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Understanding the response of ecosystems to increasing human pressures and climate change – management options

Edited by
Stelios Katsanevakis, Sebastian Christoph Alexander Ferse, Heliana Teixeira, Angel Borja and Elena Gissi

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Understanding the response of ecosystems to increasing human pressures and climate change – management options

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Editorial: Understanding the response of ecosystems to increasing human pressures and climate change – management options

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Editorial on the Research Topic
Understanding the response of ecosystems to increasing human pressures and climate change – management options

1 Introduction

The escalating human footprint and climate change (Halpern et al., 2015; Halpern et al., 2025; Korpinen et al., 2021) are driving significant and often poorly understood shifts in marine ecosystems, challenging our ability to predict and manage ecological tipping points (Scheffer et al., 2001). Effective conservation requires a clearer understanding of the causal mechanisms behind these changes, supported by interdisciplinary research, innovative monitoring technologies, and comprehensive assessments of management strategies (Sutherland et al., 2004; Borja et al., 2024). Critical issues such as Harmful Algal Blooms (HABs), jellyfish blooms, biological invasions, climate-induced range shifts, marine heatwaves, deoxygenation, pollution, coastal habitat modification, biodiversity loss, and the decline of top predators demand targeted, science-based solutions. Addressing these knowledge gaps, framed as Grand Challenges in Marine Ecosystem Ecology (Borja et al., 2020), is essential for sustaining ocean health and informing ecosystem-based management (EBM).

This Research Topic was conceived to "take the pulse" of current advances addressing these grand challenges. The contributing articles encompass new methods for assessing cumulative impacts, case studies of ecosystem responses to specific pressures, and state-of-the-art reviews on managing phenomena such as invasive species, jellyfish blooms, HABs, and the decline of top predators. Collectively, they illuminate pathways toward more effective EBM in an era of intensifying human pressures.

2 New tools and frameworks for cumulative impact assessment and ecosystem management

Multiple contributions introduce innovative conceptual frameworks and tools to assess and manage the cumulative effects of human pressures on marine ecosystems. Borja et al. present a comprehensive conceptual framework model and toolbox for evaluating cumulative impacts under the EU Marine Strategy Framework Directive (MSFD). Their policy-focused approach outlines an integrated framework – including risk assessment and vulnerability matrices and decision-support tools – to link human activities with pressures and ecosystem components, supporting sustainable use of the seas. In a similar vein, Papadopoulou et al. offer a critical interrogation of available marine EBM tools, emphasizing that different management objectives ("horses for courses") require tailored approaches. By systematically comparing tools ranging from ecosystem models to indicator frameworks, they guide practitioners in selecting appropriate methodologies for specific EBM challenges.

Focusing on the Black Sea, Lazar et al. introduce a robust semi-quantitative framework that combines a habitat sensitivity matrix (scoring the vulnerability of ecosystem components to various pressures) with fuzzy cognitive mapping via the Mental Modeler software to quantitatively prioritize drivers–pressures–impacts linkages. They then apply these tools under future "Shared Socioeconomic Pathways" (SSP1, SSP2, SSP5) scenarios to simulate and compare cumulative impacts across trajectories of management and development. Together, these novel integrations enable adaptive scenario-based assessments and provide decision-makers with a science-based roadmap to target the most damaging pressures under resource or capacity constraints.

Several original research articles tackle the problem of limited data and high uncertainty in impact assessments. Matos et al. develop "impact chains" (i.e. structured cause-effect pathways) for deep-sea ecosystems with limited data, a novel method to map in a transparent, modular framework how multiple stressors propagate through the ecosystem. Using this framework, they assess human pressure footprints on the deep-sea benthic habitats and identify critical knowledge gaps under conditions of uncertainty. Pham et al. apply an expert-based risk assessment in the Barents Sea, demonstrating how expert elicitation can evaluate risks to key ecosystem services when empirical data are limited. Their approach integrates certainty assessment into a mixed-method expert-based risk evaluation building on the DAPSI(W)R(M) framework (Elliott et al., 2017), prioritizing pressures that most endanger the delivery of ecosystem services in a rapidly changing Arctic environment.

Other studies focus on improving monitoring and assessment frameworks to better capture ecosystem change. Devlin et al. review and redesign the eutrophication assessment regime in UK waters, which is fundamental for water quality management. They highlight successes and gaps in current monitoring, then propose a future assessment structure that integrates new indicators, climate considerations, and "shifting baselines" to reflect rapid ecological change. This forward-looking framework aims to enhance alignment between directives and incorporate ecosystem impacts of climate-driven stressors (e.g. warming, hypoxia) into coastal water quality evaluations. Likewise, Olano-Arbulu et al. test the utility of linking ecosystem functioning to human benefits using the Common International Classification of Ecosystem Services (CICES) cascade (Haines-Young and Potschin, 2012). Focusing on the Bay of Biscay, they find that many indicators in past studies were misassigned to cascade components, emphasizing the need for standardized classifications. Their case study of the anchovy fishery demonstrates that the CICES cascade can effectively trace connections between environmental health and the sustainable supply of ecosystem services. By identifying disconnects and correlations in the service cascade, this work contributes to refining how we quantify the benefits humans derive from well-managed ecosystems.

3 Addressing biological invasions, jellyfish and algal blooms, the decline of top predators, and emerging stressors

Human-driven ecosystem changes often manifest as biological disturbances – such as invasive species spread, jellyfish blooms and HABs, or loss of top predators – which pose major challenges for environmental managers. Additionally, emerging stressors such as microplastics, noise, and light also contribute to cumulative impacts. This Research Topic includes several comprehensive reviews that address these phenomena and offer guidance for mitigation and policy.

Katsanevakis et al. provide a timely review of marine invasive alien species (IAS) in Europe, evaluating progress nine years after the EU adopted its IAS Regulation (European Union (EU), 2014). They synthesize data on the introduction and spread of marine non-indigenous species across European seas, revealing persistent gaps in monitoring and management. The review emphasizes that effective IAS management hinges on coordinated data sharing (through networks like EASIN and AquaNIS) and rapid response strategies. They recommend strengthening biosecurity measures, public awareness, and research on the impacts of invasive species, as invasions can lead to native biodiversity decline, regime shifts, altering food webs, and compromising ecosystem functioning (e.g. Tsirintanis et al., 2022). This echoes the broader call for science-based interventions to curb biological invasions, which rank among the prominent human-induced stressors on marine ecosystems.

HABs, traditionally managed as public health issues (e.g., causing beach or shellfish bed closures), also have complex ecological and socio-economic linkages. Recognizing this, Sagarminaga et al. introduce new tools for managing HABs under an ecosystem-based framework. To support Good Environmental Status (GES) goals (according to the EU Marine Strategy Framework Directive), the authors develop two decision-support

tools: GES4HABs, a decision tree for determining management actions based on bloom status and causes, and MAMBO (environMental mAtrix for the Management of BlOoms), a matrix that categorizes regions by natural trophic state and human influence. These tools help managers identify when and where proactive mitigation of HABs is feasible, versus when preventive management (e.g., reducing nutrient inputs) is more appropriate. By streamlining assessment and reporting of HAB conditions, this work enhances our capacity to integrate HAB management into broader marine policy and management.

A complementary review by Sagarminaga et al. tackles jellyfish outbreaks and how to manage them to achieve GES. This systematic review compiles knowledge on the drivers of jellyfish proliferations (from climate warming and overfishing of competitors to coastal habitat modification) and evaluates control measures ranging from bloom forecasting to jellyfish removal. Managing jellyfish blooms is notoriously difficult, but the review highlights that early warning systems, public engagement through citizen science, and addressing root causes (e.g. rebuilding predator fish stocks, reducing eutrophication that favors jellyfish) can mitigate impact. The authors note that jellyfish management needs to be embedded in EBM, treating blooms as symptoms of broader ecosystem imbalances (often human-induced) rather than isolated nuisances. This perspective aligns with the holistic approach advocated across this Research Topic. Fernández-Alías et al. provide a comprehensive review of scyphozoan jellyfish bloom dynamics, highlighting the persistent unpredictability of bloom events despite decades of research. They identify overlooked sources of ecological variability – ranging from larval-stage mortality and substrate competition to microbiome interactions – that modulate bloom intensity and challenge forecasting efforts. The authors argue for species- and site-specific models that integrate both biotic and abiotic controls across life stages to improve predictive capacity.

Marine top predators are critical for ecosystem functioning, yet many are in decline due to cumulative human impacts like overfishing, bycatch, and climate change. Fortuna et al. review the ecological implications of these losses, such as trophic cascades and altered community structure when apex predators are removed. They also review traditional and emerging monitoring tools, highlight successful mitigation measures (from establishing marine protected areas and sustainable fisheries regulations to reducing bycatch through technological innovation), and stress the need for integrated, adaptive EBM. The review calls for embedding predator conservation into governance frameworks that address ecological, social, and economic dimensions.

Stanton and Cowart shine light on an underappreciated anthropogenic stressor: artificial lighting at night (ALAN). In their perspective, they review the effects of ALAN on the circadian biology of marine animals. From disrupted feeding and reproduction in corals and fish to altered behavioral rhythms, ALAN emerges as an "ecological light pollution" that can compound other stressors in coastal ecosystems. The authors call for incorporating ALAN into marine management considerations, noting that as human coastal development grows, so does the footprint of nocturnal light.

4 Case studies: ecosystem responses to climate and anthropogenic pressures

Multiple contributions provide empirical insights from specific regions and species, illustrating how marine ecosystems are responding to intensifying pressures. These case studies, spanning multiple taxa and geographies, reveal both common patterns and context-specific dynamics in ecosystem change.

Several studies document responses to climate change, particularly warming, in marine populations. Liao et al. focus on a small endemic euryhaline fish in the South China Sea and document significant habitat changes under warming. Using field surveys and species distribution modeling, they show that rising temperatures and shifting salinity regimes are contracting the suitable habitat for this estuarine species. Their findings exemplify how climate change is already driving range shifts and localized population stress for coastal species, particularly in relatively understudied tropical systems.

In European waters, de Fouw et al. analyze long-term data on the bivalve *Spisula subtruncata* in the North Sea to decipher drivers of its population fluctuations. Their spatio-temporal analysis evaluates the roles of climate and hydrographic change, fishing pressure, predation, and other variables in driving bivalve population swings. Understanding these population dynamics is critical, as such suspension feeders play key roles in coastal food webs and water clarity. Understanding natural variability versus human-induced change can inform thresholds for intervention.

Other case studies focus on ecosystem responses to localized human activities and habitat modifications. Huang et al. investigate Indo-Pacific humpback dolphins' responses to a megaproject construction, the Hong Kong–Zhuhai–Macao Bridge. Through field observations, they document changes in dolphin behavior and habitat use during bridge construction, indicating disturbance from increased undersea noise, vessel traffic, and habitat alteration. Their findings emphasize that even marine megafauna in urban coastal seas can be significantly affected by infrastructure development, highlighting the need for mitigation (e.g. noise reduction, temporal work closures) to protect top predators during coastal construction.

In a different context of coastal development, Liu et al. report on the proliferation of green macroalgae in China's Nanhui tidal flat following land reclamation. They found that the newly formed mudflat wetlands experienced blooms of opportunistic green algae, likely due to altered hydrology and nutrient conditions post-reclamation. This case study illustrates how coastal engineering can trigger unforeseen ecological shifts, such as nuisance algal outbreaks, with implications for wetland management and restoration efforts.

The systematic review by Marguin et al. synthesizes evidence on how fishing alters the trophic structure of fish populations and assemblages in the Mediterranean, highlighting that high fishing pressure—especially from industrial trawling—tends to lower trophic levels and disrupt food web functioning. It identifies major knowledge gaps and emphasizes the need for improved monitoring tools, EBM, and the inclusion of trophic indicators to

assess and mitigate cumulative impacts of fishing and climate change on coastal ecosystems.

Erbay et al. present the first comprehensive assessment of marine recreational fishing in the Turkish Black Sea, revealing high participation rates (about 4.5 million marine recreational fishers) and a significant retained biomass, surpassing commercial landings for some species. The study highlights both the economic value of this sector and its potential ecological impacts, emphasizing the urgency of including recreational fisheries in stock assessments and management frameworks. It also notes encouraging signs of conservation-minded behavior among fishers, such as widespread catch-and-release practices, suggesting potential leverage points for sustainable governance.

Ussi et al. analyze over 20 years of coral reef monitoring data and find a clear long-term change in reef community composition, with increases in dead coral, due to bleaching, particularly during strong El Niño events, crown-of-thorns starfish (COTS) outbreaks, and chronic local human pressures. They observed coral recovery with lower human impact and COTS removal in well-managed sites. The study highlights the need for stronger local management and long-term monitoring to inform ecosystem-based responses and protect reef functions.

Perrois et al. investigate the environmental drivers shaping sessile benthic communities around Jeju Island, a temperate-subtropical transition zone undergoing rapid ecological change. This study highlights the importance of marine climatic transition zones as sentinels of climate-driven faunal turnover, offering critical insights for predicting and managing biogenic habitat shifts under warming scenarios.

Effective management also hinges on accurate monitoring and recognition of novel stressors, and several papers in this Research Topic tackle this challenge. Hill et al. provide a striking example from the Southern Ocean: they show how apparent trends in Antarctic krill populations can be confounded by shifts in sampling methods over time. As surveys transition from net catches and acoustics to autonomous moorings, gliders, and meta-genetics the authors caution that observed "changes" in krill abundance may partly reflect methodological differences rather than true ecological shifts. Their analysis, focusing on a keystone pelagic species, highlights the broader point that long-term ecological datasets must be interpreted in light of evolving techniques. Maintaining continuity in monitoring or calibrating among methods is essential to reliably detect biological change.

5 Nature-based solutions

Ter Hofstede and van Koningsveld explore solutions by integrating nature-based approaches into construction of human infrastructure. They advance this concept, defining operational objectives to achieve system-scale ecological benefits. Using examples from the Dutch North Sea, they argue that engineered structures (like wind farms, artificial reefs, dikes) can be deliberately designed or retrofitted to support biodiversity and ecosystem functions. Establishing clear objectives, such as enhancing fish habitat connectivity or promoting reef community development, is key to assessing the success of these interventions. This work aligns with the growing recognition that nature-based solutions and habitat restoration can help offset some impacts of development and bolster ecosystem resilience in the face of global change.

Rasowo et al. review Kenya's pioneering blue carbon initiatives, including mangrove conservation, carbon credit schemes, and seaweed farming, highlighting their dual role in climate mitigation and community development. These projects are notable for their participatory governance—linking national policy frameworks with grassroots co-management—and for empowering local stakeholders, particularly women and youth, through sustainable income generation. By aligning with multiple United Nations Sustainable Development Goals, the initiatives exemplify how blue economy strategies can deliver integrated environmental and socio-economic benefits.

Da Conceição Felisberto Macamo et al. assessed a community-based mangrove management initiative in Nhangau, Mozambique, revealing partial success in restoring 10 ha of mangrove forest and promoting local awareness and alternative livelihoods. They discuss challenges in law enforcement and long-term financial sustainability, limiting its capacity to curb illegal harvesting and fully implement regulatory mechanisms.

Wang et al. present a novel seascape connectivity modeling framework tailored to China's coastal seas, integrating species dispersal potential with hydrodynamic and habitat data to identify conservation priorities. Their approach reveals key connectivity corridors and larval sources across fragmented coastal systems, offering actionable guidance for designing spatially coherent marine protected area networks. The study demonstrates the value of connectivity-informed planning in achieving effective and ecologically representative conservation outcomes.

6 Toward resilient marine ecosystems: synthesis and future directions

The diverse contributions in this Research Topic collectively reinforce key themes for future marine ecosystem management. First, the need for interdisciplinary, integrated ecosystem-based approaches is clear, in which humans are recognized as integral components of marine ecosystems. Single indicators or sectoral perspectives are no longer sufficient when dealing with complex problems like cumulative impacts from multiple anthropogenic pressures and natural stressors in an era of climate change. Many authors advocate for combining tools and breaking silos between disciplines (oceanography, ecology, social science, policy) to improve predictability of ecosystem responses.

Second, the importance of proactive management and early warning comes through strongly. Whether it is anticipating regime shifts, identifying tipping points, or forecasting blooms, timely information can enable managers to act before irreversible damage occurs. The decision-support systems, tools, and frameworks proposed in the Research Topic are valuable steps toward that goal.

Third, many studies highlight ecosystem resilience and nature-based solutions as cornerstones of long-term sustainability. Enhancing resilience might involve restoring top predators and

keystone species (to control invasive species or jellyfish), implementing marine protected areas and habitat restoration, or designing climate-ready conservation strategies. For example, nature-inclusive design of infrastructure and habitat-focused planning can create win-win scenarios for development and conservation.

Finally, a recurring message is the need to close knowledge gaps through continued research and monitoring. From the deep sea to coastal wetlands, understanding cause-effect linkages – especially for emerging issues like microplastic pollution, artificial lighting, or ocean noise – remains a priority. The contributions in this Research Topic not only advance scientific understanding but also translate that knowledge into practical recommendations for managers and policymakers.

Author contributions

SK: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing. AB: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing. EG: Conceptualization, Writing – original draft, Writing – review & editing. SF: Conceptualization, Writing – original draft, Writing – review & editing. HT: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing.

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Addressing the cumulative impacts of multiple human pressures in marine systems, for the sustainable use of the seas

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Human activities at sea have increased, causing subsequent degradation of ocean health and affecting ecosystem services and societal goods and benefits. Climate change further exacerbates the cumulative effects of these activities and their associated pressures. Hence, effective management of these multiple activities is imperative to ensure the sustainable use of the ocean. In response to these challenges, we have developed a comprehensive conceptual framework model within an ecosystem-based approach. This framework encompasses a versatile toolbox designed to assess cumulative pressures effects and the environmental status under the European Marine Strategy Framework Directive, in compliance with the Birds and Habitats Directives requirements and the need to secure the maintenance of ecosystem services and provision of societal benefits. Although we use European examples in the current discussion, we consider that there are similar challenges in many seas worldwide and so the recommendations here are widely applicable. Our aim is to facilitate the validation, harmonization, and demonstration of this toolbox across European regional seas and several countries, at different scales, from local to regional, including overseas territories. This approach aims to foster comparability in environmental status assessments. We anticipate that the proposed methodologies will serve as a foundational benchmark against which progress can be assessed in line with expectations and policy requirements. Additionally, this work prepares the groundwork for the forthcoming evaluation of the suitability, robustness, and applicability of these solutions and tools, thereby assisting managers in achieving Good Environmental Status (GES), both in European and wider global contexts, to address challenges which are common worldwide.

KEYWORDS

cumulative effects, risk management, ecological status, environmental status, assessment tools, ecosystem-based management, policy support

1 Introduction

Human activities at sea, such as the production and extraction of living and non-living resources, maritime transport, maritime infrastructure construction, and land-based activities affecting marine ecosystems, have significantly expanded in recent decades. These activities impose substantial pressures with a subsequent degradation of ocean health (Halpern et al., 2008, 2015; Reker et al., 2019; Korpinen et al., 2021; United Nations., 2021a,b), and, ultimately, affecting human wellbeing (Borja et al., 2020). Each activity has a designated area of operation (an activity footprint), in turn creating footprints of pressures (mechanisms of effect), and footprints of effects on the natural and social systems (Elliott et al., 2020a). These footprints then require to be addressed and managed, using management response-footprints (Cormier et al., 2017). As yet, the greatest challenge in marine management is in addressing the cumulative footprints of all activities and their associated pressures to mitigate the risk of adverse effects of their combined effects on ecosystem structure and functions (Stelzenmüller et al., 2018; Lonsdale et al., 2020).

Despite efforts to create a Sustainable Blue Economy and the European Green Deal to minimize human impacts on marine ecosystems and their services and societal goods and benefits (European Commission et al., 2022), maritime and upstream activities, driven by increasing human demands (Nash et al., 2020), are likely to increase. While regulations and planning tools exist, including maritime spatial planning (e.g., in Europe, the Maritime Spatial Planning Directive, MSPD; European Union, 2014), their cumulative impacts may translate to severe impacts on human welfare. The cumulative impacts of human activities and their pressures can be further enhanced by the effects of climate change (Gissi et al., 2021; IPCC, 2021), which is altering the ocean, with large-scale and severe effects on marine biodiversity worldwide (Duarte, 2014; Poloczanska et al., 2016; Pecl et al., 2017; Pörtner et al., 2021; Nikolaou and Katsanevakis, 2023).

