., 2020) that are candidate areas to consider for future management interventions (Ramírez et al., 2021).

Our study showed clear spatially distinct changes in the life history traits of anchovy and sardine populations in the western Mediterranean Sea. A formal consideration of these differences could alter the current perception of the stock status from the stock assessment arena. Consequently, definition of the stock status, ecological analyses and management advice, in general, could benefit from taking into account these heterogeneously distributed differences. Currently, stock assessment evaluations of sardine and anchovy do not consider the north and central areas (GSA-06) differently. Although both areas are genetically very similar, we observed how input parameters that are important in stock assessment, such as length at age and length at first maturity of sardine, differed between areas. Therefore, the life history traits of sardine described in this study should be taken into consideration when evaluating the stock status but further research is needed to identify if these differences between areas will persist in the future. Life history traits that rapidly respond to environmental changes, such as body condition, might be good indicators to anticipate further declines in populations as has been previously highlighted by other studies (Lloret et al., 2012; Véron et al., 2020a). Most notably, Vargas-Yáñez et al. (2020) found that in the Alboran Sea the body condition of spawning sardine, which is closely linked to food availability in a preceding year, is the main success factor for recruitment. Therefore, the recent decline in body condition that has been observed for sardine and anchovy in the Alboran Sea should be heeded as a possible first sign for future declines of these species in the southernmost area of this study, with a future risk to show similar declines as observed in the north. This issue requires close monitoring and evaluation.

DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available because the dataset is available by request to the Spanish Institute of Oceanography. Requests to access the datasets should be directed to webmaster@ieo.es.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the biological samples were obtained from landings of commercial fishing vessels.

AUTHOR CONTRIBUTIONS

MA-P, MP, MH, JB, and MC designed the study. AC, AG, and PT performed the data collection and created the database. JS performed the environmental data analysis. MA-P, MP, JG, MH, MC-R, and MC performed and analyzed the data. MA-P wrote the first version of the manuscript assisted by MC and MP. All authors contributed significantly to revisions and improvements of the final manuscript.

FUNDING

This study was carried out within the Spanish Research project PELWEB (CTM2017-88939-R) funded by Spanish

Ministry of Science, Innovation and Universities and the European Research Contract SPELMED (SC NR 02-TENDER EASME/EMFF/2016/032XXX) funded by EC EASME. Fisheries data collection has been co-funded by the EU through the European Maritime and Fisheries Fund (EMFF) within the National Program of collection, management and use of data in the fisheries sector and support for scientific advice regarding the Common Fisheries Policy (Regulation, EU 2017/1004).

ACKNOWLEDGMENTS

We wish to thank all the participants in the fisheries data collection through all these years in the different harbors along the Spanish Mediterranean coast. We are also grateful to Marc Farré and Federico Quattrocchi for their useful advice on the analysis of data, and reviewers for their constructive comments and suggestions. This study has been conducted using E.U. Copernicus Marine Service Information. MP thank the IMPRESS Project (RTI2018-099868-B-I00), ERDF, Ministry of Science, Innovation and Universities – State Research Agency.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.570354/full#supplementary-material

REFERENCES

Agostini, V. N., and Bakun, A. (2002). 'Oceantriads'in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engrauli sencrasicolus*). *Fish. Oceanogr.* 11, 129–142. doi: 10.1046/j.1365-2419.2002.00201.x

Albo-Puigserver, M., Sánchez, S., Coll, M., Bernal, M., Sáez-Liante, R., Navarro, J., et al. (2020). Year-round energy dynamics of sardine and anchovy in the north-western Mediterranean Sea. *Mar. Environ. Res.* 159:105021. doi: 10.1016/j.marenvres.2020.105021

Alemany, F., and Álvarez, F. (1993). Growth differences among sardine (*Sardina pilchardus* Walb.) populations in Western Mediterranean. *Sci. Mar.* 57, 229–234.