Ensuring sustainable and regulated marine and coastal human activities is crucial to achieving established goals, such as the Biodiversity Strategy targets for 2030 (European Commission, 2020); Good Environmental Status (GES) under the Marine Strategy Framework Directive (MSFD; European Commission, 2008); the Good Ecological and Chemical Status under the Water Framework Directive (WFD; European Commission, 2000), for transitional and coastal waters; and the Favorable Conservation Status of vulnerable habitats and species [Birds and Habitats Directives, BHD (92/43/EEC)]. This aligns with the United Nations (UN) Decade of Ocean Science for Sustainable Development (2021–2030) (Claudet et al., 2020) and the UN Sustainable Development Goals (SDGs) (e.g., Molony et al., 2022). Additionally, the recently proposed EU Nature Restoration Law (European Commission, 2022) and the UN Decade of Ecosystems Restoration (Waltham et al., 2020) link sustainable use, planning of human activities, and the no deterioration clause with binding targets for ecosystem recovery by 2050. Achieving these goals will increase the likelihood of maintaining the provision of marine and coastal ecosystem services and societal goods and benefits under climate change, increasing the resistance and resilience of marine and societal systems (Runting et al., 2017; Gissi et al., 2021).

In this context, we present a conceptual model (Figure 1) developed as part of the Horizon Europe research project GES4SEAS[1]. The goal is to guide marine governance processes on minimizing the cumulative human pressures and their impacts on coastal and marine biodiversity and ecosystem functioning while maintaining the sustainable delivery of ecosystem services. Here, marine governance is defined as the sum of policies, politics, administration and legislation required to manage the marine system across all sectors (fisheries, shipping, seabed extraction, etc.), for tackling these complex issues (Elliott and Wither, 2023). We aim to achieve this objective by developing an innovative toolbox, tested, validated, and demonstrated in the context of adaptive ecosystem-based management (EBM) (Cormier et al., 2017). The co-creation of a toolbox with a focus on real problem-solving must start by understanding the uppermost assessment needs faced by stakeholders as well as their expectations regarding the main features or capacities of such an environmental assessment toolbox.

This toolbox will allow the competent marine authorities and regional seas conventions to assess and predict the effect of multiple stressors (including climate change) and pressures from human activities at the national, sub-regional, regional, and European levels, take informed management decisions, implementing measures that ultimately, will contribute to achieving GES. This framework is operating under the above environmental, socio-economic, and governance context, as shown in Figure 1.

Human activities are the result of socio-economic drivers and societal needs (Figure 1), leading to pressures that typically overlap in space and time, making the effects of their interactions cumulative (e.g., additive, synergistic, antagonistic, or a combination of these) (Elliott et al., 2020a; Lonsdale et al., 2020). Even though they are often studied in isolation, our knowledge of these interactions and their effects on the marine environment has increased in recent years (Crain et al., 2008; Ban et al., 2010; Coll et al., 2012; Korpinen and Andersen, 2016; Simeoni et al., 2023), but huge challenges remain to be solved. This includes our ability to consider the effects of all components of an activity, of all activities in an area and all areas constituting a marine management region on all receptors (ecological components).

Although physical and chemical processes can be predicted and based on deterministic relationships, marine physical, chemical and biological dynamics are often not linear. The consequence is that there is little predictability regarding stochastic ecological processes with which to inform decision-making processes, especially on ecological tipping points and thresholds of change (Dudney and Suding, 2020; Wedding et al., 2022), which, if exceeded, could inflict irreversible ecosystem damage (Lauerburg et al., 2020). In this context, an ecosystem-based and systems analysis approach to the management of human activities at sea and on land (Borja et al., 2016; Link and Browman, 2017; Elliott et al., 2020b) should ensure that the combined pressure of such activities is kept within levels that are compatible with the requirements of GES, against a background of climate change (Figure 1). This means that the

1 GES4SEAS: "Achieving good environmental status for maintaining ecosystem services, by assessing integrated impacts of cumulative pressures", (www.ges4seas.eu).

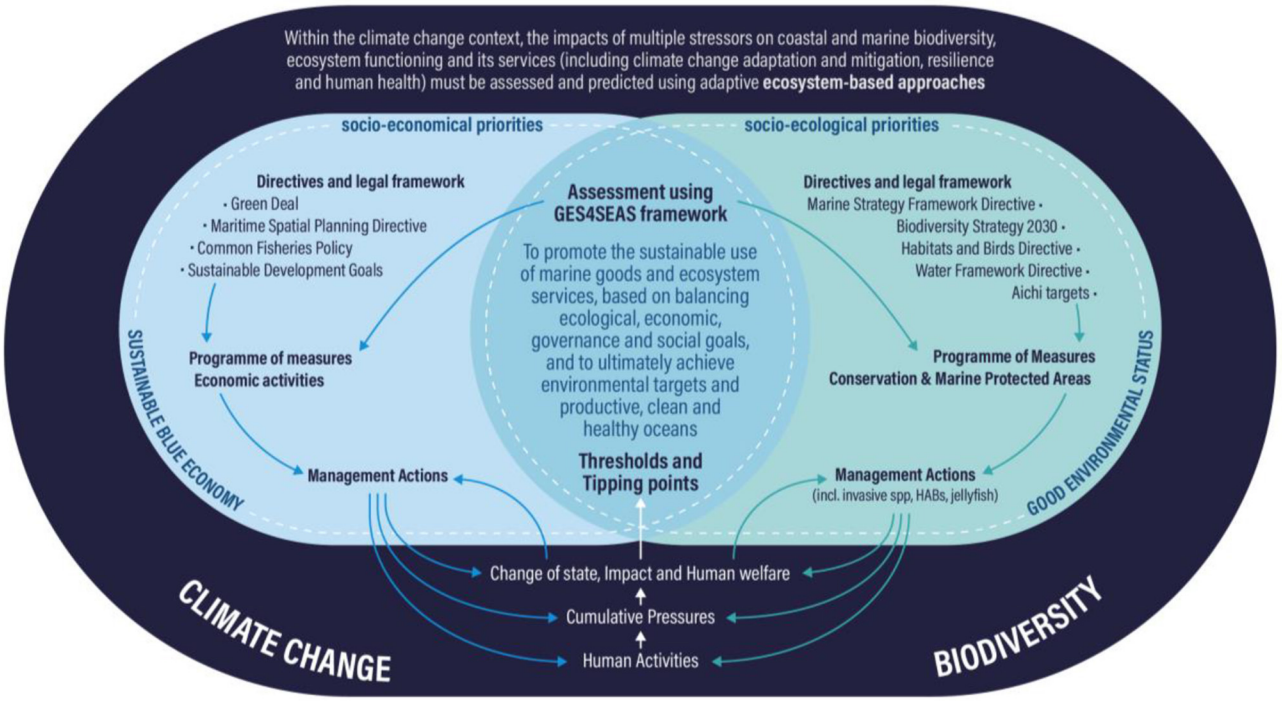

FIGURE 1
Socio-ecological, socio-economic and governance context of cumulative pressures effects management at sea, in which the project GES4SEAS is embedded.

capacity of marine and coastal ecosystems to respond to human-induced changes is not compromised, enabling the sustainable provision and use of marine goods and benefits by present and future generations. Furthermore, marine systems need to be kept resistant and resilient to rapid climate and environmental changes, as advocated by the Green Deal, IPBES, and IPCC (IPCC, 2021; Pörtner et al., 2021). However, more information is needed to reduce the gaps in spatial and temporal marine data (Maes et al., 2020) and in our understanding and knowledge of the impacts of cumulative pressures on ecosystem functioning.

Critical changes in ecosystem components leading to degraded ecosystem health are, for example, the shifts from high diversity habitats to unnaturally low diversity ones, the accumulation and increasing spread of invasive species or the increased frequency of harmful algal blooms (HABs) and jellyfish outbreaks, hence challenging the management of human activities (Fortuna et al., 2023; Katsanevakis et al., 2023; Sagarminaga et al., 2023a,b). Therefore, achieving "clean, healthy and productive oceans," *sensu* MSFD, is a delicate balance between the socio-economic needs and the socio-ecological goals (Figure 1), framed by existing agreed thresholds and observed/anticipated tipping points.

Our perspective of the combined effects of traditional and new sustainable Blue Economy activities is summarized in Figure 2. In principle, without human activities offshore, in coasts, or land, seas could be considered in GES. The sea can be regarded as having a finite assimilative capacity to accommodate human activities, their pressures and effects without adverse effects being manifest. With each additional activity permitted in a sea area, a portion of that assimilative capacity is then used up and so current activities can compromise achieving GES without adequate management measures (Elliott et al., 2018). The total sum of such management actions is defined in European terms as the Programme of Measures (PoM), *sensu* MSFD and WFD and those PoM will include mitigation and/or compensation methods to reduce the adverse effects of the activities and therefore recover some of the lost Assimilative Capacity; hence it is valuable to consider the carrying capacity of an sea area to support human activities without damage to ecosystem health (Elliott and Wither, 2023). Eventually, if mitigation cannot remove all adverse consequences, the number of activities and their pressures and effects would exceed GES and hence breach the national obligation to maintain a sea area in GES. Each of the Blue Economy activities can degrade environmental status, even if carried out in the most sustainable manner. Therefore, in consequence, without management or with poor management, the assimilative capacity of the system can be exceeded, despite existing solutions (Claudet, 2021).

There is an urgency in making the Blue Sustainable Economy compatible with the objectives of existing environmental policies for which tools are needed (European Commission, 2021). We aim at contributing to balanced, sustainable development, linking climate change and the cumulative effects of multiple activities on environmental status, ecosystem processes, functions, and services. A major challenge in marine management is to describe and quantify the impacts on specific ecosystem components, accounting for space and time lags, especially when the impacts do not all co-occur in space and/or time (Mazaris et al., 2019; Galparsoro et al., 2022). Therefore, here we propose methodologies and approaches to develop a framework for adaptive EBM, which

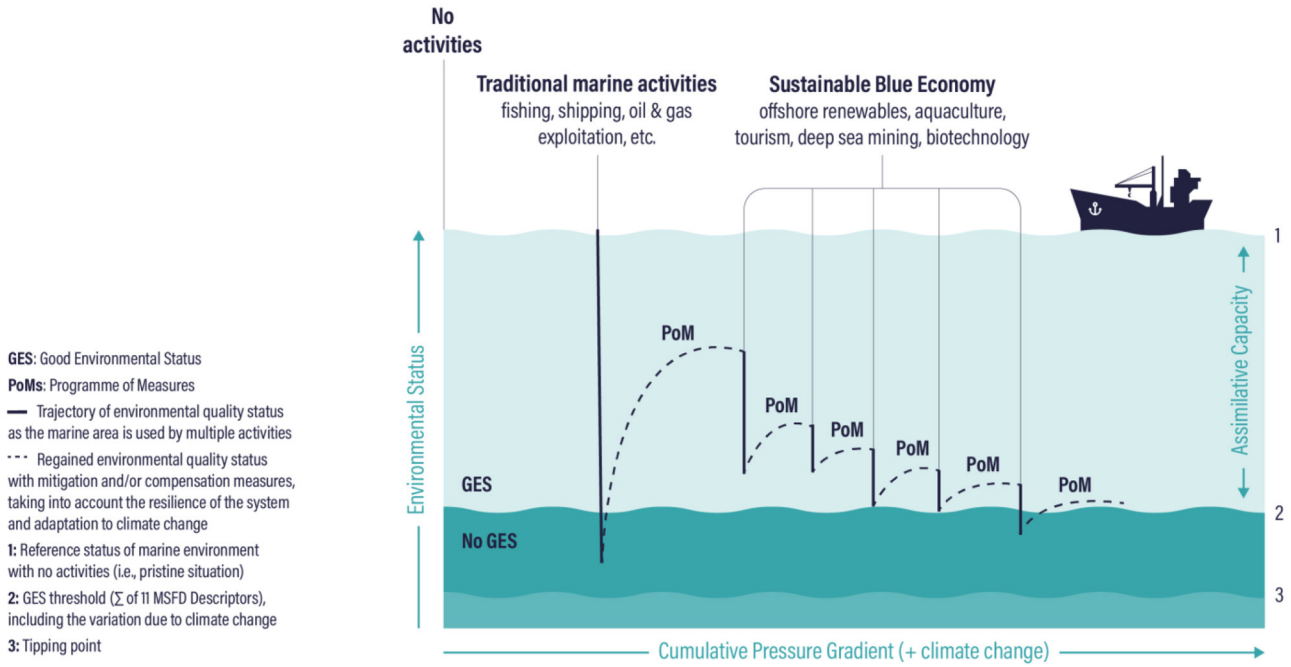

FIGURE 2
Illustration of the relationship between cumulative pressures, environmental status and the achievement of Good Environmental Status (GES). The magnitude of impact/recovery as well as the order by which activities are included in the figure are illustrative only [adapted from Elliott et al. (2018)].

by necessity includes a toolbox to assess cumulative pressures effects, the status under the MSFD and the BHD requirements (which use implementation cycles, favoring such an adaptive approach), and the maintenance of ecosystem services, in line with the goals of the EU Biodiversity Strategy 2030, the Green Deal and Mission Starfish 2030, for restoring ocean and seas (European Commission et al., 2020). This toolbox would be validated, harmonized, and demonstrated across EU regional seas and countries, at different scales, from local to regional, including overseas territories, allowing comparability in the GES assessments and use by the Member States and Regional Sea Conventions. We anticipate that this effort would serve as a baseline against which to check the progress against expectations and policy needs as well as fitness, robustness, and applicability of solutions and tools of this framework, to address challenges which are common worldwide.

2 Stakeholder involvement in a co-creation process

To achieve the abovementioned objective and meet the relevant policy objectives of the Biodiversity Strategy, Regional Seas Conventions, the MSFD, WFD and BHD, we consider that stakeholder involvement is crucial, guaranteeing a fit-for-purpose, pragmatic and validated outcome (Figure 3). Setting the scene with stakeholders has a pivotal role, identifying the policy and societal needs and validating the solutions proposed, engaging key stakeholders in the co-development of the framework and its accompanying toolbox. Therefore, as part of the stakeholder involvement process, a Practitioner Advisory Board (PAB) is required, including key actors to guide the co-creation approach.

Meeting the expectations of stakeholders on the main features or capacities expected from an environmental assessment toolbox is key to its acceptance. A preliminary survey engaging 22 stakeholders occupying key roles in marine governance and assessment (from the GES4SEAS project Stakeholder Initial Survey, 2022) retrieved 78 suggestions, many of which reflect a common desire for policy and regulatory compliance, flexibility of the toolbox, a clear link to pressures and to management, consideration of confidence of the assessments, compatibility and interoperability and clear guidance on its use (Supplementary Table S1), and compiled in Figure 4. A strong PAB together with other relevant stakeholders is also crucial to identify the main challenges currently faced by those carrying out or using the information from environmental assessments and drive science knowledge toward solutions and well-suited developments (Figure 4). Hence, the main outcome outlined above can be achieved and ensure compliance with policy and regulatory obligations, focusing on real problem-solving and following an iterative and incremental development approach (Larman and Basili, 2003), including communication and dissemination. This approach would also be used for software creation, which involves deconstructing the required comprehensive management system into smaller, manageable items. The iteration process should comprise several stages: Planning, Designing, Implementing, Testing, and Evaluating. As such, the proposed framework will need

to progress through feedback loops and reiteration stages that refine the toolbox until it meets the objectives, under the guidance of the PAB.

This iterative process can partly be achieved through consultation during which different social research tools are used (e.g., focus groups, interviews) which include information-enhancing loops between the stakeholders and scientists (learning and showcasing bi-directionally). The concept of "learning" is central in this framework, which therefore should include a series of Learning Sites (i.e., case-study test areas), connecting stakeholders and scientists in the co-development and co-learning process, and bridging end-user needs with the scientific activities.

It is critical for the success of this collaborative process to involve those stakeholders that have an influence on both the specific goals and end-products to be achieved. The implementation of the Green Deal and the new EU Biodiversity Strategy requires that Member States collaborate, supported by Regional Seas Conventions, to enable meeting the targets required by these major environmental policies [also including MSFD, BHD, WFD, Common Fisheries Policy (CFP)]. Often, such policies are misaligned spatially and temporally to a certain degree regarding monitoring, reporting and targets (e.g., Franco et al., 2021). This is despite them often converging and overlapping partially in their objectives.

These outcomes would be communicated and promoted by being adapted for dissemination to external and wider audiences, and future exploitation. This co-creation approach provides legitimacy to the outputs developed, i.e., their validity within the targeted policies context; commitment to its future use, as key stakeholders are more likely to feel a co-ownership of the solutions generated, and increased efficiency of its implementation. The ultimate outcome would be knowledge transfer, real use and uptake by the practitioners of a co-developed toolbox, necessary for implementing the EBM approach.

3 A conceptual framework to solve problems

The conceptual framework and theory, underpinning the whole process to be operationalized in the different phases, should be defined (Figure 5). It should indicate the boundaries for the models to be used, the scenarios related to human activities and climate change predictions, and the toolbox required to be used in the Learning Sites, in a logical sequence to fit or contribute to EBM approaches (Figure 5). It will identify all relevant human activities both at sea and on land and how their pressures impact the ecosystem and its components and guide EBM toward achieving GES. Based on existing work (e.g., Culhane et al., 2019), we are determining how the ecosystem service capacity depends on marine ecosystems and GES (Elliott, 2023; Van de Pol et al., 2023). As the focus is on the sustainable use of coastal and marine ecosystems to perform services from which society obtains goods and benefits and be resistant and resilient to the effects of unmanaged exogenous pressures (e.g., climate change) (Borja et al., 2010), we are focusing on those ecosystem services that are sensitive to ecosystem change and health status, including the way they lead to societal goods and benefits, including human health and welfare (e.g., Charles et al., 2016; Elliott, 2023).

Within this framework, exogenic unmanaged pressures are defined as "causes of change which have their origin outside of a management system and cannot be controlled by local measures whereas the consequences which occur in the management site are subject to management measures" while endogenic managed pressures are defined as "anthropogenic pressures which originate within management system, i.e., the causes of change can be controlled and their consequences addressed" (Smith et al., 2022; Elliott and Wither, 2023). All this work provides the theoretical and practical basis, and it guides the process of data analyses and model building that constitutes the knowledge-base required to address the policy and stakeholder requirements. This includes data and methods for determining the spatial and temporal activity-, pressure-, effect-, and management response- footprints (Elliott et al., 2020a) and will separate these according to endogenic and exogenic pressures using the causes-consequences-responses pathways (e.g., Elliott et al., 2017; Cormier et al., 2019). To do this, a solid commitment to building on the work of previous projects, and the conceptual approaches they have developed (e.g., Knights et al., 2015; Patrício et al., 2016; Smith et al., 2016; Borgwardt et al., 2019; Pedreschi et al., 2019), is necessary.

The background and approaches to fill knowledge gaps in our assessment of effects of multiple pressures on the ecosystem and its functioning, i.e., using meta-analyses quantifying the direction and magnitude of links between activities-pressures-ecosystem components-processes-functions-ecosystem services-societal goods and benefits and how these can inform EBM are central to the proposed approach. In addition, having monitoring data, based on the background related to possible lines of physical-chemical, ecotoxicological and ecological evidence, it could be possible to detect acute and chronic changes related to anthropogenic activities. Having thus increased our understanding on the response of organisms, ecosystems, processes, functions and services to anthropogenic pressures and environmental changes, the results from the information analysis would (i) support analyses toward methods to identify reference levels and potential tipping points, (ii) set thresholds where possible (Lauerburg et al., 2020), and (iii) evaluate the consequences of management options aimed at protecting marine habitats and species, building on previous studies (Halpern et al., 2008; Cormier et al., 2013, 2017, 2019; Andersen et al., 2015; Elliott et al., 2017, 2020a,b; Korpinen et al., 2019; Lonsdale et al., 2020). However, differentiating between service capacity and its human use is needed. That service capacity can be linked to GES, but its use may not, as not all services are linked to GES (Elliott, 2023).

In addition to the cause-consequence-response framework DAPSI(W)R(M) [Drivers, Activities, Pressures, State changes (on the natural system including ecosystem services), Impacts (on human Welfare, including the effects on societal goods and benefits), Responses (using management Measures)] (Elliott et al., 2017), as a unifying approach, we are incorporating the Commission Staff Working Document recommendation to use

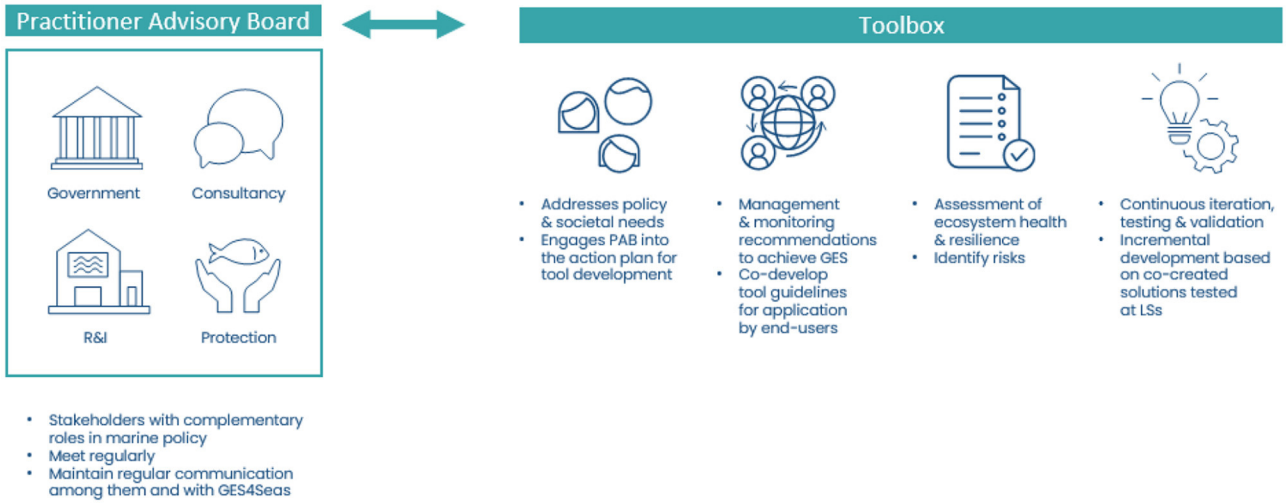

FIGURE 3
Stakeholder engagement to co-create suitable tools for marine management. GES, Good Environmental Status; LSs, Learning Sites; PAB, Practitioner Advisory Board.