Anderson, C. N. K., Hsieh, C. H., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., et al. (2008). Why fishing magnifies fluctuations in fish abundance. *Nature* 452, 835–839. doi: 10.1038/nature06851

Bachiller, E., Albo-Puigserver, M., Giménez, J., Pennino, M. G., Marí-Mena, N., Esteban, A., et al. (2020). A trophic latitudinal gradient revealed in anchovy and sardine from the Northwestern Mediterranean Sea using a multi-proxy approach. *Sci. Rep.* 10:17598. doi: 10.1038/s41598-020-74602-y

Bakun, A. (2006). Wasp-waist populations and marine ecosystem dynamics: navigating the "predator pit" topographies. *Prog. Oceanogr.* 68, 271–288. doi: 10.1016/J.POCEAN.2006.02.004

Balbín, R., López-Jurado, J. L., Flexas, M. M., Reglero, P., Vélez-Velchí, P., González-Pola, C., et al. (2014). Interannual variability of the early summer circulation around the Balearic Islands: driving factors and potential effects on the marine ecosystem. *J. Mar. Syst.* 138, 70–81. doi: 10.1016/j.jmarsys.2013.07.004

Barneche, D. R., White, C. R., and Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science* 360, 642–645.

Basilone, G., Guisande, C., Patti, B., Mazzola, S., Cuttitta, A., Bonanno, A., et al. (2006). Effect of habitat conditions on reproduction of the European anchovy (*Engraulis encrasicolus*) in the Strait of Sicily. *Fish. Oceanogr.* 15, 271–280. doi: 10.1111/j.1365-2419.2005.00391.x

Basilone, G., Mangano, S., Pulizzi, M., Fontana, I., Giacalone, G., Ferreri, R., et al. (2017). European anchovy (*Engraulis encrasicolus*) age structure and growth rate in two contrasted areas of the Mediterranean Sea: the paradox of faster growth in oligotrophic seas. *Mediterr. Mar. Sci.* 15, 739–752. doi: 10.12681/mms.2059

Bellido, J. M., Brown, A. M., Valavanis, V. D., Giráldez, A., Pierce, G. J., Iglesias, M., et al. (2008). Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. *Hydrobiologia* 612, 171–184. doi: 10.1007/s10750-008-9481-2

Bolzon, G., Cossarini, G., Lazzari, P., Salon, S., Teruzzi, A., Feudale, L., et al. (2020). "Mediterranean sea biogeochemical analysis and forecast (CMEMS MED-biogeochemistry 2018-2021)," in *Copernicus Monitoring Environment Marine Service (CMEMS).* doi: 10.25423/CMCC/MEDSEA_ANALYSIS_FORECAST_BIO_006_014_MEDBFM3 (accessed July 25, 2018).

Bosc, E., Bricaud, A., and Antoine, D. (2004). Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. *Global Biogeochem. Cycl.* 18:GB1005. doi: 10.1029/2003gb002034

Breheny, P., and Burchett, W. (2017). Visualization of Regression Models Using Visreg. *R J.* 9, 56–71.

Brockwell, P. J., and Davis, R. A. (2002). *Introduction to Time Series and Forecasting*, 2 Edn. Berlin: Springer.

Brosset, P., Fromentin, J.-M., Ménard, F., Pernet, F., Bourdeix, J.-H., Bigot, J. L., et al. (2015a). Measurement and analysis of small pelagic fish condition: a suitable method for rapid evaluation in the field. *J. Exp. Mar. Bio. Ecol.* 462, 90–97. doi: 10.1016/j.jembe.2014.10.016

Brosset, P., Ménard, F., Fromentin, J., Bonhommeau, S., Ulses, C., Bourdeix, J., et al. (2015b). Influence of environmental variability and age on the body condition of small pelagic fish in the Gulf of Lions. *Mar. Ecol. Prog. Ser.* 529, 219–231. doi: 10.3354/meps11275

Brosset, P., Fromentin, J. M., Van Beveren, E., Lloret, J., Marques, V., Basilone, G., et al. (2017). Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. *Prog. Oceanogr.* 151, 149–162. doi: 10.1016/j.pocean.2016.12.002

Brosset, P., Le Bourg, B., Costalago, D., Bănaru, D., Van Beveren, E., Bourdeix, J. H., et al. (2016a). Linking small pelagic dietary shifts with ecosystem changes in the Gulf of Lions. *Mar. Ecol. Prog. Ser.* 554, 157–171. doi: 10.3354/meps11796

Brosset, P., Lloret, J., Muñoz, M., Fauvel, C., Beveren, E., Van, et al. (2016b). Body reserves mediate trade - offs between life - history traits: new insights from small pelagic fish reproduction. *R. Soc. Open Sci.* 3:160202. doi: 10.1098/rsos.160202

Checkley, D., Alheit, J., Oozeki, Y., and Roy, C. (eds) (2009). *Climate Change and Small Pelagic Fish*. Cambridge: Cambridge University Press.

Coll, M., Albo-Puigserver, M., Navarro, J., Palomera, I., and Dambacher, J. M. (2019). Who is to blame? Plausible pressures on small pelagic fish population changes in the northwestern Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 617, 277–294. doi: 10.3354/meps12591

Coll, M., and Bellido, J. M. (2019). *Evaluation of the Population Status and Specific Management Alternatives for the Small Pelagic Fish Stocks in the Northwestern Mediterranean Sea (SPELMED) - Final Report SC NR 02. TENDER EASME/EMFF/2016/32 – SPELMED*. Luxembourg: Publications Office of the European Union.

Coll, M., Palomera, I., Tudela, S., and Dowd, M. (2008). Food-web dynamics in the South Catalan Sea ecosystem (NW Mediterranean) for 1978–2003. *Ecol. Model.* 217, 95–116. doi: 10.1016/J.ECOLMODEL.2008.06.013

De Roos, A. M., Boukal, D. S., and Persson, L. (2006). Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proc. R. Soc. B Biol. Sci.* 273, 1873–1880. doi: 10.1098/rspb.2006.3518

De Roos, A. M., Persson, L., and McCauley, E. (2003). The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecol. Lett.* 6, 473–487. doi: 10.1046/j.1461-0248.2003.00458.x

Dessier, A., Dupuy, C., Kerric, A., Mornet, F., Authier, M., Bustamante, P., et al. (2018). Variability of energy density among mesozooplankton community: new insights in functional diversity to forage fish. *Prog. Oceanogr.* 166, 121–128. doi: 10.1016/j.pocean.2017.10.009

Dickey-Collas, M., Nash, R. D. M., Brunel, T., van Damme, C. J. G., Marshall, C. T., Payne, M. R., et al. (2010). Lessons learned from stock collapse and recovery of North Sea herring: a review. *ICES J. Mar. Sci.* 67, 1875–1886. doi: 10.1093/icesjms/fsq033

D'Ortenzio, F., Alcal, M. R., Biologica, O., Dohrn, S. Z. A., and Comunale, V. (2009). On the trophic regimes of the Mediterranean Sea: a satellite analysis. *Biogeosci. Discuss* 5, 2959–2983. doi: 10.5194/bgd-5-2959-2008

Enberg, K., and Heino, M. (2007). "Fisheries-induced Life History Changes in Herring (*Clupea harengus*)," in *ICES CM Documents 2007 - ICES Annual Science Conference*. Laxenburg: International Institute for Applied Systems Analysis.

Erauskin-Extramiana, M., Alvarez, P., Arrizabalaga, H., Ibaibarriaga, L., Uriarte, A., Cotano, U., et al. (2019). Historical trends and future distribution of anchovy spawning in the Bay of Biscay. *Deep. Res. Part II Top. Stud. Oceanogr.* 159, 169–182. doi: 10.1016/j.dsr2.2018.07.007

Ernande, B., Dieckmann, U., and Heino, M. (2004). Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proc. R. Soc. B Biol. Sci.* 271, 415–423. doi: 10.1098/rspb.2003.2519

FAO. (2018). *FAO Yearbook: Fisheries and Aquaculture Statistics 2016*. Rome: FAO.

Fernandez-Corredor, E., Albo-Puigserver, M., Pennino, M. G., Bellido, J. M., and Coll, M. (2021). Influence of environmental factors on different life stages of European anchovy (*Engraulis encrasicolus*) and European sardine (*Sardina pilchardus*) from the Mediterranean Sea: a literature review. *Estuar. Coast. Shelf Sci.* 41:101606. doi: 10.1016/j.rsma.2020.101606

Feuilloley, G., Fromentin, J.-M., Stemmann, L., Demarcq, H., Estournel, C., and Saraux, C. (2020). Concomitant changes in the Environment and small pelagic fish community of the Gulf of Lions. *Prog. Oceanogr.* 186:102375. doi: 10.1016/j.pocean.2020.102375

Font, J. (1990). A comparison of seasonal winds with currents on the continental slope of the Catalan Sea (northwestern Mediterranean). *J. Geophys. Res.* 95, 1537–1545. doi: 10.1029/JC095iC02p01537

Font, J., Salat, J., and Julià, A. (1990). Marine circulation along the Ebro continental margin. *Mar. Geol.* 95, 165–177. doi: 10.1016/0025-3227(90)90114-Y

Fox, J., and Weisberg, S. (2011). *An R Companion to Applied Regression*. Thousands Oaks: Sage Publications.