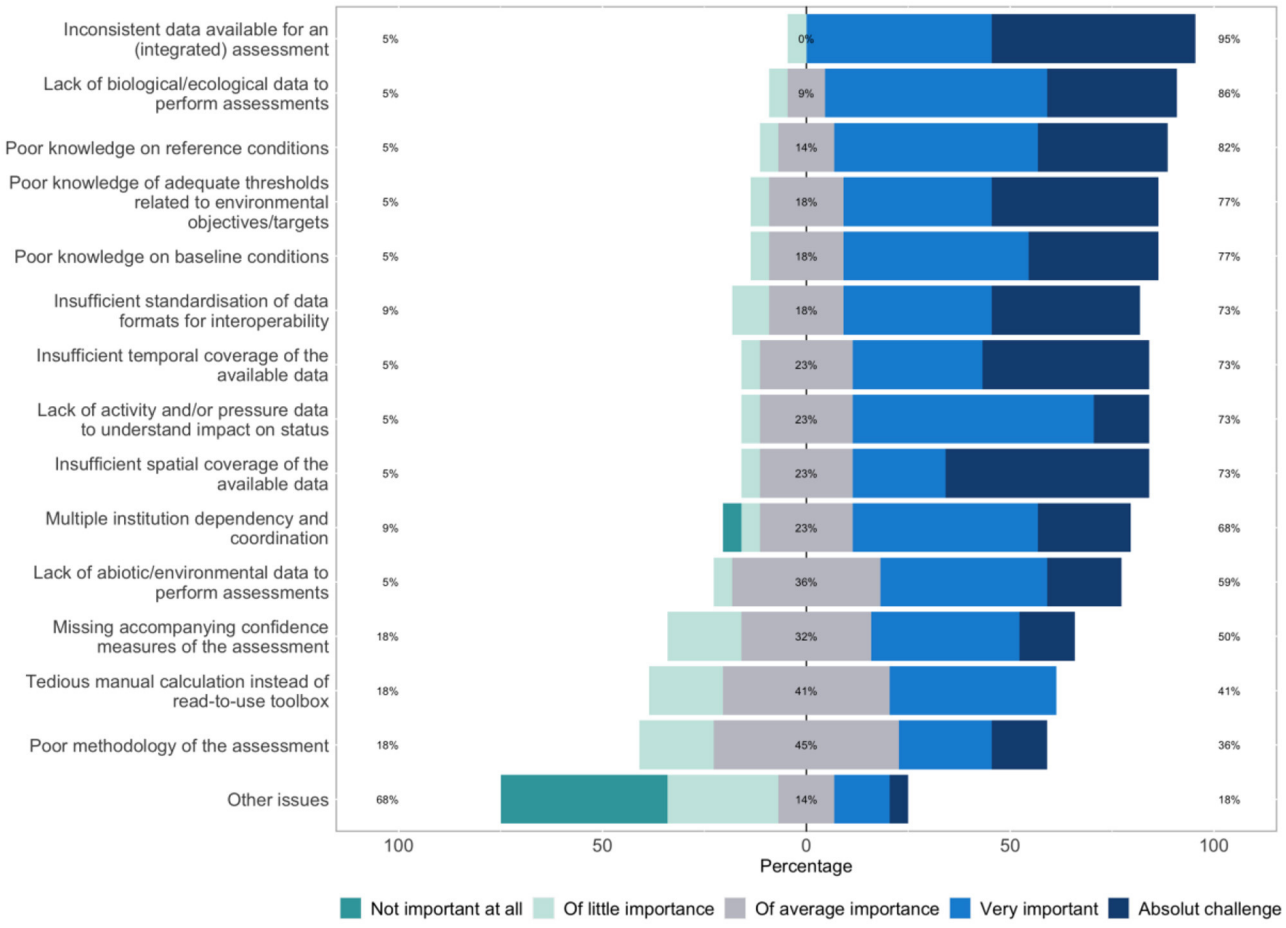

FIGURE 4
Main challenges faced with environmental assessments. Perspective from 22 stakeholders occupying key roles in marine governance and assessment in national ministries and competent authorities, NGO's, Regional Sea Conventions, European Commission and agencies (from the GES4SEAS project Stakeholder Initial Survey, 2022).

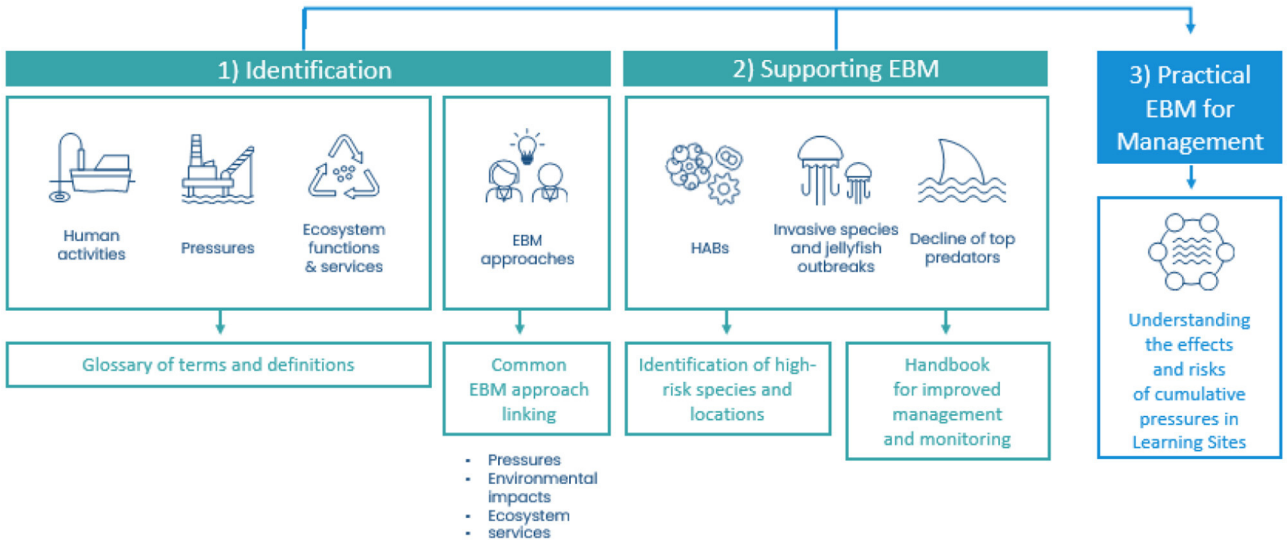

FIGURE 5
Developing a conceptual framework and knowledge base for Ecosystem-Based Management (EBM). HABs, Harmful Algal Blooms.

the DAPSES-MMM approach[2], which is similar but which adds confusion through the explicit separation into natural ecosystem services and societal ecosystem services (cf. Elliott, 2023), as well as goods and benefits, including human health and welfare. However, the latter approach extends the acronym to mention monitoring, measures and management, linked to MSFD (e.g., articles 11 and 13) and inherently included in R(M), in DAPSI(W)R(M). These frameworks give the ability to develop a unified approach that connects activities with pressures to state change on the natural system and impact on the human system, and the capacity to supply ecosystem services which then, after inputting human complementary assets and capital, provides goods and benefits for human health and wellbeing, combining the model components together into a coherent system.

In turn, this would be made operational at the Learning Sites, in close collaboration with the PAB, in showing how to develop solutions (responses and management measures) (Stelzenmüller et al., 2020). A risk-based approach based on Exposure × Effect or Hazard × Vulnerability links (see Galparsoro et al., 2021), such as the widely used and ISO standard Bow-tie method and software, should be also included (Cormier et al., 2019). It would also use a modified method to give stakeholder-led assessment and opportunities in marine environmental management (Elliott et al., 2020c). Importantly, this involves defining the role of all actors well in advance by showing what to expect from whom. For example, bringing into the spotlight marine invasive species, HABs, jellyfish outbreaks, and the decline of top predators that affect the biodiversity of all European marine regions (Katsanevakis et al., 2014, 2016; Sanseverino et al., 2016; Prieto, 2018; Tsiamis et al., 2018; Karlson et al., 2021; Zingone et al., 2021) we have reviewed in depth the Drivers, Pressures, State change, and affected ecosystem services (Fortuna et al., 2023; Katsanevakis et al., 2023; Sagarminaga et al., 2023a,b). Best practices and existing knowledge in monitoring, assessment, predicting, and managing these issues, and compiling a set of guidelines and tools for improved management, also accounting for the potential of new technologies and novel methods, such as eDNA, metabarcoding, remote sensing, and biologgers, have been also completed (Fortuna et al., 2023; Katsanevakis et al., 2023; Sagarminaga et al., 2023a,b).

4 Understanding the mechanisms of cumulative effects

The proposed approach is also underpinned by our development of the knowledge base to quantify, assess and forecast the consequences of anthropogenic perturbations on ecosystem sustainability, productivity, and resilience, from the conceptual and theoretical framework raised previously, under scenarios of climate change by 2050 (including particular aspects, such as sex segregation of species, depending on environmental factors, and extreme events). The objective is to understand the mechanisms that determine cumulative effects (Figure 6).

This includes refining methods and using existing models to set thresholds and establish tipping points. Here, tipping points are defined as "zones of rapid change in a non-linear relationship between the state of an ecosystem or ecosystem component and intensity of a driver, human activity or pressure. This leads to abrupt transitions beyond a critical level, in which the system is unable to return to the precedent stable stage" [term adapted after Selkoe et al., 2015 and Stelzenmüller et al., 2018 in Smith et al. (2022)]. Thresholds are defined as "a value or range of values that allows for an assessment

2 DAPSES-MMM: Drivers, Activities, Pressures, State of Change, Ecosystem Services, Management, Measures, Monitoring, (https://data.consilium.europa.eu/doc/document/ST-9161-2020-ADD-5/en/pdf).

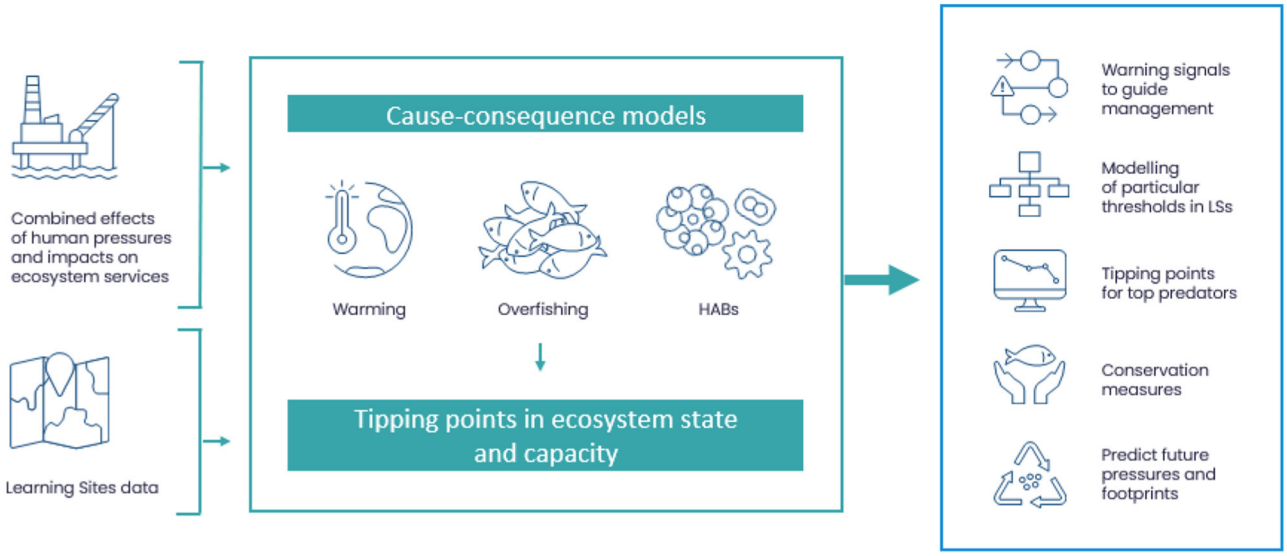

FIGURE 6
Understanding the mechanisms that determine the cumulative effects of human activities and climate change. HABs, Harmful Algal Blooms.

of the quality level achieved for a particular criterion, thereby contributing to the assessment of the extent to which GES is being achieved" [after the European Commission, 2017, in Smith et al. (2022)].

Mechanistic models would need to be parametrized from data analyses together with existing knowledge [analysis on impact-chains covering each of the two main risk aspects (i.e., exposure and potential effect)], stakeholder input and specific analyses at the Learning Sites, and their outcomes (codes and interfaces) should be then implemented. The integration of two approaches would be needed: combined effects (pressures) and environmental status and dynamics, making this integration operational. This would enable the assessments relevant to the implementation of the MSFD, BHD and Biodiversity Strategy, to be included in the toolbox. In generating the approach proposed here, by necessity, we are building upon the work from previous projects and other initiatives, in linking human activities and pressures and impacts/state/ecosystem services, using a variety of models (Coll et al., 2012, 2016, 2019, 2020; Uusitalo et al., 2016b; Lynam et al., 2017; Stelzenmüller et al., 2018, 2020; Cormier et al., 2019). This work sets the scene and defines the ways to undertake the work in the Learning Sites and the further development of the software toolbox as well as the inclusion of the links between GES and the capacity to deliver ecosystem services (Broszeit et al., 2017; Leenhardt et al., 2017), using the Common International Classification of Ecosystem Services (CICES; Haines-Young Potschin, 2018). Models are being used to investigate the most appropriate ways to obtain thresholds and tipping points, building on previous evidence (Scheffer and Carpenter, 2003; deYoung et al., 2008; Scheffer et al., 2009; Lynam et al., 2016; Dudney and Suding, 2020; Hillebrand et al., 2020; Lauerburg et al., 2020; Rogers et al., 2020; Thrush et al., 2021) and tools (e.g., Fulton et al., 2015) under the climate change context.

5 Developing a software tool for assessing the status of the ocean

The approach proposed here relies on integrative and holistic solutions which are being operationalized to identify a scientific framework and software toolbox for mapping, analyzing and assessing (i) cumulative pressures [Cumulative Impact Assessment/Combined Effects Assessment (CIA/CEA)], (ii) GES, and (iii) ecosystem services in a systematic and holistic way (Figure 7). To date, these three assessments have often been carried out separately, in some projects and by Regional Seas Conventions. Nonetheless, there is a high degree of interaction and dependencies within these three assessments (Birk et al., 2020; Culhane et al., 2020). These assessments have the potential to be aligned, starting by combining and improving existing tools and frameworks [e.g., Nested Environmental status Assessment Tool –NEAT (Borja et al., 2016), the CIA and EcoImpactMapper methods (Halpern et al., 2008; Stock, 2016), and the "Marine Ecosystem Capacity for Service supply Assessment" method (MECSA) (Culhane et al., 2020)]. Hence, this would produce an innovative and flexible toolbox, which can deliver science-based assessments with both numerical and spatial output; in consequence, the toolbox will also enable guiding the management process [in terms of DAPSI(W)R(M), see Elliott et al., 2017], to inform decision making (e.g., as required under the MSFD, BHD, Biodiversity Strategy) (Loiseau et al., 2021). An added value of such integration is the improved incorporation of the spatial extent of both human activities and ecosystem components and the possibility to cross-refer and validate the assessment results to the various data sources used. The toolbox should be iteratively adjusted, tested and validated at the Learning Sites, in collaboration with feedback from the PAB.

This integrative toolbox will be required/invaluable for use by managers and decision-makers for assessing the effects of pressures on both the ecosystem status (e.g., MSFD GES, or

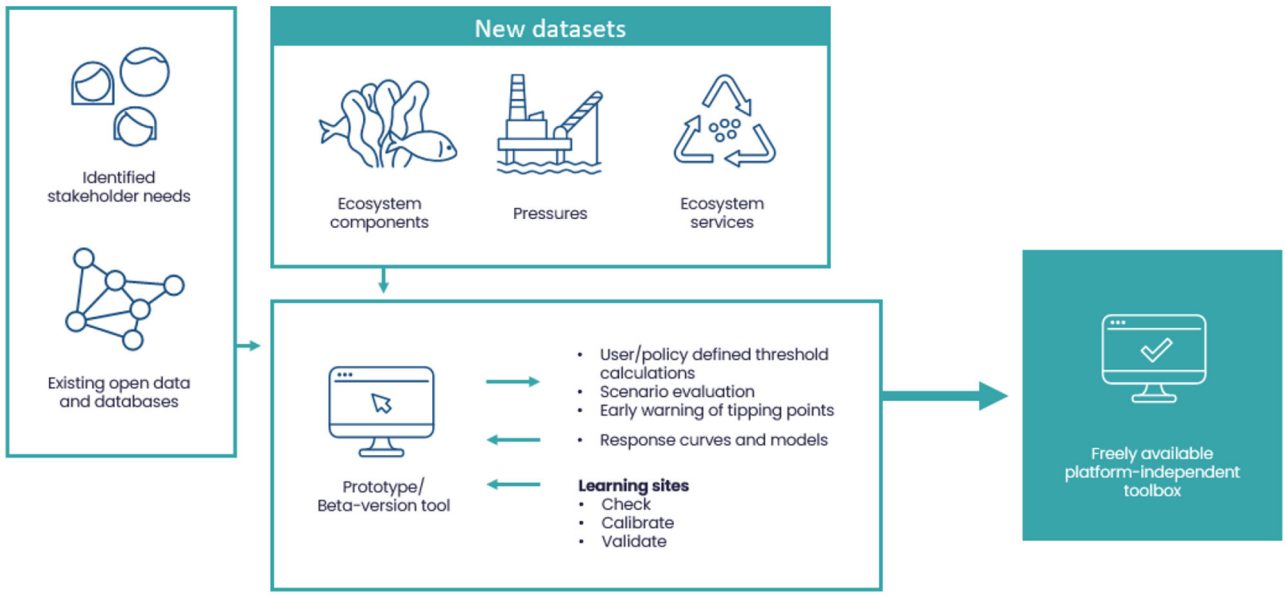

FIGURE 7
Linking pressure and status assessment with the capacity to supply ecosystem services into a unifying holistic framework and nested toolbox.

BHD favorable conservation status) and on the capacity to supply ecosystem services within contrasting scenarios of human activities and climate change. The objective is to advance from the current situation with multiple disparate assessment frameworks and tools (see Smit et al., 2021, for an overview) to a comprehensive integrative and hierarchical framework with multiple inputs and outputs, linkages and/or crosswalks between them, and an accompanying confidence assessment. It is further emphasized that the ability to understand and manage such a complex socio-ecological system therefore requires a systems analysis approach which has a solid underpinning theoretical framework, but which is then able to be implemented by stakeholders (Elliott et al., 2020b). As such, a simplicity of implementation, flexibility, and transparency are key to this process, as it enhances acceptance by key stakeholders, especially as a decision support tool (Nygård et al., 2020; Schumacher et al., 2020).

To meet the overall objectives, an iterative and incremental development approach is required to be applied, following the steps: (i) development of a prototype based on existing tools and software, after inputs from PAB stakeholder needs; (ii) co-development of an assessment framework and a tool that overcome weaknesses of existing approaches, and (iii) based on rigorous testing of the toolbox, in Learning Sites, with further improvement (iterations with PAB) and dissemination to stakeholders (Figure 3). Key challenges to overcome in the three steps are:

- Step 1: Combining existing tools into a unifying toolbox. This would be achieved by initially combining three existing tools: (i) NEAT (Borja et al., 2016, 2021; Uusitalo et al., 2016a; Pavlidou et al., 2018), (ii) EcoImpactMapper, an open-source tool for mapping of cumulative effects (Stock, 2016), and (iii) the MECSA methodology (Culhane et al., 2020).
- Step 2: Improving existing and widely used frameworks/tools. The prototype toolbox developed in step 1 would be further developed, focusing on a range of well-known weaknesses (e.g., Quemmerais-Amice et al., 2020) that will be overcome, e.g.,: (i) supplement the linear and unidirectional relation between pressures and ecosystem responses with response curves and thresholds models; (ii) enhance the current flat/sectoral structure to a hierarchical one using e.g., conceptual ecosystem models connecting ecosystem components with pressures and the resulting state changes and the ecosystem services and resultant societal goods and benefits that they provide (e.g., Griffiths et al., 2017); (iii) supplement the use of expert judgement (currently extensively applied) for the setting of weighting factors with data-driven/evidence-driven approaches; (iv) allowing flexibility in the selection of aggregation/integration methods, depending on the regional needs; (v) include uncertainty assessment as an output from the tool (e.g., Uusitalo et al., 2016a; Quemmerais-Amice et al., 2020; Carstensen et al., 2023), and (vi) define data structures and interfaces that enable direct linkage between existing data and databases and the tool, and thus minimize the need for manual data input, a hurdle to key stakeholders characterizing many standalone assessment tools.
- Step 3: Based on the testing of the toolbox in Learning Sites with more data, and the risk-based approach, the modules could be fine-tuned, tested in Learning Sites with limited data and upscaled to regional seas, documented and published as a final version of the toolbox, also engagement with PAB to anchor the developed tool within the stakeholder community.

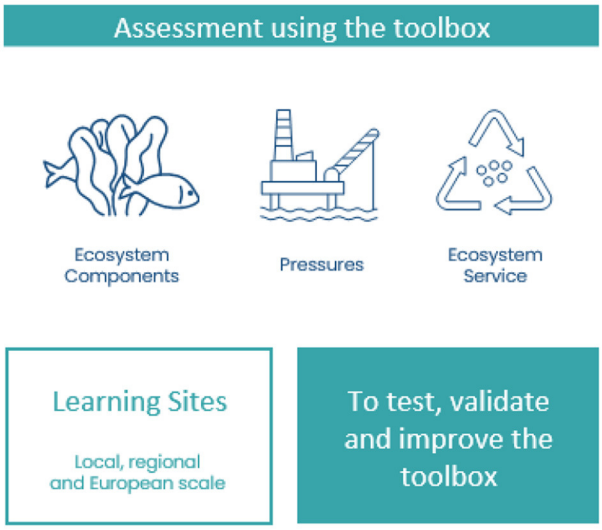

FIGURE 8
Learning sites to test and validate the toolbox and synthesize recommendations for stakeholders.

6 Learning together, by testing together

Working with the Learning Sites and the PAB, the proposed strategy would contrast different approaches and extract clear, concise, operational, and harmonized conclusions (Figure 8). A central aim for all Learning Sites would be to provide the developing, testing and demonstration ground for the assessment toolbox and validate its value with respect to the EBM and specifically, the risk of adverse effects on GES, selected ecosystem services, functions and processes, human health and wellbeing, in the face of cumulative human pressures and climate change scenarios.

The Learning Sites should facilitate mutual learning and collaboration, providing additional skills (e.g., modeling, use of integrative tools, etc.), or knowledge and skills-exchange transverse to the sites (i.e., use of satellite data to set HABs extent, molecular methods to detect invasive species, etc.). This ensures that knowledge is transferred from one site to another, experiences from stakeholders are shared from a regional sea to another, and finally, the outputs can be shared, harmonized and understood in different geographical areas and at various spatial scales, readily applicable to stakeholders. To increase this knowledge transfer, cooperation should be established with main actors in marine assessment, by providing and harnessing data and applying an integrated conceptual framework, both at national and international level. Furthermore, this gives the much-needed potential to take experience from skills and data-rich areas to areas with a lesser experience of these aspects.

With this aim, Learning Sites should cover a broad variety of human activities and pressures affecting the marine environment, as well as the different environmental (MSFD Descriptors) and ecosystem services and societal goods and benefits (CICES: Haines-Young Potschin, 2018; Elliott, 2023) affected. In order to test and validate fully the approach, Learning Sites should vary greatly in terms of geographical scope and spatial scales (i.e., local, subregional, regional, continental, overseas), political context (i.e., EU and non-EU countries), state of knowledge regarding cumulative impacts, ecosystem services and their interplay with climate change, as well as data and knowledge availability. The sharing and use of data from portals such as EMODnet[3], WISE Marine[4], and Copernicus[5] should be promoted. The stocktake of current knowledge also comprises data from other resources such as national data reported to the EU under different directives, to the Regional Seas Conventions, or published literature. The Learning Sites would enable the ability to:

- Explore the specificities of Learning Sites stemming from different geographical locations, especially with regards to the impacts of cumulative pressures (including climate change) in the functioning of ecosystems (and the capacity for providing ecosystem services, and benefits for human health), so they can be better managed. To this end, Learning Sites with different sets of activities, pressures, impacts, ecosystem services and societal goods and benefits should be covered in detail.
- Determine how the toolbox developed can work at a large pan-European scale, exploring comparability and harmonization across regional seas, integrating cumulative pressures, impacts (status) and ecosystem services delivery.
- Gain understanding on the functioning of transverse topics, such as invasive species, HABs and jellyfish blooms, as well as aspects related to top predator monitoring (Ferrer et al., 2015; Ferrer and Pastor, 2017; Ferrer and González, 2021); in addition, it would encompass developing and testing methods based on biologging, remote sensing, and genomics (eDNA), for different ecosystem components.
- Learn how to best manage transboundary issues, especially with non-EU countries, including barriers to coherence and equivalence of outcomes, which may often hinder the process and/or successful policy implementation and effectiveness (e.g., Elliott et al., 2023).
- Internationalize outputs and receive inputs by going beyond the EU frontier reaching other non-EU Seas. This is of particular interest as while sharing the SDGs framework, the marine management approaches elsewhere may or may not differ from those in the EU.
- Identifying requirements and potential limitations for the application of the toolbox and, in an iterative process, adapt them to the stakeholder needs, thereby testing, validating, and demonstrating the toolbox in areas with different amounts of data, and upscaled to regional seas and all European seas.
- Implementing cumulative impact models (Katsanevakis et al., 2016) associated with hazardous events.
- Synthesizing the lessons learnt across Learning Sites with regard to (a) cumulative impacts, from different pressures on marine biodiversity and ecosystems components and

3 https://emodnet.ec.europa.eu/en
4 https://water.europa.eu/marine
5 https://www.copernicus.eu/en

functions, as required by the MSFD, (b) estimating extinction risks of species, communities and structures that are essential to ecosystem functioning and the conservation of marine biodiversity, (c) advanced understanding of approaching tipping points, (d) assess the risks to ecosystem services, and to societal goods and benefits including human health and wellbeing, and (e) mitigation strategies to achieve GES targets, in relation to the MSFD PoM. All these lessons will set the basis for an EBM approach, which would be completed in close collaboration with PAB.

Given the above requirements, actions and activities, there is the need to make solutions available and ready to use. The lessons learnt at the Learning Sites, and the outputs generated, will need to be transferred to the stakeholders, but also further afield as the proposed approach will enhance societal and public engagement and understanding of ecosystem functioning and human health through ocean literacy, ensuring adequate dissemination and exploitation. The dissemination would be based on an innovative set of tasks, which use ocean literacy (based on IOC-UNESCO guidelines). Importantly, this will contribute to behavioral change in society, as well as educating and training (i.e., school and adult education, summer schools, citizen science platforms) a new generation of researchers in tools developed, using the lessons learnt. This additionally has the benefit of ensuring cooperation with international organizations and initiatives, by providing and harnessing data and applying an integrated conceptual framework, in close cooperation with PAB.

7 Enhancing the impact of the outcomes

With its results, outcomes and impacts, the proposed approach described here will contribute to accelerate the ecological transition required by the European Green Deal, specifically within the Destination "Biodiversity and ecosystem services," as proposed in Table 1.

The outcomes and results would then need to be disseminated, exploited and communicated following a plan that can be carefully designed based on the Lasswell's Communication Model. This model focuses on "Who says What to Whom in Which channel and with What effect," as a means to maximize the impact of any action (Figure 9).

Usually, maximizing the impact outputs requires (i) reaching key stakeholders so that they can better manage pressure impacts and (ii) bridging the existing gap between science and other sectors (i.e., competent implementing authorities/policy-makers, scientists, society at large, and younger generations) by increasing ocean literacy. This objective can be achieved through dedicated workshops, selecting the key messages on which we want to focus, e.g., what and why is ocean functioning so complex? What do cumulative pressures mean in the ocean context? How can we integrate information to conclude whether the oceans are healthy or not?

In such workshops, the main target groups should be identified e.g., (i) key stakeholders (national and statutory authorities implementing and reporting the MSFD, BHD, CFP, Biodiversity Strategy and Regional Seas Conventions, EEA, DG-ENV and DG-MARE), (ii) scientists working on cumulative pressures and impacts (e.g., in working groups in ICES and elsewhere), including experts providing services, from private consultancies, and early career researchers, (iii) society at large, and (iv) young people and educators.

8 Challenges to complete the proposed framework

Here, we have proposed a framework for an adaptive EBM of multiple human activities and pressures at sea. As identified here and in the accompanying references, this builds on a large body of knowledge, experience and expertise. However, we are conscious that each of the steps explored in each section, presents multiple challenges that can prevent completing the objectives. For each step, some of the most important challenges have been identified and listed below.

- ***Stakeholder involvement in a co-creation process***: stakeholder fatigue, which can result in a lack of engagement, is one of the most common challenges in science-policy projects, needing specific actions to overcome this problem (Durham et al., 2014). Another could come from not involving the most influential stakeholders, in terms of legitimacy of the solutions proposed, due to the complex relations in the science-policy interface (Støttrup et al., 2019).
- ***A conceptual framework to solve problems***: difficulty to determine quantitatively the assimilative capacity of the systems (Elliott et al., 2018), and, as such, not being able to determine when it has been exceeded.
- ***Understanding the mechanisms of cumulative effects***: inability to assess the individual characteristics or link in the chain of activity-pressure-impact-welfare, especially when integrating across multiple activities and pressures and climate change (Gissi et al., 2021). Also, the knowledge on reference conditions, thresholds, and tipping points, is still poor (Dudney and Suding, 2020; Hillebrand et al., 2020).
- ***Developing a software tool for assessing the status of the ocean***: from previous assessment tools development, we are aware of some challenges (Borja et al., 2019), which can include: (i) combination of different tools into a unique software, (ii) solving the types of relationships between pressures and ecosystem components (linear, non-linear, unidirectional, etc.), (iii) defining the adequate hierarchical structure to integrate species, indicators, ecosystem components or areas, (iv) how to set weighting factors in an objective way, (v) how flexible should be the tool, to meet the stakeholder expectations, or (vi) technicalities linked to the use of existing massive datasets and outputs from the software, among others. However, recent advances in Artificial Intelligence to interrogate large data sets may indicate solutions.
- ***Learning together, by testing together***: one of the most common challenges could be the lack of actual qualitative or quantitative suitable data (either from pressures, ecosystem components or services) (Borja et al., 2019). But also,

TABLE 1 Description of the expected results toward the outcomes and impacts required by the European Commission, including the indicators to measure the success and final impact.

Required outcome (OUT)	Expected results	Expected outcomes	Expected impact	Indicator
OUT1- Policy implementing authorities at national and regional level can assess and predict impacts (including tipping points) of multiple stressors on coastal and marine biodiversity, ecosystems functioning and relevant services (including CC).	Capacity-building on the use of a validated, tested and demonstrated toolbox, including holistic assessment of pressures, impacts on biodiversity and ecosystem services delivery, taking into account CC.	Key stakeholders master the use of the toolbox that facilitates the reporting for MSFD, Regional Seas Conventions, BHD and Biodiversity Strategy.	Policy implementing authorities are able to more efficiently report in a comparable and flexible way across MSs and Regional Seas Conventions, and they anticipate and respond to tipping points.	Number of MSs and Regional Seas Conventions experts trained and capable to use the toolbox by 2026.
OUT2- Better management and impact assessment of invasive species, harmful algal and jellyfish blooms.	Proposal for better management of these impacts, based on the results from Learning Sites, which include transverse testing across Regional Seas Conventions.	Adoption of approaches by implementing authorities.	Most accurate assessment of invasive spp., HABs and jellyfish, having harmonized monitoring and assessment methods.	DG-ENV incorporates the suggestions in the guidelines for MSs and Regional Seas Conventions and they adopt them.
OUT3- Implementation of the MSFD by determining pressure levels that clearly equate to acceptable levels of environmental impact on the GES.	A proposal for a systemic approach for the integrated impact assessment of cumulative pressures, based on the validated, tested and demonstrated toolbox.	Use of the approach and toolbox by key stakeholders to assess and predict impacts from multiple pressures and reporting.	Policy implementing authorities are able to determine pressure levels that prevent GES and favorable status from being achieved.	Number of MSs, Regional Seas Conventions, EEA, scientists, and consultancies using the systemic approach by 2026.
OUT4- EBM approaches and policy measures for activities to reduce pressures to ensure GES and will enable the sustainability of coastal and marine ecosystems to deliver services and be resilient to rapid climate and environmental changes.	Proposal, after testing in Learning Sites, of an EBM approach and policy measures for activities to reduce pressure impacts, including effects from CC, to ensure GES.	Use by key stakeholders of the EBM approach and policy measures, including its use for CFP.	Contribution to attaining GES, by MSs, Regional Seas Conventions and EEA adopting the EBM approach and policy measures proposed	Number of MSs and Regional Seas Conventions adopting EBM proposal by 2026, and DG-MARE.

D, Deliverable; CC, climate change; MSFD, Marine Strategy Framework Directive; EEA, European Environment Agency; MSs, Member States; BHD, Birds and Habitats Directives; HABs, Harmful Algal Blooms; EBM, Ecosystem-Based Management; CFP, Common Fisheries Policy; GES, Good Environmental Status; DG-ENV, Directorate General of the Environment; DG-MARE, Directorate General of Maritime Affairs; MS, Member State.

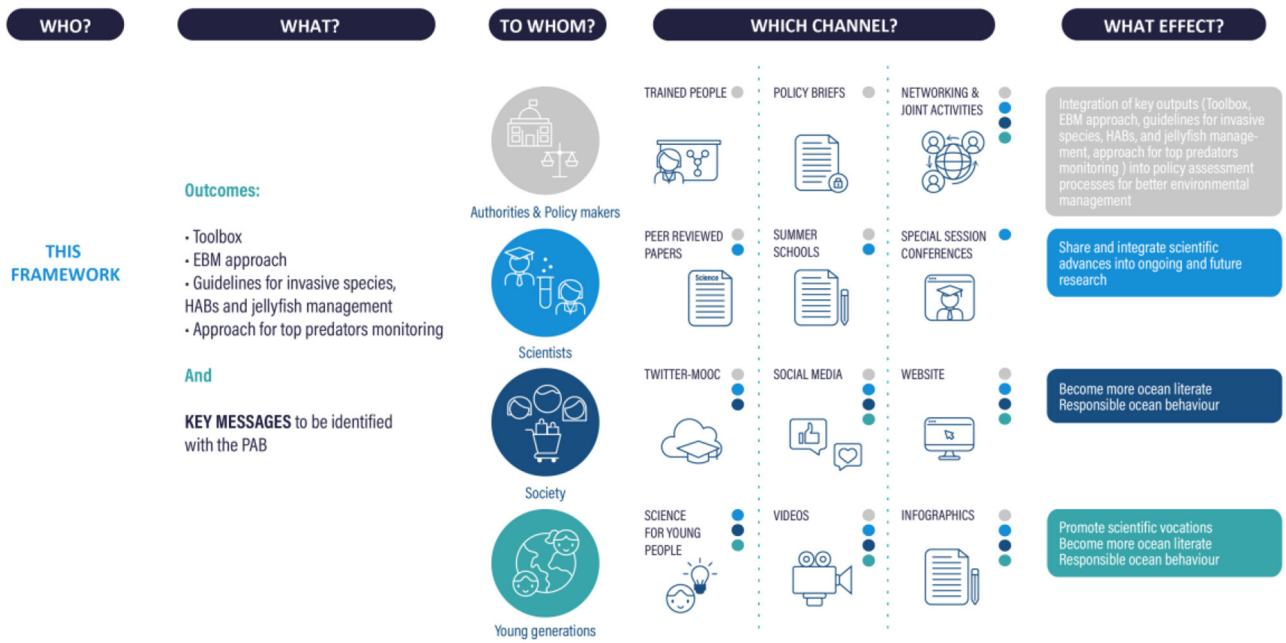

FIGURE 9
An example of applying the Lasswell's communication model to disseminate, exploit and communicate activities within the proposed framework. Only main channels are included. EBM, Ecosystem-based management; PAB, Practitioner Advisory Board; HABs, Harmful Algal Blooms.

there are difficulties for harmonizing data for an effective intercomparison in support of decision-making, the difficulties in cooperation among partners and stakeholders (e.g., cultural drawbacks, transboundary issues, etc.), or a difficulty to validate the toolbox (not only from a scientific point of view, but also by the influential stakeholders, deciding on methodologies to be used officially by Member States or Regional Seas Conventions).

- ***Enhancing the impact of the outcomes***: they can be various, but we consider the most important the challenge to reach key stakeholders, and an inadequate identification of key messages, which can hamper the dissemination and future exploitation of the tools.

Some of these challenges can be overcome with collaboration among partners, stakeholders, different national and international projects working in the same topics, and with Regional Seas Conventions. New techniques aimed at extracting, combining and interrogating data and information, even using textural analysis and Artificial Intelligence, may help to overcome some of these challenges. Similarly, it is noted that the many marine projects currently underway as part of the European Horizon Europe programme will create data, skills and tools that may help to overcome these challenges.

9 Final considerations

Despite the challenges identified, with this proposed approach we aim to advance considerably the knowledge of cumulative effects of multiple pressures on marine ecosystems and their services, to provide a toolbox to stakeholders which can allow them to assess pressures, impacts and provision of goods and benefits. More importantly this will allow them to support the sustainable use of the seas and to take EBM decisions to reverse the situation if their assessment areas are failing to achieve GES. This policy and practice review paper serves to set the scene of knowledge on these topics and, throughout the methodology proposed and already in the process of being developed, envisage the potential achievements and the impacts they can have on marine management in Europe and worldwide. Once the outputs currently being developed have been finalized, this policy paper can serve to measure the success of the research and implementation carried out and the progress of the topic in implementation of the proposed framework.

Author contributions

AB: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Writing—original draft, Writing—review & editing. ME: Conceptualization, Investigation, Methodology, Writing—original draft, Writing—review & editing. HT: Conceptualization, Formal analysis, Investigation, Methodology, Validation, Writing—original draft, Writing—review & editing. VS: Conceptualization, Formal analysis, Investigation, Methodology, Validation, Writing—original draft, Writing—review & editing. SK: Conceptualization, Investigation, Methodology, Validation, Writing—original draft, Writing—review & editing. MC: Conceptualization, Investigation, Methodology, Validation, Writing—original draft, Writing—review & editing. IG: Conceptualization, Investigation, Methodology, Validation, Writing—original draft. SF: Conceptualization, Investigation, Methodology, Validation, Writing—original draft, Writing—review & editing. NP: Conceptualization, Investigation, Methodology, Validation, Writing—original draft, Writing—review & editing. CL: Conceptualization, Investigation, Methodology, Validation, Writing—original draft, Writing—review & editing. TB: Conceptualization, Investigation, Methodology, Validation, Writing—original draft, Writing—review & editing. JA: Conceptualization, Investigation, Methodology, Validation, Writing—original draft, Writing—review & editing. JC: Conceptualization, Investigation, Methodology, Validation, Writing—original draft, Writing—review & editing. ML: Conceptualization, Methodology, Validation, Visualization, Writing—original draft, Writing—review & editing. MU: Conceptualization, Funding acquisition, Investigation, Methodology, Validation, Writing—original draft, Writing—review & editing.

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Conflict of interest

ME is employed by IECS Ltd. and ML by Science Crunchers. TB was employed by MariLim Aquatic Research GmbH.

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.

The authors AB, HT, SK, IG, and JA declared that they were an editorial board member of Frontiers, at the time of

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/focsu.2023.1308125/full#supplementary-material

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'*Horses for courses*' – an interrogation of tools for marine ecosystem-based management

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Marine Ecosystem-Based Management (EBM) approaches are a well-established and fundamental component of international agreements and treaties, regional seas conventions, assessment strategies, European Directives and national and regional instruments. However, there is the need to interrogate and clarify the implementation of EBM approaches under current marine management. Although particular focus here is within the European Union Marine Strategy Framework Directive (MSFD), all lessons learned are applicable to marine assessments and management in seas worldwide given that all marine management instruments aim to ensure sustainability in marine ecosystems and human uses. Notably, the MSFD aims to ensure that Good Environmental Status (GES) will be achieved thereby enabling the sustainability of coastal and marine ecosystems to deliver ecosystem services and societal goods and benefits while at the same time being adaptive to rapid climate and environmental changes. As a clear understanding of EBM and the tools available to achieve it is needed for practitioners, regulators and their advisors, the analysis here firstly presents the current understanding of EBM (including its origin and application) and the wider 26 principles on which it is based. Secondly, we identify the key elements that are addressed by those

principles (18 key EBM elements). Thirdly, we identify the types of tools available for use in the EBM context (19 tool groups). Fourthly we analyze the suitability of tool types to deliver the key EBM elements using an expert judgement approach. Finally, we conclude with the lessons learned from the use of those tools and briefly indicate how they could be combined to help achieve EBM in the most effective way. It is emphasized that no single tool is likely to satisfy all aspects of EBM and therefore employing a complementary suite of tools as part of a toolbox is recommended.