Ganias, K. (2009). Linking sardine spawning dynamics to environmental variability. *Estuar. Coast. Shelf Sci.* 84, 402–408. doi: 10.1016/j.ecss.2009.07.004

García, A., Cortés, D., Ramírez, T., Giráldez, A., and Carpena, Á (2003). Contribution of larval growth rate variability to the recruitment of the Bay Málaga anchovy (SW Mediterranean) during the 2000-2001 spawning seasons. *Sci. Mar.* 67, 477–490. doi: 10.3989/scimar.2003.67n4477

García, A., and Palomera, I. (1996). Anchovy early life history and its relation to its surrounding environment in the western Mediterranean basin. *Sci. Mar.* 60, 155–166.

García-Martínez, M., del, C., Vargas-Yáñez, M., Moya, F., Santiago, R., Muñoz, M., et al. (2019). Average nutrient and chlorophyll distributions in the Western Mediterranean: RADMED project. *Oceanologia* 61, 143–169. doi: 10.1016/j.oceano.2018.08.003

Garrido, S., Rosa, R., Ben-Hamadou, R., Cunha, M. E., Chícharo, M. A., and van der Lingen, C. D. (2007). Effect of maternal fat reserves on the fatty acid composition of sardine (*Sardina pilchardus*) oocytes. *Comp. Biochem. Physiol. B. Biochem. Mol. Biol.* 148, 398–409. doi: 10.1016/j.cbpb.2007.07.008

GFCM. (2019). *Working Group on Stock Assessment of Small Pelagic Species (WGSASP). Scientific Advisory Committee on Fisheries (SAC). 9–14 December 2019*. Rome: FAO.

Giannoulaki, M., Iglesias, M., Tugores, M. P., Bonanno, A., Patti, B., De Felice, A., et al. (2013). Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages. *Fish. Oceanogr.* 22, 69–89. doi: 10.1111/fog.12005

Giráldez, A. (2009). *Estudio de la variabilidad temporal de los parámetros reproductivos del boquerón (Engraulis encrasicolus L.) en el mar de Alborán*. Spain: Instituto Español de oceanografía.

Giráldez, A., and Abad, R. (1995). Aspects on the reproductive biology of the Western Mediterranean anchovy from the coasts of Málaga (Alborán Sea). *Sci. Mar.* 59, 15–23.

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., et al. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nat. Commun.* 6:7615. doi: 10.1038/ncomms8615

Hidalgo, M., Olsen, E. M., Ohlberger, J., Saborido-Rey, F., Murua, H., Piñeiro, C., et al. (2014). Contrasting evolutionary demography induced by fishing: the role of adaptive phenotypic plasticity. *Ecol. Appl.* 24, 1101–1114. doi: 10.1890/12-1777.1

Hidalgo, M., Rouyer, T., Bartolino, V., Cerviño, S., Ciannelli, L., Massutí, E., et al. (2012). Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of a harvested species. *Ecography* 35, 637–649. doi: 10.1111/j.1600-0587.2011.07314.x

Hidalgo, M., Rouyer, T., Molinero, J. C., Massutí, E., Moranta, J., Guijarro, B., et al. (2011). Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Mar. Ecol. Prog. Ser.* 426, 1–12. doi: 10.3354/meps09077

Holmes, E. E., Scheuerell, M. D., and Ward, E. J. (2021). *Applied Time Series Analysis for Fisheries and Environmental Data*. Maryland: Northwest Fisheries Science Center(NOAA).

Hsieh, C. H., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M., and Sugihara, G. (2006). Fishing elevates variability in the abundance of exploited species. *Nature* 443, 859–862. doi: 10.1038/nature05232

Hunter, A., Speirs, D. C., and Heath, M. R. (2015). Fishery-induced changes to age and length dependent maturation schedules of three demersal fish species in the Firth of Clyde. *Fish. Res.* 170, 14–23. doi: 10.1016/j.fishres.2015.05.004

Hyndman, R., Athanasopoulos, G., Bergmeir, C., Caceres, G., Chhay, L., O'Hara-Wild, M., et al. (2020). *Forecast: Forecasting Functions for Time Series and Linear Models. R Package Version 8.13*.