KEYWORDS

Ecosystem-Based-Management, EBM elements, assessment tools, marine policies, Marine Strategy Framework Directive

1 Introduction

Managing human activities impacting marine systems focuses on one central theme – the need to have the appropriate physical, chemical and biological conditions, in order to protect and maintain ecological structure and functioning while at the same time ensuring that the natural system delivers the ecosystem services from which society gains goods and benefits after inputting human capital and complementary assets (Elliott, 2013, 2023). For example, in the marine system, physical, chemical and biological conditions can ensure that fish stocks are maintained but then complementary assets of time, money, energy, skills and knowledge and the ability to be sentient are required to ensure that society benefits from those fish (Haines-Young and Potschin, 2018). Hence, marine management and governance must be aimed at ensuring sustainable marine systems in which the above central theme is satisfied (Borja et al., 2010).

Sustainable development, management and governance rely on an adequate understanding of the complex interplay of science, technology, and management skills (Borja et al., 2024). However, there are fundamental management philosophies which underpin the holistic approach required to achieve sustainable development and management of coastal and marine activities. The main underlying philosophy for these is summarized as managing the ecosystem in which humans are regarded as an integral part. The 'Ecosystem Approach' (EA or EcAp), 'Ecosystem-Based Approach' (EBA) and/or 'Ecosystem-Based Management' (EBM), and their variants are the terms commonly used for this philosophy (Kirkfeldt, 2019). However, it can be argued that the term 'based' is redundant as any ecosystem approach must be based in the ecosystem, with its natural and human features. Despite this, the semantics of these terms have been interrogated and even subtle but meaningful differences between the terms have been analyzed (e.g., Kirkfeldt, 2019); here, the term EBM is taken to include all variants of the concept.

Given this implied uncertainty, the research here uses a structured expert evaluation to identify and interrogate current EBM approaches and policy measures to reduce the adverse effects of human activities; in doing so, it provides the best assessment of the most appropriate approaches/tools to reach policy objectives. The particular focus is within the European Union (EU) Marine Strategy Framework Directive (MSFD; EC, 2008) to ensure that Good Environmental Status (GES) can be achieved thereby enabling the sustainability of coastal and marine ecosystems to deliver ecosystem services and societal goods and benefits while at the same time being adaptive to rapid climate and other environmental changes (Borja et al., 2013). Despite that EU focus, this interrogation is relevant to all marine areas where similar policies/legislation are applied and marine ecosystem assessments are required; for example, Cormier et al. (2022) indicated that Canada has also followed large elements of the MSFD.

The analysis here is structured to firstly present the current understanding and context of EBM and the wider principles on which it is based. Secondly, we identify the key elements that are addressed by the EBM principles. Thirdly, we identify the types of assessment tools available to support EBM. Fourthly, we analyze the suitability of tool types to deliver the key EBM elements. Finally, the paper presents conclusions regarding the use of those tools and briefly indicates the way in which they could be combined to achieve EBM.

2 Ecosystem-Based Management in theory: the concept and principles

The term EBM has several definitions although these are not always very clear and unambiguous (Kirkfeldt, 2019; Delacámara et al., 2020); however, with respect to the MSFD, the following is used:

> *"Ecosystem-based approach (to management), aka an 'ecosystem-based approach' or 'ecosystem-based management', is an integrated approach to management of human activities that considers the entire ecosystem including humans. The goal is to maintain ecosystems in a healthy, clean, productive and*

> *resilient condition so that they can provide humans with the services and goods upon which we depend. It is a spatial approach that builds around a) acknowledging connections, b) cumulative impacts and c) multiple objectives"* (modified slightly from CSWD, 2020).

Ecosystem-Based Management recognizes the full array of interactions within a marine ecosystem, including humans, rather than considering single issues, species, or ecosystem services in isolation (see also McLeod et al., 2005). It encompasses the comprehensive integrated management of human activities based on the best available scientific knowledge about the ecosystem and its dynamics, helping to ensure activities are monitored and managed accordingly with the relevant legislation (ICES, 2020). It aims to identify and act on influences which are critical to the health of marine ecosystems, thereby achieving the sustainable use of goods and services and maintenance of ecosystem integrity (ICES, 2003).

Ecosystem-Based Management is under-pinned by several fundamental or key principles required for its operationalization and implementation. Using literature up to 2010, Long et al. (2015) reviewed the evolution of the concept of the set of EBM principles in their definition of EBM, which adds a spatial connotation compared to the previous definitions: *"Ecosystem-based management is an interdisciplinary approach that balances ecological, social and governance principles at appropriate temporal and spatial scales in a distinct geographical area to achieve sustainable resource use"* (Long et al., 2015). That study selected the 15 most important/commonly cited EBM principles from a list of 26 principles. They noted three emerging Key Principles such as 'Consider Cumulative Impacts', 'Apply the Precautionary Approach' and 'Explicitly Acknowledge Trade Offs' that could help to shape and successfully apply EBM.

Other projects and expert working groups globally have since further considered this list of principles and consequently chosen the EBM principles that most fit their aims/mandate. For example, a United States, EU and Canadian working group on the ecosystem approach to ocean health and stressors was established in 2016 under the Atlantic Ocean Research Alliance (AORA) to investigate the implementation of EBM in the North Atlantic. They reviewed and contrasted 20 Principles for implementation (Dickey-Collas et al., 2022), including those such as *'the ecosystem approach should seek the appropriate trade-off (balance) between, and integration of, conservation and use of marine resources (e.g., biological diversity)'*, *'the ecosystem approach should consider all forms of relevant information, including scientific and indigenous and local knowledge, innovations and practices'* and *'the ecosystem approach should involve all relevant sectors of society and scientific disciplines'*. As a further example, to clarify and codify the priorities for EBM in New Zealand, a set of narratives and EBM principles were developed around seven themes including recognition that *'humans along with their multiples uses and values for the marine environment are part of the ecosystem'* and EBM should be *'tailored, place and time specific, recognizing all ecological complexities and connectedness, and addressing cumulative and multiple stressors'* (Hewitt et al., 2018; Le Heron et al., 2020). Guilhon et al. (2021), working on Areas Beyond National Jurisdiction and deep-sea mining (DSM), grouped EBM principles into 8 categories: core, ecological, impacts, knowledge, management, participation, socio-economic and spatial-temporal scales. The inclusion of the words 'tailored' and 'management' in this definition implies that EBM must be an adaptive system to accommodate changing circumstances. Similarly, by necessity it should have feedback loops so that lessons learned can be incorporated into future management actions (Elliott et al., 2020a; Roux and Pedreschi, 2024; Smith et al., 2025).

3 Ecosystem-Based Management in practice: application from global to local scales

3.1 At the global level

Although previous regional approaches, such as the North Sea Conferences (e.g. NSC, 2002) mention the Ecosystem Approach, it was first codified by the UN Convention for Biological Diversity (CBD, 2000, 2004) as a set of 12 principles (CBD 1992, 2007). This defined it as *'a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way'* and so its application aims to achieve these three objectives of the Convention. It is based on applying appropriate scientific methodologies focused on levels of biological organization, which encompass the essential processes, functions and interactions among organisms and their environment. Furthermore, it recognizes that humans, with their cultural diversity, are an integral component of ecosystems.

At a global level, EBM is not explicitly stated in the CBD although it is implicit in the original 12 principles and, at the 5th Conference of Parties (COP) meeting in 2000, the EBA was set as the primary framework for action under the Biodiversity Convention (CBD, 2000, COP 5, Decision V/6). The recent (12/2022) 15th CBD COP adopted the "Kunming-Montreal Global Biodiversity Framework" (GBF) in which three of 23 targets express the need to apply EBAs and nature-based solutions (CBD, 2022).

The UN Convention on the Law of the Sea (UNCLOS) defines the rights and responsibilities of nations concerning their use of the world's oceans as well as the management of marine resources (Cormier et al., 2022). At present, the concept of the Ecosystem Approach is only implicit in the Convention, through a reference to a clear obligation to protect and preserve the marine environment (Article 192). Similarly, the use of measures is included to protect and preserve rare or fragile ecosystems as well as the habitat of depleted, threatened or endangered species and other forms of marine life (Article 194(5)).

3.2 At the regional level

Regional Sea Conventions, together with various organizations, such as the European Environment Agency (EEA), have included

EBM in their science and evidence planning and have included its principles in their data, science and advisory programs. EBM is therefore an approach for addressing 'wicked' environmental problems, i.e., complex problems that involve many interdependent factors and strong links between the socio-economic and ecological spheres (Termeer et al., 2019). As such, it recognizes the need to incorporate systems thinking into natural resource management (O'Higgins et al., 2020; Elliott et al., 2020a; Smith et al., 2025). It is important to acknowledge that due to the complexities involved in marine and aquatic social-ecological systems, there is neither a one-size-fits-all EBM approach nor only one EBM implementation path (Delacámara et al., 2020; Roux and Pedreschi, 2024). Indeed, progress towards EBM is more likely to proceed incrementally; it is essential therefore that approaches are regularly reviewed and that any produced EBM toolbox includes new tools and tool combinations to improve and support the process. This also ensures that EBM is an adaptive management approach which can accommodate changing conditions and the results of previous management actions.

The monitoring and assessment strategy of the Baltic Sea Marine Environment Protection Commission (HELCOM) is built on the ecosystem approach concept (HELCOM, 2013). This strategy covers all the components of a marine ecosystem and the pressures impacting it, and more recently includes climate change. The HELCOM integrated assessments are based on a few key features: (i) commonly agreed assessment areas, which are defined in a nested way for each assessment indicator; (ii) quantitative core indicators which have been developed following commonly agreed criteria; (iii) indicator threshold values, which define good environmental status, and (iv) multi-metric indicator-based assessment tools.

The HELCOM assessment strategy not only covers the state of the environment but also gives due focus to human activities, pressures and their impacts on the ecosystem and society. In 2010, the HELCOM holistic assessment introduced the cumulative impact assessment of anthropogenic pressures (see Korpinen et al., 2012), following the global assessment method by Halpern et al. (2008). Since then, this includes the HELCOM multi-metric indicator-based assessment tools (HEAT, BEAT and CHASE), cumulative impact assessment (CIA) and a tool to estimate the effectiveness of measures (Ahtiainen et al., 2024).

The Barcelona Convention for the Mediterranean adopted the EcAp in 2008 as the guiding principle to all policy implementation for healthy marine and biological ecosystems that are productive and biologically diverse for the benefit of present and future generations (UNEP, 2008). The Integrated Monitoring and Assessment Program (IMAP) was adopted in 2016, as part of the implementation of the EcAp Roadmap. The current EcAp contributes to Sustainable Development Goal 14 (Cormier et al., 2021), the achievement of CBD Aichi Biodiversity Target 11 and the implementation of the MSFD (see below). The EcAp includes ecological objectives that mirror the MSFD descriptors and also aims towards operational objectives with indicators and target levels through regular monitoring programs.

For the Black Sea, although the Bucharest Convention (http://www.blacksea-commission.org/_convention.asp) does not explicitly mention EBM and the EcAp, the main actions are linked to combating pollution from land-based sources and maritime transport, achieving sustainable management of marine living resources, and pursuing sustainable human development, i.e. by definition an EcAp. Black Sea action plans require a holistic approach to the ecosystem, which has led to the development of the Black Sea Integrated Monitoring and Assessment Program (BSIMAP). Integrated evaluation tools are still generally missing from BSIMAP with the exception of eutrophication assessment tools, TRIX (Trophic Status Index; Vollenweider et al., 1998) and BEAST (Black Sea Eutrophication Assessment Tool; Slobodnik et al., 2017).

In the North-East Atlantic Ocean, the Oslo and Paris (OSPAR) Convention (https://www.ospar.org/convention) considers a framework for the regulation of most human activities, which are likely to influence marine ecosystems and the overall biodiversity. Both, the HELCOM and OSPAR Commissions have in their vision and mission the need to consider the concept of a defined Ecosystem Approach (given as "*the comprehensive integrated management of human activities based on the best available scientific knowledge about the ecosystem and its dynamics, in order to identify and take action on influences which are critical to the health of marine ecosystems, thereby achieving sustainable use of ecosystem goods and services and maintenance of ecosystem integrity*" - Helsinki and OSPAR Commissions, 2003). The OSPAR North-East Atlantic Environment Strategy 2030 provides further detail to this definition of the Ecosystem Approach to incorporate reference to "*drivers, activities and pressures that adversely affect the health of marine ecosystems*" in place of "*on influences which are critical to the health of marine ecosystems*" (OSPAR, 2021). Applying the ecosystem approach integrates conservation and management approaches, such as marine protected areas or measures targeted at single species and habitats, as well as other approaches, including cumulative effects.

In the case of the EEA, under its high level policy objective of achieving sustainability in Europe, its multifaceted work addresses key EBM principles. These include Ecological integrity and biodiversity, and Cumulative effects and support EU policies and strategies with evidence-based knowledge to help the EEA member countries and the EU to assess progress towards achieving their vision. The EEA outputs include the State of Environment reports. The EEA Marine Messages III addressing key EBM elements (as with marine Messages II, European Environment Agency, 2019), is being prepared for 2026.

3.3 At the European Union level

The EU, in policy, legal instruments (such as Directives), strategies and with support from numerous research projects, focuses on understanding marine ecosystems, their interactions and pressures. Therefore, this implicitly requires applying EBM as an iterative process (Haugen et al., 2024) although there is no definition of EBM embedded in EU law (O'Hagan, 2020). The EU Integrated Maritime Policy contains the fundamental pillars of the MSFD (EC, 2008) and the Maritime Spatial Planning Directive

(MSPD; EU, 2014). The MSFD text (EC, 2008) does not provide a definition (see also CSWD, 2020 and Section 4) of an EBA to management but requires its application. The 11 descriptors of the MSFD form the different sectors of the EBA as seen by the EU, as they include the most important ecosystem features of concern as well as human pressures on the ecosystems and their resulting effects (Berg et al., 2015).

While the MSFD is the first piece of EU legislation to adopt an EBA aiming at the protection of the full range of marine biodiversity, the European Commission considers the Natura 2000-regime (the network of sites to safeguard the habitats and species of community interest) as one of the legal components of the implementation of this approach for the marine environment. This EBA considers the concepts of favorable conservation status and good ecological status as required respectively by the Habitats Directive (HD) and the Water Framework Directive (WFD) (Bastmeijer, 2018; Elliott and Wither, 2024). Both Natura 2000 and WFD objectives are in line with some of the EBM principles (e.g., ecosystems must be managed within the limits of their functioning, assess cumulative impacts, conserve ecosystem structure and functioning to maintain ecosystem services) and therefore the Ecosystem Approach is considered appropriate to aid their implementation (Vlachopoulou et al., 2014; Bastmeijer, 2018).

The MSPD (EU, 2014) explicitly acknowledges that an EBA will contribute to promoting the sustainable development and growth of the maritime and coastal economies and the sustainable use of marine and coastal resources, supported by maritime spatial planning. The MSPD is increasingly regarded as the mechanism for the Program of Measures needed to achieve Favorable Conservation Status, for HD, and GES, for the MSFD (Elliott and Wither, 2024).

The EU Common Fisheries Policy (CFP) (EU, 2013), whilst focused on fisheries, implements an EBA to fisheries management within ecologically meaningful boundaries. This aims to ensure that negative impacts of fishing activities on the marine ecosystem are minimized, and ensures that activities avoid the degradation of the marine environment.

The more recent EU Biodiversity Strategy 2030 (EC, 2020) again does not define EBM but reiterates the benefits of its application. It also introduces the EU Nature Restoration Law (EC, 2022; Hering et al., 2023; now adopted as EU, 2024) and the Action Plan to conserve fisheries resources and protect marine ecosystems (EC, 2023). With this action plan, the EC aims to achieve a more consistent implementation of the EU environmental policy and the Common Fisheries Policy with its three – environmental, economic and social - sustainability pillars.

4 Sector, single activity or single-policy EBM applications

Marine management has to address the full range of human activities and their resulting pressures and effects on both the natural and human systems (Elliott et al., 2020b). A key aspect of EBM is in recognizing the full array of marine ecosystem interactions (including humans) rather than focusing on specific sectors in isolation hence only on a subset of related activities and pressures to be managed. An early example of this is the adoption of Ecosystem Approach to Fisheries (EAF) management (EAFM) (FAO, 2003). While the EAF deals with all the ecological consequences of fishing, it also recognizes the social and economic implications of fishing and especially its management (FAO, 2021). Although the EAF concept has been introduced in the European CFP (e.g. see Garcia et al., 2003; Morishita, 2008; Jennings and Rice, 2011), its operationalization and implementation in European fisheries management so far have been limited (Wakefield, 2018; FAO, 2021).

The application of the EBM to a single sector (e.g. offshore energy) and activity (e.g. monopile and turbine placement) is also seen in the development of offshore wind farms (OWF) in line with conservation objectives (Pezy et al., 2020; Copping et al., 2020; Galparsoro et al., 2022; Maldonado et al., 2022). Similarly, Guilhon et al. (2021) review the adoption of EBM by deep-sea mining (DSM) concluding that the mere recognition of EBM principles in the regulatory framework does not guarantee their implementation and further clarification on the meaning of the Ecosystem Approach in the DSM context is needed. In another sectoral example, an 'ecosystem approach to aquaculture' (EAA) is defined as a strategy for the integration of its activities within the wider ecosystem such that it promotes sustainable development, equity, and resilience of interlinked social-ecological systems (FAO, 2010).

Ecosystem-based marine spatial planning (EB-MSP) is a relatively recent practice (see Andersen et al., 2020). EB-MSP has been extensively researched and reviewed in its concepts, tools and critical issues for its implementation (Katsanevakis et al., 2011, 2020; Kirkfeldt, 2019; Stelzenmueller et al., 2013, 2018, 2020). EBA is often presented as a concept or broad implementation philosophy to 'give space to ecology' within the MSP process and decisions. The guidance of the main steps of the MSP process (EC et al., 2021) presents a set of key actions to operationalize EBA.

Other EBM applications include approaches linked to Integrated Ecosystem Assessments (IEAs). First developed by the US National Oceanic and Atmospheric Administration (NOAA), IEAs are seen as an approach to operationalizing EBM (Levin et al., 2009, 2014; Samhouri et al., 2014; Dickey-Collas, 2014), and have been adopted by ICES as a key tool to achieve EBM (ICES, 2023) along with fisheries assessments and ecosystem overviews (ICES, 2021a; 2022).

5 Key EBM principles, elements and tools

Having defined EBM, it is then important to determine and interrogate the tools available for achieving it and its outcomes. To this end, the 26 EBM principles from Long et al. (2015) were reviewed together with more recent literature (Rudd et al., 2018; Hewitt et al., 2018; Clark et al., 2021; Dickey-Collas et al., 2022). The principles were reworded to add clarity and to aid their

operationalization (Table 1). To make the analysis more manageable, only 16 of the 26 EBM principles were selected here as this study primarily focused on the assessment of environmental state change and pressures and Good Environmental Status in the marine environment. Accordingly, the current analysis omitted principles that apply exclusively to the management implementation part of the system, e.g., acknowledging trade-offs (principle 21), use of incentives (principle 26) and applying the precautionary approach to management (principle 18) (Table 1). Trade-off analysis can be used to advice on potential fisheries closures based on fisheries data and bioeconomic modelling (ICES, 2021b). Trade-offs between small-scale fisheries and aquaculture can be studied using a mixed methods approach (including literature reviews, conceptual models, quantitative and qualitative data and insights) to meet social and environmental goals (Mansfield et al., 2024). Trade-off scenarios between fisheries, offshore wind farms and MPAs, based on spatially-explicit trophic models, can also be used to advise on future sea space e.g. for planned offshore wind farms and new MPAs (Püts et al., 2023). However, whether trade-offs are actually considered formally, consistently and transparently by decision makers and national authorities when designing their management measures, i.e. the

TABLE 1 Ecosystem-Based Management (EBM) Principles (Long et al., 2015) and reworded as instructions.