Hyndman, R. J., and Khandakar, Y. (2008). "Automatic time series forecasting: the forecast package for R. *J. Stat. Softw.* 26, 1–22.

ICES. (2008). *Report of the Workshop on Small Pelagics (Sardina pilchardus, Engraulis encrasicolus) Maturity Stages (WKSPMAT), 10-14 November 2008*. Italy: Mazara del Vallo.

ICES. (2017). *Report of the Workshop on Age estimation of European anchovy (Engraulis encrasicolus). WKARA2 2016 Report 28 November - 2 December 2016*. Pasaia: ICES.

Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., et al. (2007). Ecology: managing evolving fish stocks. *Science* 318, 1247–1248. doi: 10.1126/science.1148089

Kendall, M., and Stuart, A. (1983). *The Advanced Theory of Statistics, Vol.3*. London: Griffin.

Le Cren, E. D. (1951). The Length-Weight Relationship and Seasonal Cycle in Gonad Weight and Condition in the Perch (*Perca fluviatilis*). *J. Anim. Ecol.* 20, 201–219. doi: 10.2307/1540

Lloret, J., Faliex, E., Shulman, G. E., Raga, J. A., Sasal, P., Muñoz, M., et al. (2012). Fish health and fisheries, implications for stock assessment and management: the mediterranean example. *Rev. Fish. Sci.* 20, 165–180. doi: 10.1080/10641262.2012.695817

Lloret, J., Palomera, I., Salat, J., and Solé, I. (2004). Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). *Fish. Oceanogr.* 13, 102–110.

Lloret, J., Shulman, G., and Love, R. M. (2013). *Condition and Health Indicators of Exploited Marine Fishes*. Hoboken: John Wiley & Sons.

Lorente, P., Piedracoba, S., Soto-Navarro, J., and Alvarez-Fanjul, E. (2015). Evaluating the surface circulation in the Ebro delta (northeastern Spain) with quality-controlled high-frequency radar measurements. *Ocean Sci.* 11, 921–935. doi: 10.5194/os-11-921-2015

Ludwig, W., Dumont, E., Meybeck, M., and Heussner, S. (2009). River discharges of water and nutrients to the Mediterranean and Black Sea: major drivers for ecosystem changes during past and future decades? *Prog. Oceanogr.* 80, 199–217. doi: 10.1016/j.pocean.2009.02.001

Macías, D., Castilla-Espino, D., García-del-Hoyo, J. J., Navarro, G., Catalán, I. A., Renault, L., et al. (2014). Consequences of a future climatic scenario for the anchovy fishery in the Alboran Sea (SW Mediterranean): a modeling study. *J. Mar. Syst.* 135, 150–159. doi: 10.1016/j.jmarsys.2013.04.014

Mangano, M. C., Mieszkowska, N., Helmuth, B., Domingos, T., Sousa, T., and Baiamonte, G. (2020). Moving Toward a Strategy for Addressing Climate Displacement of Marine Resources: a Proof-of-Concept. *Front. Mar. Sci.* 7:408. doi: 10.3389/fmars.2020.00408

Martín, P., Bahamon, N., Sabatés, A., Maynou, F., Sánchez, P., and Demestre, M. (2008). European anchovy (*Engraulis encrasicolus*) landings and environmental conditions on the Catalan Coast (NW Mediterranean) during 2000-2005. *Hydrobiologia* 612, 185–199. doi: 10.1007/s10750-008-9482-1

McBride, R. S., Somarakis, S., Fitzhugh, G. R., Albert, A., Yaragina, N. A., Wuenschel, M. J., et al. (2015). Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish Fish.* 16, 23–57. doi: 10.1111/faf.12043

Mercado, J. M., Cortés, D., García, A., and Ramírez, T. (2007). Seasonal and inter-annual changes in the planktonic communities of the northwest Alboran Sea (Mediterranean Sea). *Prog. Oceanogr.* 74, 273–293. doi: 10.1016/j.pocean.2007.04.013

Morales-Nin, B., and Pertierra, P. J. (1990). Growth rates of the anchovy *Engraulis ecransicolus* and the sardine *Sardina pilchardus* in the Northwestern Mediterranean Sea. *Mar. Biol.* 107, 349–356.