No	EBM Principles	Reworded principles
1	Consider ecosystem connections*	Determine and ensure connectivity within and between areas
2	Appropriate spatial and temporal Scales*	Assess at temporal and spatial scales, appropriate to the ecosystem components of concern
3	Adaptive management*	Use adaptive management in employing measures
4	Use of scientific knowledge*	Use best and fit-for-purpose scientific knowledge
5	Integrated management*	Ensure integrated management is carried out
6	Stakeholder involvement*	Ensure a fair and transparent stakeholder involvement at all stages
7	Account for dynamic nature of ecosystem*	Ensure ecosystem functioning is assessed at relevant spatial and temporal scales accounting for change
8	Ecological integrity and biodiversity*	Determine ecological integrity and biodiversity
9	Sustainability*	Ensure the managed systems are sustainable in the long-term
10	Recognise coupled social-ecological systems*	Include and integrate both ecological and social systems (humans are part of the marine system)
11	Decisions reflect Societal Choice	Ensure the outcomes respect societal choice
12	Distinct boundaries*	Consider ecosystem and jurisdictional boundaries. Include spatial and temporal boundaries in the assessments.
13	Inter-disciplinarity*	Ensure the assessments are multidisciplinary, including social and natural scientists
14	Appropriate monitoring*	Perform appropriate and fit-for-purpose monitoring
15	Acknowledge uncertainty*	Measure and record uncertainty in the assessments
16	Acknowledge ecosystem resilience	Acknowledge ecosystem resilience in a narrative, in planning and when assessing the resilience of existing plans to current and emerging pressures.
17	Consider economic context	Determine the economic repercussions of action and non-action
18	Apply the Precautionary Approach	Apply the precautionary approach in management
19	Consider cumulative impacts*	Assess the risk, identify and measure the cumulative impacts/effects (on both natural and social systems)
20	Organizational change	Identify if organizational change is required in management and make recommendations
21	Explicitly acknowledge Trade-offs	Determine whether and what are the trade-offs in management measures
22	Consider effects on adjacent ecosystems	Determine the effects and connectivity of an area on adjacent systems and vice versa
23	Commit to principles of equity	Ensure that actions and outcomes are just and equitable to nature and society
24	Develop long term objectives	Record the long-term vision and ensure objectives are SMART: Specific, Measurable, Achievable, Relevant, and Time-Bound and link to indicators
25	Use of all forms of knowledge*	Use best-available natural and social sciences, including indigenous knowledge
26	Use of incentives	Use economic, societal and ecological incentives to achieve outcomes

Principles marked with an asterisk (*) are the most relevant to this study focus on assessing Good Environmental Status under the Marine Strategy Framework Directive.

suggestion of the omitted EBM principle 21, is questionable (Howe et al., 2014; Fortnam et al., 2023) and not the focus of this work. Similarly, EBM principle 23 suggests that managers and decision makers should be committing to principles of equity ensuring that measures and outcomes are just for nature and society, while EBM 26 suggests the use of economic, societal and ecological objectives to achieve outcomes.

The current assessment identified key elements of EBM relevant to the selected 16 principles (as the operations to undertake and aspects to be considered and assessed to satisfy each principle as part of the overall EBM process; Table 2). It considers these together with the appropriate assessment approaches and tools that can be used to deliver, singly or in combination with others, these different EBM elements (Table 3). The selection of EBM principles, EBM elements and associated assessment tools was based on the judgement of 20 experts who were researchers with direct experience of GES assessment, EBM and use of the tools to deliver it; these experts were taken from the partners and advisors in the GES4SEAS project (www.ges4seas.eu) and are included as authors here. The experts (with an estimated >150,000 citations) were chosen based on their wide and documented experience working on major relevant marine policies (e.g. MSFD, WFD, MSP), on thematic assessments (e.g. non-indigenous species, benthic seafloor assessments, eutrophication, ecosystem services), tool development or use (e.g. AMBI, CIMPAL, NEAT, MARXAN, various models, risk based and cumulative impact assessment tools) and all the relevant EBM aspects and principles (e.g. assessing ecological integrity and biodiversity, cumulative impacts, distinct boundaries, appropriate spatial and temporal scales).

The experts deconstructed and matched the principles into elements (i.e., all those essential topics that need to be addressed/assessed to satisfy a principle) following a co-creation and consensus approach. For the next step, the experts matched the elements to tools/tool types/methodological approaches required to address/satisfy the elements based on expert knowledge and literature checks by subject focusing on marine applications. An example matching the principles to elements and corresponding tool groups/assessment methodologies is given in S1. The tools were then grouped in relevant tool groups following a co-creation with key stakeholders and a consensus approach based on their main characteristics (e.g. from conceptualizing to modelling, from assessing state to addressing risk, and within modelling from

TABLE 2 Elements of Ecosystem-Based Management (EBM) (and their applications) relevant to Ecosystem Assessments (full descriptions in Supplementary Materials S2).

#	EBM element	Brief description
1	Cumulative effects assessments -CEA	Cumulative Effects Assessment (CEA) is the assessment of ecosystem changes that accumulate from multiple stressors, both natural and human made (Dubé et al., 2013). CEAs are holistic evaluations of the combined effects of human activities and natural processes on the environment, constituting a specific form of environmental impact assessments.
2	GES MSFD assessments	The assessment undertaken for the purposes of the MSFD. It is a formal procedure by which information is collected and evaluated following agreed methods, rules and guidance. It is carried out periodically to determine the level of available knowledge and to evaluate the environmental status. The resulting output is a report that synthesizes the findings, and leading to a classification of status in relation to the determination of GES (CSWD, 2020).
3	Whole ecosystem assessments	Whole ecosystem assessments are similar to the previous but without the same strict structure and requirements of the MSFD. These include regional assessments, e.g., in the Baltic Sea (HELCOM), Atlantic Ocean (OSPAR Commission), Mediterranean (UNEP-MAP), or in the Black Sea (Todorova et al., 2019) and ICES ecoregions (ICES, 2023).
4	Ecosystem services (delivery, impacts, valuation)	This includes assessments of ecosystem services (ES) in terms of delivery and impacts as well as of value. Ecosystem services are the final outputs or products from ecosystems that lead to societal goods and benefits that are directly consumed, used (actively or passively) or enjoyed by people.
5	Special biotic effects/impacts	Examples include sex-changing and sex segregation (i.e., when sexes of a species live apart, either singly or in single-sex groups). Documenting the underlying causes of sexual segregation is important for management and conservation reasons as differential exploitation of the sexes (e.g., by spatially focused fishing in key areas) can lead to population decline.
6	Specific ecosystem functions (and impacts on functions)	The MSFD in line with its requirement for *good environmental status* and '*clean, healthy and productive oceans and seas within their intrinsic conditions*', additionally requires that *the structure, functions and processes of the constituent marine ecosystems…. allow those ecosystems to function fully and to maintain their resilience to human-induced environmental change* (EC, 2008).
7	Pressures-activities footprint	Determining the overall effects of human activities as a precursor to management, requires quantifying: (i) the area in which the human activities take place, (ii) the area covered by the pressures generated by the activities on the prevailing habitats and species, and (iii) the area over which any adverse effects occur. These three features correspond to activities-footprints, pressures-footprints and effects-footprint (Elliott et al., 2020b).
8	Effects or Impacts footprints	As with the category Pressure-Activities footprint, this category brings in a spatial element in the assessments of impacts and effects which is an essential part of EBM and EU conservation policies (e.g., HD and MSFD). As effects and impacts are more difficult to identify and assess, activity and pressure footprints are often used as proxies.

(Continued)

TABLE 2 Continued

#	EBM element	Brief description
9	Links activities pressures impacts	Linking activities, pressures and impacts is an essential part of the MSFD and a crucial element of EBM. DAPSI(W)R(M) (Drivers, Activities, Pressures, State change, Impacts on human Welfare, Responses by Measures) or DAPSES-MMM (socio-economic Drivers, human Activities, Pressures, State of environment, Ecosystem Services – Management (policies and governance), Measures, Monitoring) are examples of the conceptual frameworks mapping these links.
10	Single MSFD descriptors/single issues	This includes primarily assessments on major issues such as Invasive alien species (IAS), Harmful Algal Blooms (HABs), jellyfish blooms and eutrophication.
11	Single species, ecosystem components state change	This includes assessments of single species status (e.g., under CFP and MSFD for commercial species) or assessments of a habitat (e.g., for reporting for HD or within an MPA) and looking at changes of status due to pressures.
12	Threatened habitats and species	This includes documenting status and distributions of species and habitats at risk at global, regional or local scales.
13	Pressure and impact reduction/mitigation	This includes targeted and specific pressure and impact reduction or mitigation measures. For example measures mitigating the impacts of marine IAS include physical removal, promotion of commercial exploitation, and environmental rehabilitation. Other examples include increasing the selectivity of the fishing gears and implementing the landing obligation to reduce bycatch and unwanted catches.
14	Spatial and other measures	This includes spatial and other measures related to the management response and management footprint. Well known spatial measures include, for example, the ban of trawling in the deep habitats in the Mediterranean and the North East Atlantic, or in particular areas (e.g., over protected habitats).
15	Climate change	Modelling tools can address changes in species distributions due to climatic effects and these insights are relevant to the planning phase to conservation spatial planning and restoration prioritization. In the evaluation and assessment phase it can inform on whether the outcomes are affected by climate change as well as the trajectory of change.
16	Uncertainty	Uncertainty applies to all the EBM process phases in that the managers prefer to get advice that includes uncertainty/confidence both in terms of consequences of planning scenarios or management plans and in assessment outcomes.
17	Risks	This includes risk from action or inaction, risks to ecosystem components due to spatial overlap with activities and pressures, risks related to specific biotic effects (e.g., sex related fishing impacts or fishing impacts on nesting or nursery areas).
18	Other policy requirements e.g., MSPD, BHD, Biodiversity Strategy	This EBM element addressed the ability of satisfying different policy needs (other than MSFD), e.g., by providing outputs relevant for the MSPD, the Biodiversity Strategy, the EU Nature Restoration Law, the BHD or the needs of RSC (e.g., OSPAR, HELCOM).

MSFD, Marine Strategy Framework Directive; GES, Good Environmental Status; HD, Habitats Directive; BHD, Birds and Habitats Directives; CFP, Common Fisheries Policy.

single species life cycle or stock assessment modeling to predictive species distribution models, multi species food web modeling, bioeconomic modelling and so on; they excluded approaches used in the ecohydrology/other coastal/terrestrial fields).

In total, 18 individual key EBM elements were identified (Table 2; full descriptions in S2). They relate to all aspects of conceptual management cycle frameworks around adaptive EBM strategy, including the PACE [plan, act, check, evaluate (BSPC, 2006)] and cause-consequence-response frameworks such as the modified DPSIR-related (Drivers, Pressures, State, Impacts, Response) frameworks DAPSES-MMM (Drivers-Activity-Pressures-State-Ecosystem Services-Management (Policies and Governance)- Measures-Monitoring; CSWD, 2020) and DAPSI(W)R(M) (Drivers-Activities-Pressures-State change-Impacts (on human Welfare)-Responses (using management Measures; Elliott et al., 2017); the cause-consequence-response frameworks are typically used as problem-solving approaches by the European Commission, Regional Seas Conventions and EU research projects.

Assessment methodological approaches and tools addressing the 18 EBM elements were identified as 19 tool groups (categories) (Table 3; full descriptions including examples of applications and required data and resources are given in S3). Scoring of the tools by the experts is given in section 6.1.

6 Assessment of tools used in EBM

6.1 Assessment method

The relevance and usefulness of the tool groups was assessed by the team of 20 experts by scoring the tool group ability to deliver on the specific elements of EBM according to a set of questions. Specifically, "can these tool groups inform on the EBM element in question? Can they offer concrete advice alone or in combination with other tools?".

The scoring system used was as follows:

- Score 5, if the tool group fully delivers on the specific element of EBM;
- Score 3, if the tool group only delivers on some aspects of the specific element of EBM;
- Score 1, if the tool group only delivers on specific aspects of the EBM element and its use in combination with other tools is required to deliver the element of EBM;
- Score 0, if the tool group does not deliver on the EBM element (in full or partially).
- Leave blank, if no score can be attributed (e.g., due to insufficient knowledge).

TABLE 3 Types of tools used to support delivery of the elements of Ecosystem-Based Management (EBM).

#	Tool group	Brief description
1	Conceptual models	Conceptual models (including mental models, mind maps, argument mapping, horrendograms, organograms, etc.) are a graphical representation of a system (e.g., natural, socio-economic or socio-ecological system). They visually summarize the complex relationships within a system through a network of nodes (the main components of a system) and vectors/links (the pathways linking those components).
2	Semi-quantitative mental models - Fuzzy cognitive mapping	Semi-quantitative mental models are an advance on conceptual models in that the linkages between nodes (the system's main components) are not just documented, but the direction and strength of interaction is specified, allowing for simple scenario investigation. Perhaps the most used Fuzzy cognitive mapping (FCM) tool is Mental modeler.
3	Knowledge graphs	A knowledge graph is a structured representation of knowledge that encapsulates information on entities, their attributes, and the relationships between them. It consists of 'nodes' (representing entities) and 'edges' (representing the relationships between them), and can be visualized as a network or a graph. A knowledge graph might be usefully viewed as a combination of a graphical network diagram, allied to a database providing information on each of the nodes and links.
4	BBN probabilistic models	Bayesian Belief Networks (BBNs) are models that graphically and probabilistically represent correlative and causal relationships among variables and which account for uncertainty. BBNs operationalize conceptual models by quantifying the linkages and the strengths of the links (the dependencies and interdependencies) between nodes (the model's variables) through conditional probability tables or distributions.
5	Risk based approaches exposure-effect-hazard-vulnerability (e.g., Bow-Tie)	Bow-Tie is an ISO and industry-standard method for producing conceptual models (Cormier et al., 2019). It addresses a risk or problem (as the central knot of the Bow-Tie) and indicates the causes of that problem (to the left of the knot) and the consequences that occur because of the problem (to the right of the knot). Various controls can be placed on the left of the hazard to prevent the hazard from occurring, or on the right to reduce/mitigate/compensate for the magnitude of any consequences.
6	Cumulative impact spatial mapping	The global human impact assessment (Halpern et al., 2008) is a spatial assessment where layers of pressures and of ecosystem components (e.g., species, species groups, habitats), spatialized across a grid of selected resolution, are combined. Their spatial overlap and weight scores representing the sensitivity of the ecosystem components to each of the pressures are used to derive an index expressing cumulative impacts/effects.
7	Impact risk ranking through linkage-chain-frameworks (e.g., ODEMM)	A risk assessment methodology which traces sector–pressure–ecosystem component pathways (also known as 'linkage chains') and scores them through expert judgement and data where available. Each link is scored for a number of attributes (e.g., spatial overlap, temporal overlap, degree of impact, resilience or resistance), giving total impact risk scores in a variety of ways depending on complexity (ODEMM: Knights et al., 2015; Pedreschi et al., 2023; SCAIRM: Piet et al., 2023).
8	Single spp. model (life cycle, stock assessment)	Single-species models are mathematical representations used to study and understand the dynamics of a particular species within an ecosystem. The models focus on population size, growth, and interactions of a single species, while often considering the species interactions with its environment and other influencing factors. These models can incorporate limited ecosystem or multispecies information.
9	Biogeochemical models	Biogeochemical models capture two-way interactions between the biology and chemistry of ecosystems. They are used to simulate how abiotic and biotic variables interact through time and across space and provide a means to explore management scenarios in relation to climate change and change in the flow of nutrients from land into the ocean.
10	Food web models (e.g., multispecies models, EWE)	Food-web models are a particular type of ecosystem models, which simulate the structure and flow of energy and nutrients between ecosystem components. Food web models aim to understand the trophic patterns, population dynamics among predators and prey, and implications for system stability. Examples include Ecopath with Ecosim (EwE) and Ecological Network Analysis (ENA).
11	Ecosystem models (e.g., End2End)	Ecosystem models are models that describe the interactions between at least two ecosystem components (e.g., populations, species, functional groups), whereby the interactions are real ecological processes (e.g., predator–prey interactions). They are a mathematical representation of an entire ecosystem, which integrates physico-chemical oceanographic descriptors and organisms ranging from microbes to higher-trophic-level organisms (including humans).
12	Species distribution models	Species distribution models (SDM, also known as habitat suitability models or predictive habitat distribution models) are used to predict the spatial distribution of a species (e.g. the likelihood of its presence or density) based on its observed relationship with environmental conditions. Different modelling techniques can be used (e.g., generalized linear or additive regression models, classification and regression trees, Random Forest, maximum entropy algorithm).

(Continued)

TABLE 3 Continued

#	Tool group	Brief description
13	Natural capital accounting, ecosystem services valuation	The natural capital approach to policy and decision-making considers the value of the natural environment for people and the economy, providing a tool to support the protection and management of the natural environment and to facilitate the engagement of stakeholders within management decisions. Natural capital accounts are developed to assess and monitor the contribution of natural resources to economic activity.
14	Bioeconomic models, socioeconomic models (CBA), societal goods and benefits valuation	This tool group includes tools such as: (i) Bio-economic models, i.e. integrated economic-ecological models used for resource management; (ii) Valuation of Societal Benefits, which determines the 'total social value' (comprising of ecological value, economic value, and socio-cultural value) of marine ecosystem services leading to benefits for society; (iii) Cost-benefit analysis (CBA), a core tool of public policy consisting of the systematic process of calculating the benefits and costs, expressed in monetary units, of policy options and projects.
15	Spatial planning models (e.g., GIS, VAPEM, related to use)	Spatial planning models are tools used to help planners and policymakers make informed decisions about the use of marine space and resources. The models are designed to provide insights into the potential impacts of different planning scenarios. Examples include Geographic Information Systems (GIS, computer-based tools used to store, analyze, and visualize spatial or geographic data) and VAPEM tool (Ecological Assessment and Marine Spatial Planning Tool, which integrates environmental risk information and with technical and socio-ecological information).
16	Conservation planning models (e.g., MARXAN)	Conservation planning is the process of locating, configuring and implementing areas that are managed to promote the persistence of biodiversity and other natural values. Systematic conservation planning (SCP) based on clear goals and targets, locates and designs new reserves. Common decision support tools to facilitate SCP include MARXAN (a suite of spatial prioritization decision support tools to design networks of protected areas) and ZONATION (operating on spatial data about ecological features, costs, and threats, also utilizing information about uncertainty and connectivity).
17	Simple assessment index (e.g., M-AMBI)	Simple assessment indices are methods for classifying marine systems according to human pressures and include those focusing on the primary community structural variables (abundance, species richness, and biomass) and derived community structural variables (e.g., diversity indices). Examples include numerous biotic indices, covering different biological elements from phytoplankton to macroinvertebrates and fishes. M-AMBI (Multivariate AZTI's Marine Biotic Index) is an example of multivariate index for macroinvertebrates (Borja et al., 2019).
18	Descriptor or theme-specific combination of indices and models (e.g., HEAT, BEAT and CHASE)	The indicator-based multi-metric assessment tools integrate quantitative indicators to inform of the integrated state of the assessment area. Tools have been developed for hazardous substances (CHASE), eutrophication (HEAT) and biodiversity (BEAT). The indicators use a threshold value indicating acceptable state from the un-acceptable state and the indicators can be grouped within the tool to best reflect the assessment topic.
19	Overarching assessment tools (e.g., NEAT and OHI)	NEAT (Nested Environmental status Assessment Tool) is a tool primarily developed for biodiversity assessment. The tool is usually applied to status assessment, describing the status of an ecosystem using target, thresholds and values of state indicators for various ecosystem components, divided into separate values for specific habitats inside a spatial assessment unit. OHI (Ocean Health Index) is a framework for assessing ocean health based on the sustainable provisioning of benefits and services people expect from healthy oceans, such as food, cultural and social value, and jobs.

Full descriptions in Supplementary Materials S3.

The scores were reported in a matrix format crossing tool groups (19 rows; Table 3) against EBM elements (18 columns; Table 2). Each expert contributed to scoring individual or multiple tools depending on their knowledge of the tools, and the confidence the experts had in this knowledge was also recorded (as high, moderate or low) for each of the tool groups they scored.

In addition, each tool was assessed for its place within the four management cycle phases based on the PACE framework (plan, act, check, evaluate) (BSPC, 2006; Andersen, 2012). PACE is compatible with the ISO9001:2015 process management PDCA model (plan, do, check, act). In the Planning phase of PACE, the overall vision and goals (e.g., GES, targets per descriptor or theme specific goals such as tackling eutrophication, in the MSFD) are set by management and all the main threats to the system are identified. In the Evaluation and Check phases, the main focus of this work, status assessments are performed and distance to goals is evaluated (e.g., is GES reached? Why GES is not achieved? Is monitoring fit-for-purpose? Are additional measures needed)?.

Score matrices were collated and averaged across contributors. Scores allocated by the contributors to tool groups with high or moderate confidence were only considered further in the analysis. Due to blanks in the matrix, the number of responses contributing to the average varied according to the tool-by-element pair. The number of responses considered in the average calculation was recorded, together with estimates of the standard deviation (SD) and range (minimum and maximum) of the scores across participants. The minimum and maximum number of entries per tool were also recorded.