Moritz, S., and Bartz-Beielstein, T. (2017). Imputets: time Series Missing Value Imputation in R. *R J.* 9, 207–218. doi: 10.32614/RJ-2017-009

Murua, H., and Saborido-Rey, F. (2003). Female reproductive strategies of marine fish species of the North Atlantic. *J. Northwest Atl. Fish. Sci.* 33, 23–31. doi: 10.2960/J.v33.a2

Nash, R. D., Witthames, P., Pawson, M., and Alesworth, E. (2000). Regional variability in the dynamics of reproduction and growth of Irish Sea plaice, Pleuronectes platessa L. *J. Sea Res.* 44, 55–64. doi: 10.1016/S1385-1101(00)00046-0

Neuheimer, A. B., and Grønkjær, P. (2012). Climate effects on size-at-age: growth in warming waters compensates for earlier maturity in an exploited marine fish. *Glob. Chang. Biol.* 18, 1812–1822. doi: 10.1111/j.1365-2486.2012.02673.x

Ospina-Alvarez, A., Catalán, I., Bernal, M., Roos, D., and Palomera, I. (2015). From egg production to recruits: connectivity and inter-annual variability in the recruitment patterns of European anchovy in the northwestern Mediterranean. *Prog. Oceanogr.* 138, 431–447. doi: 10.1016/j.pocean.2015.01.011

Palomera, I. (1992). Spawning of anchovy *Engraulis encrasicolus* in the northwestern Mediterranean relative to hydrographic features in the region. *Mar. Ecol. Prog. Ser.* 79, 215–223. doi: 10.3354/meps079215

Palomera, I., Olivar, M. P., Salat, J., Sabatés, A., Coll, M., García, A., et al. (2007). Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Prog. Oceanogr.* 74, 377–396. doi: 10.1016/j.pocean.2007.04.012

Pascual, M., Rives, B., Schunter, C., and Macpherson, E. (2017). Impact of life history traits on gene flow: a multispecies systematic review across oceanographic barriers in the Mediterranean Sea. *PLoS One* 12:e0176419. doi: 10.1371/journal.pone.0176419

Peck, M. A., Reglero, P., Takahashi, M., and Catalán, I. A. (2013). Life cycle ecophysiology of small pelagic fish and climate-driven changes in populations. *Prog. Oceanogr.* 116, 220–245. doi: 10.1016/J.POCEAN.2013.05.012

Pennino, M. G., Coll, M., Albo-Puigserver, M., Fernandez-Corredor, E., Steenbeek, J., Giráldez, A., et al. (2020). Current and future influence of environmental factors on small pelagic fish distributions in the Northwestern Mediterranean Sea. *Front. Mar. Sci.* 7:622. doi: 10.3389/fmars.2020.00622

Pertierra, J. P., and Lleonart, J. (1996). NW Mediterranean anchovy fisheries. *Sci. Mar.* 60, 257–267.

Pinot, J. M., López-Jurado, J. L., and Riera, M. (2002). The CANALES experiment (1996-1998). Interannual, seasonal, and mesoscale variability of the circulation in the Balearic Channels. *Prog. Oceanogr.* 55, 335–370. doi: 10.1016/S0079-6611(02)00139-8

Planque, B., Fromentin, J. M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., et al. (2010). How does fishing alter marine populations and ecosystems sensitivity to climate? *J. Mar. Syst.* 79, 403–417. doi: 10.1016/j.jmarsys.2008.12.018

Quattrocchi, F., Mamouridis, V., and Maynou, F. (2016). Occurrence of adult anchovy in Catalonia (NW Mediterranean) in relation to sea surface conditions. *Sci. Mar.* 80, 457–66. doi: 10.3989/scimar.04413.24a

Quattrocchi, F., and Maynou, F. (2017). Environmental drivers of sardine (*Sardina pilchardus*) in the Catalan Sea (NW Mediterranean Sea). *Mar. Biol. Res.* 13, 1003–1014. doi: 10.1080/17451000.2017.1331039

Queiros, Q., Fromentin, J. M., Gasset, E., Dutto, G., Huiban, C., Metral, L., et al. (2019). Food in the sea: size also matters for pelagic fish. *Front. Mar. Sci.* 6:385. doi: 10.3389/fmars.2019.00385

Quintanilla, J. M., Laiz-Carrión, R., Uriarte, A., and García, A. (2015). Influence of trophic pathways on daily growth patterns of western Mediterranean anchovy *Engraulis encrasicolus* larvae. *Mar. Ecol. Prog. Ser.* 531, 263–275. doi: 10.3354/meps11312

R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ramírez, F., Afán, I., Davis, L. S., and Chiaradia, A. (2017). Climate impacts on global hot spots of marine biodiversity. *Sci. Adv.* 3:e1601198.

Ramírez, F., Pennino, M. G., Albo-Puigserver, M., Steenbeek, J., Bellido, J. M., and Coll, M. (2021). SOS small pelagics: a Safe Operating Space for small pelagic fish in the Western Mediterranean Sea. *Sci. Total Environ.* 756:144002. doi: 10.1016/j.scitotenv.2020.144002

Ramírez-Amaro, S., Picornell, A., Arenas, M., Castro, J. A., Massutí, E., Ramon, M. M., et al. (2018). Contrasting evolutionary patterns in populations of demersal sharks throughout the western Mediterranean. *Mar. Biol.* 165, 1–16. doi: 10.1007/s00227-017-3254-2

Rochet, M. (1998). Short-term effects of fishing on life history traits of fishes. *ICES J. Mar. Sci.* 55, 371–391. doi: 10.1006/jmsc.1997.0324

Ruiz, J., Macías, D., Rincón, M. M., Pascual, A., Catalán, I. A., and Navarro, G. (2013). Recruiting at the Edge: kinetic Energy Inhibits Anchovy Populations in the Western Mediterranean. *PLoS One* 8:e55523. doi: 10.1371/journal.pone.0055523

Sabatés, A., Salat, J., Palomera, I., Emelianov, M., De Puelles, M. L. F., and Olivar, M. P. (2007). Advection of anchovy (*Engraulis encrasicolus*) larvae along the Catalan continental slope (NW Mediterranean). *Fish. Oceanogr.* 16, 130–141. doi: 10.1111/j.1365-2419.2006.00416.x

Salat, J. (1996). Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. *Sci. Mar.* 60, 21–32.

Salat, J., Garcia, M. A., Cruzado, A., Palanques, A., Arín, L., Gomis, D., et al. (2002). Seasonal changes of water mass structure and shelf slope exchanges at the Ebro shelf (NW Mediterranean). *Cont. Shelf Res.* 22, 327–348. doi: 10.1016/S0278-4343(01)00031-0

Salgado-Hernanz, P. M., Racault, M. F., Font-Muñoz, J. S., and Basterretxea, G. (2019). Trends in phytoplankton phenology in the Mediterranean Sea based on ocean-colour remote sensing. *Remote Sens. Environ.* 221, 50–64. doi: 10.1016/j.rse.2018.10.036

Saraux, C., Van Beveren, E., Brosset, P., Queiros, Q., Bourdeix, J.-H., Dutto, G., et al. (2019). Small pelagic fish dynamics: a review of mechanisms in the Gulf of Lions. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 159, 52–61. doi: 10.1016/J.DSR2.2018.02.010

Sharpe, D. M. T., and Hendry, A. P. (2009). Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evol. Appl.* 2, 260–275. doi: 10.1111/j.1752-4571.2009.00080.x

Silva, A., Santos, M. B., Caneco, B., Pestana, G., Porteiro, C., Carrera, P., et al. (2006). Temporal and geographic variability of sardine maturity at length in the northeastern Atlantic and the western Mediterranean. *ICES J. Mar. Sci.* 63, 663–676. doi: 10.1016/j.icesjms.2006.01.005

Simoncelli, S., Fratianni, C., Pinardi, N., Grandi, A., Drudi, M., Oddo, P., et al. (2019). "Mediterranean sea physical reanalysis (CMEMS MED-physics) [data set]," in *Copernicus Monitoring Environment Marine Service (CMEMS)*. doi: 10.25423/MEDSEA_REANALYSIS_PHYS_006_004

Stahl, J. P., and Kruse, G. H. (2008). Spatial and Temporal Variability in Size at Maturity of Walleye Pollock in the Eastern Bering Sea. *Trans. Am. Fish. Soc.* 137, 1543–1557. doi: 10.1577/T07-099.1

Stawitz, C. C., and Essington, T. E. (2018). Somatic growth contributes to population variation in marine fishes. *J. Anim. Ecol.* 88, 315–329. doi: 10.1111/1365-2656.12921

Stearns, S. C. (1989). Trade-Offs in Life-History Evolution. *Funct. Ecol.* 3, 259–268. doi: 10.2307/2389364