A Group average algorithm cluster analysis, based on Euclidean distance, was applied to the matrix data (average of scores across contributors) to identify groupings of (i) elements of EBM based on the similarity of tools used, and (ii) the tool abilities to deliver the

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specific element of EBM, i.e. Q and R-mode analyses (respectively analyzing attributes by cases and vice versa, Southwood and Henderson (2000)). A SIMPROF test was applied to identify clusters of elements that do not significantly (P>0.05) differentiate based on the tools used to deliver them. The contingency table from the clustering of both EBM elements and tools was explored and the score matrix rearranged accordingly to identify which tool groups better deliver for which EBM elements (or groups of elements within a cluster). The *a priori* categorization based on the EBM process phases (PACE) was also considered as a means to interpret the data-based clusters. The analyses were undertaken in PRIMER v6 (Clarke and Gorley, 2006).

6.2 Assessment results

On average, there were 11 entries per methodological tool group across all contributors, ranging from 7 (Knowledge Graphs) to 15 (Overarching Assessment Tools). The mean scores attributed to the tool groups according to their ability to deliver on the specific elements of EBM are shown in Table 4. The EBM elements (columns) and tool groups (rows) in Table 4 are grouped with separators according to the results of the cluster analysis undertaken between EBM elements (Figure 1 shows 5 groups differentiated at Euclidean distance 5) and tool groups (Figure 2 shows 5 groups differentiated at Euclidean distance 5). The cells in Table 4 are colored to reflect the variability of the mean score of tool groups within each column (the lowest score in the column is white, highest score in the column is dark blue).

All tool groups are noted in italics and all EBM elements are in bold in the following sections. *Risk based approaches accounting for exposure-effect-hazard-vulnerability* (e.g., Bow-Tie; tool group #5); *BBN probabilistic tools* (#4) and *Impact risk ranking through linkage-chain-frameworks* (#7) together with *Knowledge graphs* (#3) and *Conceptual models* (#1), were identified as the most suitable (with mean score values between 4.2-4.8 out of a maximum of 5) for the assessment of **Links between activities, pressures and impacts** during the planning phase of the EBM process. *Risk based approaches* alone were also identified as the most suitable tool for the assessment of **Risks** and of **Pressure and impact reduction/mitigation**, with mean score values 4.7 (Table 4). This tool group is also best suited to deliver the **requirements of other policies** (e.g., MSPD, BHD, Biodiversity Strategy), although the mean score in this case is lower (3.8) compared to the other EBM elements mentioned above.

The use of *Descriptor or theme-specific combinations of indices and models* (e.g., HEAT, BEAT and CHASE; #18) and *Overarching assessment tools* (e.g., NEAT and OHI; #19) also scored high overall. They were considered the most suitable tools to deliver **GES MSFD assessments** during the Check/Evaluation phases of the EBM process (both tools scoring >4.5). *Descriptor or theme-specific combinations of indices and models* (#18) were also the most suitable tool (score 4.8) to assess **Single MSFD descriptors and single issues** (e.g., eutrophication, NIS, HABs), while the *Overarching assessment tools* (#19) were also the best option to undertake **Whole ecosystem assessments** (score 4.5), together with

TABLE 4 Mean scores assigned to each tool group (rows) based on their ability to deliver on a specific element of Ecosystem-Based Management (EBM) (columns).

Tool No.	Main group	Tool Group	EBM elements: 4 ES (delivery, impacts, valuation)	9 Links activities pressures impacts	15 Spatial and other measures	3 Whole ecosystem assessments	2 GES MSFD assessments	10 Single MSFD Descriptors/ single issues	13 Climate change	14 Pressure and impact reduction/ mitigation	15 Other Policy Requirements	5 Specific biotic effects	6 Specific functions	16 Uncertainty	11 Single species, State change	12 Threatened habitats and species	17 Risks	1 Cumulative assessments	7 Pressures-Activities footprint	8 Impacts footprints
13		Natural capital accounting, ES valuation	4.7	0.7	1.3	0.8	0.0	0.3	0.8	1.3	1.8	1.2	2.7	1.5	0.5	1.0	1.2	0.3	1.0	1.0
14		Bioecon., socioec. models, SG&B valuation	5.0	1.5	0.0	1.5	0.0	0.0	0.5	0.5	1.5	0.5	0.5	0.0	0.0	0.0	0.5	2.0	0.5	1.5
9		Biogeochemical models	0.3	0.0	0.7	1.3	0.7	1.3	2.0	1.0	1.0	1.0	0.7	1.5	1.3	1.0	0.5	0.3	0.0	0.0
17		Simple assessment index	0.8	1.2	1.4	1.3	3.0	2.5	0.7	1.6	2.4	3.1	2.2	1.3	1.9	2.4	0.9	1.1	0.8	1.0
8		Single spp. models	0.6	1.0	1.9	0.9	1.3	2.0	1.7	1.3	1.6	2.6	1.4	2.1	3.3	2.4	1.7	0.1	0.9	0.5
12		SDM models	1.7	1.2	2.1	1.2	2.0	1.9	2.4	1.3	2.0	2.5	1.7	1.9	2.8	3.2	1.8	1.8	1.1	1.2

(Continued)

TABLE 4 Continued

Tool No.	Tool Group	Main group	EBM elements																			
			4 ES (delivery, impacts, valuation)	9 Links activities pressures impacts	15 Spatial and other measures	3 Whole ecosystem assessments	2 GES MSFD assessments	10 Single MSFD Descriptors/ single issues	13 Climate change	14 Pressure and impact reduction/ mitigation	15 Other Policy Requirements	5 Specific biotic effects	6 Specific functions	16 Uncertainty	11 Single species, State change	12 Threatened habitats and species	17 Risks	1 Cumulative assessments	7 Pressures-Activities footprint	8 Impacts footprints
6	Cumulative impact spatial mapping		1.7	3.1	2.6	2.7	2.6	2.3	1.9	2.1	2.6	1.7	1.8	1.5	0.9	1.9	2.5	4.7	4.0	3.8
15	Spatial planning models		1.7	2.7	4.3	1.3	1.5	1.4	1.2	1.9	2.5	1.7	1.2	1.5	1.0	1.5	2.1	2.8	2.9	2.5
16	Conservation planning models		0.8	1.9	4.6	0.8	0.7	0.7	1.6	2.3	3.1	0.9	0.8	2.0	1.0	2.7	1.6	1.8	2.2	1.8
18	Descriptor or theme-specific combination of indices & models		1.9	2.6	2.6	3.3	4.8	4.8	1.7	2.1	2.9	2.3	2.5	3.1	2.5	2.6	1.4	2.4	1.5	1.6
19	Overarching assessment tools		1.5	2.5	3.7	4.5	4.5	3.3	1.9	2.5	3.0	1.5	1.4	4.0	2.9	3.1	0.7	2.7	2.7	2.8
7	Impact risk - linkage-chain-frameworks		2.0	4.8	1.3	3.2	1.9	2.8	1.6	3.3	2.8	2.3	3.0	1.6	2.2	1.7	3.9	4.1	3.1	2.9
4	BBN probabilistic		2.4	4.6	1.6	2.6	1.9	3.0	2.9	3.2	2.6	3.0	3.2	3.8	2.7	3.3	3.6	3.4	1.8	2.0
5	Risk based approaches		2.4	4.5	1.9	2.3	2.1	3.5	2.7	4.3	3.8	3.3	3.0	2.6	2.5	2.8	4.7	3.8	1.9	1.9
3	Knowledge Graphs		1.2	4.6	1.0	1.4	1.2	2.6	3.4	3.0	2.8	1.8	1.6	0.8	1.0	2.6	1.2	1.4	1.0	1.0
1	Conceptual models		2.6	4.2	2.0	2.5	2.0	2.6	2.9	2.8	2.1	2.7	3.0	1.8	2.2	2.4	1.9	2.6	2.6	2.3
2	Semi-quantitative mental models		2.0	3.5	1.4	2.1	1.4	2.6	2.6	2.5	2.1	2.0	2.0	1.3	2.0	2.3	1.9	2.3	1.7	1.6
10	Food web models		1.7	2.0	2.5	3.0	2.3	3.0	2.6	2.7	1.9	3.6	4.0	2.6	3.1	2.6	1.8	2.1	1.3	2.0
11	Ecosystem models		2.1	2.4	2.0	3.5	2.0	2.4	2.3	2.0	2.1	2.5	3.3	1.7	2.4	2.4	1.8	2.3	1.0	1.1
	ProcessPhase		PA	PA	PA	CE	CE	PA	Gen	PA	Gen	CE	PA	Gen	CE	CE	Gen	PA/CE	PA	PA

Scores assigned with high or medium confidence only were considered to calculate the mean values across all contributors. EBM elements and tool groups are grouped based on cluster analysis between EBM elements (Figure 1) and tools (Figure 2), respectively (gaps between columns and rows separate cluster groups at Euclidean Distance = 5). Links between EBM elements and the EBM process phases are also shown at the bottom of the table (P, Plan; A, Act; C, Check; E, Evaluate; Gen, General relevance). Cells in the table are colored in a monochrome gradient to reflect the variability of the mean score from lowest (white) to highest (dark blue) value overall, indicating therefore the highest score-match between tool groups and EBM elements.

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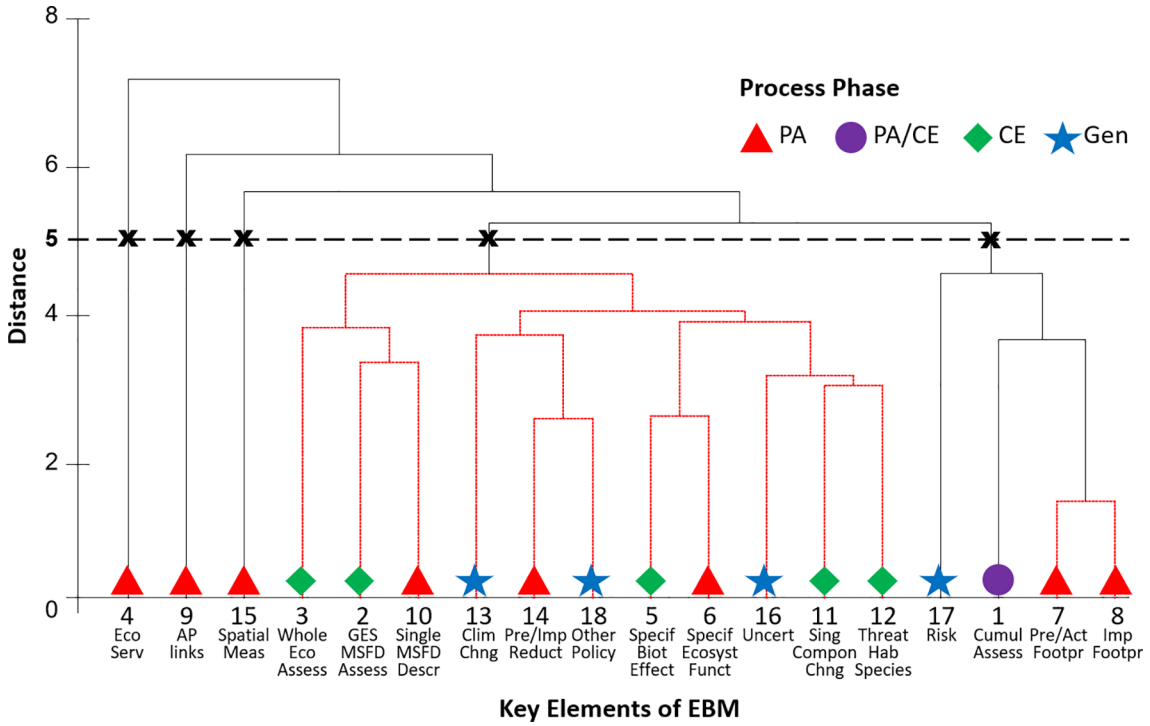

FIGURE 1
Cluster analysis of the elements of Ecosystem-Based Management (EBM) based on similarity of tools used and their ability to deliver the specific element of EBM (mean of scores with high or medium confidence). See Table 2 for full name and reference number of the EBM elements. Symbols indicate EBM process phases: P, Plan; A, Act; C, Check; E, Evaluate; Gen, General relevance. Group average algorithm was applied for the cluster analysis, based on Euclidean distance. Elements connected by red lines do not significantly differentiate based on the tools used to deliver them (SIMPROF test, P>0.05). Bold crosses identify the cluster groups differentiated at Euclidean Distance of 5 (black dotted line), as reported in Table 4).

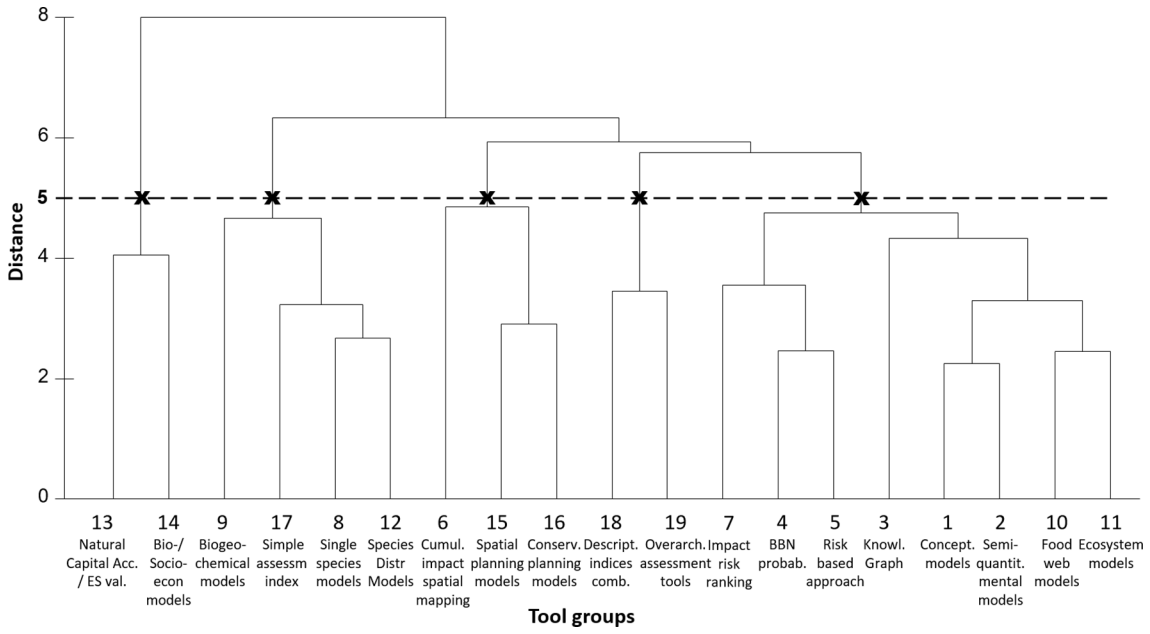

FIGURE 2
Cluster analysis of the tool groups based on similarity in the Ecosystem-Based Management (EBM) elements they can deliver (mean of scores with high or medium confidence). See Table 3 for full name and reference number of the tool groups. Group average algorithm was applied for the cluster analysis, based on Euclidean distance. Bold crosses identify the cluster groups differentiated at Euclidean Distance of 5 (black dotted line), as reported in Table 4).

Ecosystem end-to-end models (#11), and for **Uncertainty assessments** (score 4.0), along with *BBN probabilistic methods* (score 3.8) (Table 5).

Spatial-based tools were best suited to deliver elements at the Planning phase of the EBM process. *Cumulative impact spatial mapping* (#6) was identified as the best option to undertake **Cumulative assessments** (score 4.7) and to assess the **footprints of pressures/activities** (score 4.0) **and of impacts** (score 3.8). *Spatial and Conservation planning models* (#15 and #16, respectively) were the most suitable option to deliver on **Spatial and other measures**.

Food web models (#10) were identified as the best option to assess **Specific ecosystem functions** (and impacts on functions) (score 4.0) and **Specific biotic effects/impact** (score 3.6) during Planning and Check/Evaluation phases of the EBM process, respectively. *Risk based approaches* (#5) and *Simple assessment indices* (#17) scored moderately in the delivery of this latter EBM element. *Food web models* were also amongst the top scoring tools (score 3.1) identified to deliver the assessment of **Single species, ecosystem components state change**, although *Single* spp. *Models* (tool group #8) were identified as the best option for this element of the EBM Check/Evaluation phases, albeit with a score in the mid-range (score 3.3). *SDM models* (#12) and *Overarching assessment tools* (#19) were also amongst the top scoring tools for the assessment of **Single species, ecosystem components state change**, but their scores suggest a better

TABLE 5 Three top-scoring tool groups for each Ecosystem-Based Management (EBM) element.

EBM element	First place	Second place	Third place
Cumulative assessments	Cumulative impact spatial mapping (e.g., Halpern et al.) [4.7]	Impact risk ranking through linkage-chain-frameworks (e.g., ODEMM) [4.1]	
GES MSFD assessments	Descriptor or theme-specific combination of indices and models (e.g., HEAT, BEAT and CHASE) [4.8]	Overarching assessment tools (e.g., NEAT and OHI) [4.5]	
Whole ecosystem assessments	Overarching assessment tools (e.g., NEAT and OHI) [4.5]		
Ecosystem services (delivery, impacts, valuation)	Bioeconomic models, socioeconomic models (CBA), societal goods and benefits valuation [5.0]	Natural capital accounting, ecosystem services valuation [4.7]	
Specific biotic effects/impacts	Food web models (e.g., multispecies models, EWE) [3.6]	Risk based approaches exposure-effect-hazard-vulnerability (e.g., Bow tie) [3.3]	Simple assessment index (e.g., M-AMBI) [3.1]
Specific ecosystem functions (and impacts on functions)	Food web models (e.g., multispecies models, EWE) [4.0]		
Pressures-activities footprint	Cumulative impact spatial mapping (e.g., Halpern et al.) [4.0]		
Impacts footprints	Cumulative impact spatial mapping (e.g., Halpern et al.) [3.8]		
Links activities pressures impacts	Impact risk ranking through linkage-chain-frameworks (e.g., ODEMM et al.) [4.8]	Knowledge Graph [4.6]	BBN probabilistic [4.6]
Single MSFD descriptors/single issues (e.g., eutrophication, NIS, HABs)	Descriptor or theme-specific combination of indices and models (e.g., HEAT, BEAT and CHASE) [4.8]		
Single species, ecosystem components state change	Single spp. model (e.g., life cycle, stock assessment) [3.3]	Food web models (e.g., multispecies models, EWE) [3.1]	
Threatened habitats and species	BBN probabilistic [3.3]	SDM models[3.2]	Overarching assessment tools (e.g., NEAT and OHI) [3.1]
Climate change	Knowledge graph [3.4]		
Pressure and impact reduction/mitigation	Risk based approaches exposure-effect-hazard-vulnerability (e.g., Bow tie) [4.3]		
Spatial and other measures	Conservation planning models (e.g., MARXAN) [4.6]	Spatial planning models (e.g., GIS, VAPEM, related to use) [4.3]	
Uncertainty	Overarching assessment tools (e.g., NEAT and OHI) [4.0]		
Risks	Risk based approaches exposure-effect-hazard-vulnerability (e.g., Bow tie) [4.7]		
Other policy requirements e.g., MSPD, BHD, Biodiversity Strategy	Risk based approaches exposure-effect-hazard-vulnerability (e.g., Bow tie) [3.8]	Conservation planning models (e.g., MARXAN) [3.1]	Overarching assessment tools (e.g., NEAT and OHI) [3.0]

Only tools with average score ≥4 are included, where present. Where not present the top 3 tools with average score between 3 and 4 were considered. The average score for each tool is shown between square brackets. MSFD, Marine Strategy Framework Directive; GES, Good Environmental Status.

suitability to deliver the assessment of **Threatened habitats and species**, along with *BBN probabilistic methods* (#4; top scoring for this EBM element, with a value of 3.3).

Tools such as *Natural capital accounting, ecosystem services valuation* (#13) and *Bioeconomic models, socioeconomic models (CBA), societal goods and benefits valuation* (#14) are clearly the best option (scores >4.6) for the assessment of **Ecosystem services (delivery, impacts, valuation)** (including societal goods and benefits) during the Planning phase of the EBM process, while these tools are poorly suited to deliver other EBM elements (with almost all scores <2, and often 0; Table 4). Finally, the best tool to account for **Climate change** in the EBM process appeared to be *Knowledge graphs* (#3), followed by *Conceptual models* (#1) and *BBN probabilistic methods* (#4), albeit with scores only between 2.9-3.4.

The three top-scoring tool groups for each EBM element are summarized in Table 5. When tools with an average score ≥4 are considered, 12 tools are selected, but these only deliver 12 of the 18 EBM elements, as some EBM elements have only tools scoring lower than 4 (e.g., Specific biotic effects/impacts; Table 4). To account for these latter EBM elements, the top 3 scoring tools with scores between 3-4 were considered in these cases. As a result of these combined selection criteria, Table 5 includes 15 out of the 19 tool groups analyzed. *Conceptual models*, *semi-quantitative mental models*, *biogeochemical models* and *ecosystem models* are not included as they did not fulfil the selection criteria.