Stenseth, N. C., and Rouyer, T. (2008). Destabilized fish stocks. *Nature* 452, 825–826. doi: 10.1038/452825a

Taboada, F. G., and Anadón, R. (2016). Determining the causes behind the collapse of a small pelagic fishery using Bayesian population modeling. *Ecol. Appl.* 26, 886–898. doi: 10.1890/15-0006/suppinfo

Teruzzi, A., Bolzon, G., Cossarini, G., Lazzari, P., Salon, S., Crise, A., et al. (2019). "Mediterranean sea biogeochemical reanalysis (CMEMS MED-biogeochemistry) [data set]," in *Copernicus Monitoring Environment Marine Service (CMEMS)*. doi: 10.25423/MEDSEA_REANALYSIS_BIO_006_008

Tugores, P., Giannoulaki, M., Iglesias, M., Bonanno, A., Tičina, V., Leonori, I., et al. (2011). Habitat suitability modelling for sardine *Sardina pilchardus* in a highly diverse ecosystem: the Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 443, 181–205. doi: 10.3354/meps09366

Van Beveren, E., Bonhommeau, S., Fromentin, J.-M., Bigot, J.-L., Bourdeix, J.-H., Brosset, P., et al. (2014). Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean. *Mar. Biol.* 161, 1809–1822. doi: 10.1007/s00227-014-2463-1

Van Beveren, E., Fromentin, J. M., Rouyer, T., Bonhommeau, S., Brosset, P., and Saraux, C. (2016). The fisheries history of small pelagics in the Northern Mediterranean. *ICES J. Mar. Sci.* 73, 1474–1484. doi: 10.1093/icesjms/fsw023

Vargas-Yáñez, M., Giráldez, A., Torres, P., González, M., García-Martínez, M., del, C., et al. (2020). Variability of oceanographic and meteorological conditions in the northern Alboran Sea at seasonal, inter-annual and long-term time scales and their influence on sardine (*Sardina pilchardus* Walbaum 1792) landings. *Fish. Oceanogr.* 29, 1–14. doi: 10.1111/fog.12477

Ventero, A., Iglesias, M., and Villamor, B. (2017). Anchovy (*Engraulis encrasicolus*) otoliths reveal growth differences between two areas of the Spanish Mediterranean Sea. *Sci. Mar.* 81, 327–3. doi: 10.3989/scimar.04615.21a

Véron, M., Duhamel, E., Bertignac, M., Pawlowski, L., and Huret, M. (2020a). Major changes in sardine growth and body condition in the Bay of Biscay between 2003 and 2016: temporal trends and drivers. *Prog. Oceanogr.* 182:102274. doi: 10.1016/j.pocean.2020.102274

Véron, M., Duhamel, E., Bertignac, M., Pawlowski, L., Huret, M., and Baulier, L. (2020b). Determinism of Temporal Variability in Size at Maturation of Sardine *Sardina pilchardus* in the Bay of Biscay. *Front. Mar. Sci.* 7:567841. doi: 10.3389/fmars.2020.567841

Viñas, J., Sanz, N., Peñarrubia, L., Araguas, R.-M., García-Marín, J.-L., Roldán, M.-I., et al. (2014). Genetic population structure of European anchovy in the Mediterranean Sea and the Northeast Atlantic Ocean using sequence analysis of the mitochondrial DNA control region. *ICES J. Mar. Sci.* 71, 391–397. doi: 10.1093/icesjms/fst132

Walsh, M. R., Munch, S. B., Chiba, S., and Conover, D. O. (2006). Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecol. Lett.* 9, 142–148. doi: 10.1111/j.1461-0248.2005.00858.x

Wei, T., and Simko, V. (2017). *R Package "corrplot": Visualization of a Correlation Matrix (Version 0.84)*. Available Online at: https://github.com/taiyun/corrplot.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag:.

Wood, S. N. (2006). *Generalized Additive Models: An Introduction With R. Texts in Statistical Science*. Boca Raton, FL: Chapman & Hall/CRC, 410.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 73, 3–36. doi: 10.1111/j.1467-9868.2010.00749.x

Yang, L., Qin, G., Zhao, N., Wang, C., and Song, G. (2012). Using a generalized additive model with autoregressive terms to study the effects of daily temperature on mortality. *BMC Med. Res. Methodol.* 12:165. doi: 10.1186/1471-2288-12-165

Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14.

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.