6.3 Selecting tools for the EBM approaches

Each of the tools have different advantages and disadvantages but, as shown above, they also have different abilities to fully or partially deliver one or multiple EBM elements. *Cumulative impact spatial mapping* and *Impact risk ranking through linkage-chain-frameworks* are the best suited tools to deliver **Cumulative assessments**, for which they both scored highly (≥4 on average, on a scale 0-5). The score closer to 5 attributed (on average) to *Cumulative impact spatial mapping* suggests that this tool alone is closer to fully deliver on this specific element of EBM at the plan and check phases. Either or both of these two top tools also appear to support the delivery of five other EBM elements which specifically address activities, pressures and impacts, through the assessment of their links or footprints during the planning phase. In turn, the top-ranking tools for **Cumulative assessments** appear to be less suited for the other elements of EBM (e.g., on ecosystem services and specific biotic effects assessments).

The best tools to deliver **GES MSFD assessments** during the Check-Evaluation phases of the EBM process are *Descriptor or theme-specific combination of indices and models* (e.g., HEAT, BEAT and CHASE) and *Overarching assessment tools* (e.g., NEAT and OHI). Both the NEAT and OHI tools scored ≥4 on average, but the use of *Descriptor or theme-specific combination of indices and model* alone appears to be closer to fully deliver on this specific element of EBM. Similarly, this tool group is also the best choice to undertake the assessment of **Single MSFD descriptors/single issues (e.g., eutrophication, contamination, NIS, HABs)** as may be required at the planning phase of the EBM process. *Overarching assessment tools* (e.g. NEAT and OHI) also inform other EBM elements at the Check-Evaluation phases, being well suited to deliver **Whole ecosystem assessments** and supporting the assessment of **Threatened habitats and species** (along with *SDM models*). *Overarching assessment tools* also deliver well on **Uncertainty** and may be used to support **Other policy requirements** (together with *Conservation planning models*). These tools are sufficiently specific to support the strict requirements of the MSFD but also, in being a combination of indices, models and integration tools can deliver to both topic related thematic and holistic assessments. In turn, the two top-ranking tools for GES MSFD assessments appear to poorly deliver on other EBM elements, both being among the lowest ranking tools for **Risks** and **Climate change**.

The top-ranking tools for the assessment of **Ecosystem services (delivery, impacts, valuation)** during the planning phase of the EBM process (*Natural capital accounting, ecosystem services valuation and Bioeconomic models, socioeconomic models (CBA), societal goods and benefits valuation*) are very well suited to deliver this specific EBM element, with scores close (for *Natural capital accounting*) or equal to the maximum of 5 (for *Bio/Socio-economic models*). However, due to their very specific nature, they are a very poor choice to inform all the other EBM elements, for which they are amongst the lowest ranking tools, and often with a value of 0 (no use) for example for **GES MSFD assessments** (both tools) and **Single MSFD descriptors/single issues, Single species/ecosystem components state change, Threatened habitats and species, Spatial and other measures**, and **Uncertainty** (*Bio/Socio-economic models*).

Food web models are the best tool choice for EBM elements of the planning phase such as the assessment of **Specific biotic effects/impacts** (also informed by *Simple assessment indices*, e.g., M-AMBI) and **Specific ecosystem functions (and impacts on functions)**, especially for the latter. *Food web models* may also inform the assessment of **Single species, Ecosystem components state change**, for which they are the top-ranking tool along with *Single* spp. *model* (e.g. life cycle, stock assessment), albeit both with scores close to 3.

The top-ranking tools to address **Spatial and other measures** during EBM planning (*Spatial planning models* e.g., GIS, VAPEM, related to use) and *Conservation planning models* (e.g., MARXAN) are well suited for this EBM element, with scores ≥4. In turn, they do not appear to be of particular use for the other EBM elements, for which they are most often amongst the lowest ranking tools. Notable exceptions being the ability of *Conservation planning models* and of *Spatial planning models* to deliver on spatial planning aspects (e.g. spatial allocation and exclusion of activities, preferred locations for conservation and restoration) of, respectively, **Other policy requirements** (e.g., advising on the best ways to reach targets such as the 10 and 30% protection targets) or **Pressures-activities footprint** (e.g. through the spatial mapping of these elements in an area).

The top-ranking tool for the general assessment of **Risks** is *Risk based approaches exposure-effect-hazard-vulnerability* (e.g., Bow-tie), which appears to be well suited to deliver this EBM element. This latter tool is also the best option for the **Pressure and impact reduction/mitigation** during the planning and act phases of the EBM process and to address **Other policy requirements** (although

with a score ≤4). It also appears to be always within the top ten ranking tools for any of the other EBM elements. Furthermore, *Knowledge graphs* appear to be the best tool to account for **Climate change** (albeit with an average score ≤4 and most likely done in a qualitative way. This tool is also within the top 3 ranking (with score ≥4) in the delivery of **Links activities-pressures-impact**, together with *BBN probabilistic tools* and *impact risk ranking through linkage-chain-frameworks*.

Finally, the best tool group for the assessment of **Single species/ Ecosystem components state change** at the planning stage of the EBM process includes *Single* spp. *model* (e.g., life cycle, stock assessment), although this type of tool cannot fully deliver all aspects of this element of EBM (scoring close to 3).

7 Discussion

The analysis here has shown that EBM is either explicit or implicit in all major policies for sustainable marine management. It is commonly regarded to be based on a set of accepted principles, presented here, and as shown here, it has been adopted widely by national, European, regional and global initiatives. Because of this, it requires tools and approaches for that adoption but is has become apparent that (i) EBM principles need to be disaggregated to all important associated EBM elements (e.g. example in S1) to be able to address them fully and correctly match them to necessary tools and methods, and (ii) not all tools are suitable for fulfilling all of those principles and thus the user needs guidance in choosing the most suitable tools – hence 'horses for courses'.

Marine EBM is essentially a risk-based process based on an understanding of natural and anthropogenic hazards, in order to determine what are the risks to the seas, how to assess and mitigate them, and how to manage the causes and consequences (Cormier et al., 2022). In essence, hazards occur in the environment (for example, by natural features such as tsunamis, and anthropogenic hazards such as contaminant inputs) and these become risks once they affect human health and welfare (Cormier et al., 2019). Hence, marine management and especially EBM is centered around cause-consequence-response frameworks (see above) relating to the human activities, their pressures, risks and effects on the natural and human systems and the management responses to prevent or mitigate those adverse consequences (e.g. CSWD, 2020; Elliott et al., 2017; Stelzenmüller et al., 2020). In order to be proactive, EBM should also enable an opportunity assessment and management process as a means to ensuring the wise and sustainable use of the seas while also maintaining and protecting the natural system (Borja et al., 2024). Key EBM elements in all these frameworks focus on ecosystem health and so identify: (i) the change in status of various ecosystem components due to single human activities or pressures, and (ii) the cumulative effects of all the activities operating in the marine space, negatively but also positively e.g., through protection, conservation and restoration actions. The analysis here shows that two key tool group categories fit this purpose: Overarching assessment tools (for GES assessments through structured ecosystem component changes assessments) and Cumulative impact spatial mapping (Halpern et al., 2008: EcoImpactMapper). Improvements can be made to these tools to further their use, for example to the Halpern et al. (2008) approach, to provide a hierarchical (*vs.* flat) structure, values for ecosystem components (*vs.* only presence/absence), and proper (*vs.* no) weighting by importance or spatial distribution of ecosystem components) (see Borja et al., 2024).

The risk-based tools (e.g. Knights et al., 2015; Piet et al., 2021, 2023) using spatial overlap and sensitivity estimates specifically intended to guide EBM), can also be used more widely in assessments, where their outcomes can be compared with those of more quantitative tools (or perhaps alternatively in data-poor cases). They can also partly inform on spatial and other measures and be integrated into science and advice frameworks (Roux and Pedreschi, 2024). However highly specialized tools such as MARXAN, ZONATION, VAPEM (see Supplementary Materials S3 for skills/software links/references) may be needed to support decision-making (for placing and zoning activities including conservation) and maritime spatial planning (see, for example, applications by Maldonado et al., 2022; Doxa et al., 2022; Fabbrizzi et al., 2023). Beyond highly specialized tools for the valuation of natural capital and ecosystem services, only food web models can address the delivery of ecosystem services and some production-related societal goods and benefits (e.g. Elliott, 2023).

Despite the continued debate and semantics regarding the EBM terms used (Kirkfeldt, 2019), the analysis here has strongly confirmed that EBM is the central pillar of the understanding, interrogation and management of the marine environment. Hence, EBM or its variants are mentioned in all major marine policy instruments at local, national, regional (European) and international levels (see Dickey-Collas et al., 2022, for a list). As such, it is notable that the analysis here is the first in which the 26 EBM principles have been reworded as instructions and 16 of them have been assessed in relation to tools for their partial or full delivery (Table 2). Despite this, while Link and Haugen (2025) recently carried out a valuable assessment to quantify the monetary repercussions of using EBM compared to a Business-As-Usual (BAU) scenario, we contend that so many bodies and instruments are using EBM that it should be regarded as BAU. However, importantly, this work reinforces the point here that EBM is good for both the ecosystem structure, functioning and services, as well as delivering societal goods and benefits.

The EBM approaches have often been related to individual components, habitats, species, activities or sectors, but it is emphasized that such a deconstructing of the marine environment would not result in an 'ecosystem-based' approach which requires all natural and societal features to be included. For example, while the FAO emphasized 'the ecosystem-based approach to fisheries management', this is only for one sector and its management is usually to the benefit of this sector and to the exclusion of other sectors (Dickey-Collas et al., 2022), thereby a misnomer not constituting EBM as defined here and elsewhere. Similarly, it is cautioned that if EBM is only considered in relation to HABs, NIS, top predators or any other individual component, no matter how important, then this would not constitute a true EBM

(Borja et al., 2024) as EBM is/should be a systematic holistic approach and the alternative to piecemeal and sectoral management (Sander, 2023).

When applied to disparate areas, EBM and its tools would have the major challenge in having to cope with different types of information, both qualitative and quantitative (Haugen et al., 2024). It also must be suitable for skills- and data-poor areas as well as skills- and data-rich areas (S3). The analysis here has shown that the priorities of scientists may differ from the priorities of managers as the two groups focus on different phases of the PACE process. Furthermore, the 19 tool groups interrogated here are not mutually exclusive and some have the same aims and outcomes, hence, the rationale for discussing tool groups in support of EBM.

Central to the task of managing marine areas is determining/assessing the footprints of activities, pressures and effects (Elliott et al., 2020b) and then enacting and integrating the horizontal and vertical management response-footprints (Cormier et al., 2022); a true EBM approach should encompass all of these aspects. The tool groups interrogated here show the importance of conceptual models as a starting point and frameworks, especially for cause-consequence-response links, such as DPSIR and its variants (see above). Among these, the most recent and increasingly widely-used variant, DAPSI(W)R(M) overcomes the difficulties in other and earlier variants (Patrício et al., 2016; Elliott et al., 2017).

Given the complexity of the marine environment and the need for its management to cope with a multi-component, multi-functioning, multi-sectoral, multi-user, multi-agency and multi-legal jurisdiction environment (Cormier et al., 2022), then it is not surprising that several or many tools would be required to be used together to support and effect EBM. Here, as designed in this particular study, the EBM principles (Table 1) were matched to assessment core objectives (e.g., quality status assessments, cumulative effects assessments, ecosystem services addressing uncertainty and acknowledging the importance of stakeholder engagement); for example, the principles determine ecological integrity and biodiversity (e.g., GES for MSFD) and consider cumulative impacts are at the core of EU Member State MSFD assessments (Borja et al., 2024).

The novel application used here of R and Q mode multivariate analyses, applied to the data elicited by expert judgement regarding the cases (experts) and attributes of the tools, has respectively grouped the most appropriate tools for EBM and the most relevant EBM principles for the tools. In summary, the analysis indicated five groups of tools according to the elements to which they relate (Figure 2): (i) socio-economic aspects, (ii) biochemical, species and habitat models; (iii) spatial mapping and planning models; (iv) indices and assessments for descriptors and wider assessment, and (v) conceptual, graphical and numerical ecosystem models encompassing natural and social features.

Given that EBM is essentially a risk and opportunity assessment and management process, this grouping is not surprising. However, the analysis could indicate a circular argument in that the overarching assessment tools (e.g. NEAT) are best at delivering an overall GES assessment. Similarly, descriptor and theme-based tools (e.g. HEAT) are good for descriptor and single issues whereas other types of assessment tools (such as single species or simple biotic indices) are appropriate for other assessments (Borja et al., 2016). Assessment, and its monitoring, are not management measures *per se*, but they are necessary to indicate what management is needed and/or whether management has been successful (Borja and Elliott, 2021; Elliott and Wither, 2024). Several tools can help with planning (through activity placement, suggested measure types or closures/MPAs, and conservation prioritization) or by risk management informed through linkage chains or exposure-effect-hazard approaches. All of these tools contribute to supporting EBM but not implement EBM. The Act phase of PACE and the Impact (Welfare) and Response (by Measures) phases of the DAPSI(W)R(M) cycle (and Management and Measures part of the DAPSES-MMM framework) require additional approaches. These include, for example, stakeholder involvement, consultation and co-creation of measures based on socio-economic tools, distance to accepted policy objectives and targets, elaborated scenarios and determination of social and economic repercussions of and need for management, thereby completing the EBM cycle (Borja et al., 2024). EBM should be then at the forefront of approaches that could address the current nature crisis (Sander, 2023).

It is emphasized throughout this review that EBM should not only gather appropriate information covering both the natural and human realms but that it has to accommodate both the changes to the system and the effects and repercussions of management measures. This implies that the management actions can be revisited by the environmental managers (often the so-called 'competent authorities' such as an Environmental Protection Agency) at prescribed intervals. Those intervals may occur whenever there are notable changes to external events, ecosystem local and global (e.g. climate change) characteristics, and levels of activities and pressures. Conversely, they may follow the monitoring and reporting cycle stipulated in the legislation, for example the 6-year cycle in the case of the MSFD. It is of note, for example, that the MSFD requires that its indicators, targets and thresholds can be adapted/modified at each reporting cycle to adjust for the so-called shifting baselines caused by climate change (Elliott et al., 2015).

Given that many of the EBM principles relate to natural and anthropogenic changes in the marine system under management (e.g. EBM principle 7, account for dynamic nature of ecosystems) then it is imperative that any tool used should be sufficiently flexible to those changes and repeated easily with the input parameters being changed/modified. This argues for not only having one tool used flexibly but also for having a suite of tools (a toolbox) which can be used to accommodate changing conditions. For example, this response to changing circumstances should include feedback loops indicating new or revised management actions, hence the central and important feature that EBM has to be related to an adequate monitoring system in which the monitoring not only indicates what management is required but also whether that management has succeeded in its aims.

8 Conclusions and recommendations

The analysis here has shown that a given complement of tools, i.e., a toolbox, is needed to satisfy the many principles of EBM. EBM

principles encompass high level concepts with many different or complementary aspects and deconstructing the principles to essential relevant EBM elements is vital for clarity and to be able to address them fully. No single tool is likely to satisfy all aspects of EBM and especially there is the need to ensure that the EBM can adapt to changing circumstances. Hence, as the result of the analysis, the EBM toolbox needs to include:

i. The starting point of a good conceptual understanding linking the ecological features to their relevant management anchored in all essential principles and elements, policy and governance through a risk and opportunity assessment and management framework.
ii. The conceptual model should include the capability to create links (again conceptual or preferably numerical) between the ecological structure and functioning, the resulting ecosystem services and the societal goods and benefits and their valuation.
iii. A tool/suite of tools for a suitably weighted cumulative impacts assessment which is based on estimating the activity-, pressures- and effects-footprints for all aspects in an area and which can help define/evaluate/check the thresholds and identify tipping points of change and then link these to management actions.
iv. A tool/suite of tools which both covers the components and features of the ecosystem, such as the MSFD descriptors, both singly and in total, including the species and habitat components and their interlinkages, and which allows an adaptive capacity in management as marine conditions change.

Developing such an EBM toolbox and applying these tools requires appropriate and fit-for-purpose data and expertise (see Supplementary Material S3) and thus EBM processes should plan for the required resources in order to advance EBM implementation. Hence, it is emphasized that for wide use globally then the tools should be suitable for skills- and data-poor areas as well as skills- and data-rich ones.

For most EBM principles (even for some of the omitted ones, as we show above) there are suitable tools to address their essential elements, but data gaps remain and impede comprehensive full-scale assessments. For example, while natural capital valuation tools are available, not many valuation studies or data are available for deep sea habitats (Jobstvogt et al., 2014). Similarly, there are tools available for trade-off analysis to allow EBM principle 11 decisions respect societal choices e.g. on planning priorities in national marine spatial plans but again valuations or willingness-to-pay studies are few and focusing on a small range of issues (e.g. Addamo et al., 2024).

The framework presented here, could be applicable to any marine system, from estuaries, to coastal and offshore waters, as well as to shallow and deep-sea areas. While it is intended to serve as basis to be used under European marine directives (e.g. MSFD, MSPD), it is emphasized that the fundamental aspects are global and applicable anywhere, in taking management decisions and measures for achieving a healthy ocean.

Author contributions

NP: Conceptualization, Investigation, Writing – original draft, Writing – review & editing. CS: Conceptualization, Investigation, Visualization, Writing – original draft, Writing – review & editing. AF: Conceptualization, Formal Analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. ME: Conceptualization, Investigation, Writing – original draft, Writing – review & editing. AB: Investigation, Writing – original draft, Writing – review & editing. JHA: Investigation, Writing – original draft, Writing – review & editing. EA: Investigation, Writing – original draft, Writing – review & editing. JPA: Investigation, Writing – original draft, Writing – review & editing. StB: Formal Analysis, Investigation, Writing – original draft, Writing – review & editing. TB: Investigation, Writing – original draft, Writing – review & editing. SiB: Writing – original draft, Writing – review & editing. DB: Investigation, Writing – original draft, Writing – review & editing. JC: Writing – review & editing, Writing – original draft. RC: Writing – original draft, Writing – review & editing. IG: Investigation, Writing – original draft, Writing – review & editing. AJ: Writing – review & editing, Writing – original draft. StK: Investigation, Writing – original draft, Writing – review & editing. SaK: Writing – original draft, Writing – review & editing. LL: Writing – review & editing. CLo: Writing – review & editing, Writing – original draft. CLy: Writing – original draft, Writing – review & editing. IM: Investigation, Writing – original draft, Writing – review & editing. CO: Investigation, Writing – review & editing. DP: Investigation, Writing – original draft, Writing – review & editing. GP: Investigation, Writing – original draft, Writing – review & editing. DR: Investigation, Writing – review & editing. IS-A: Writing – review & editing, Writing – original draft. VS: Investigation, Writing – original draft, Writing – review & editing. JT: Writing – review & editing, Writing – original draft. LU: Writing – review & editing, Writing – original draft. MU: Investigation, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors AF, ME, EA, JHA, StB, DB, are employed by IECS Ltd, TB by MariLim Aquatic Research GmbH and SiB by Environmental Resources Management Ltd.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1426971/full#supplementary-material

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Methodology for prioritizing marine environmental pressures under various management scenarios in the Black Sea

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This study aims to develop a methodology for identifying predominant pressures on the marine ecosystem, emphasizing the significance of examining these pressures and the necessity for management scenarios. The research focuses on how the Black Sea ecosystem responds to the combined effects of human pressures, climate change, and policies. An in-depth analysis was conducted on environmental pressures affecting the Romanian Black Sea, highlighting dominant pressures such as physical habitat loss, hydrocarbon introduction, and non-indigenous species invasion. The research employs a novel methodological approach to assess the implications of these pressures under different Shared Socioeconomic Pathways (SSPs): SSP1 "Taking the Green Road", SSP2 "Middle of the Road", and SSP5 "Taking the Highway". The findings reveal a complex interplay between economic development and environmental conservation, with each pathway presenting distinct outcomes for marine ecosystems. Recent developments, including beach rehabilitation, maritime transport, and oil and gas exploitation, have overshadowed traditional pressures such as nutrient introduction and fishing. The study identifies the increasing vulnerability of critical habitats to anthropogenic pressures, with the rehabilitation of these ecosystems remaining challenging even under reduced pressures. The results underscore the need for adaptive management strategies to enhance the Black Sea ecosystem's sustainability and resilience. The study's insights are important for developing management strategies that address ongoing environmental challenges. This research provides knowledge for policymakers and stakeholders involved in marine management and conservation efforts in the Black Sea region, emphasizing the importance of adaptive strategies to mitigate the adverse effects of human activities and climate change on marine ecosystems.

KEYWORDS

Black Sea, human pressures, climate change, biodiversity, sustainability, environmental pressures, management scenarios

1 Introduction

In today's rapidly changing world, the marine environment has faced various threats, emphasising the imperative need for developing a systematic approach to prioritising these pressures to ensure the preservation of its ecological balance and long-term health (Halpern et al, 2008; Halpern et al, 2015; Borgwardt et al, 2019; Sundblad et al., 2021; IPCC, 2022; Smit et al., 2022). Understanding how to effectively assess and rank these mechanisms, through which human activities or natural events have altered the marine ecosystem, is paramount for its protection (Ma et al., 2023; Wu et al., 2023; Borja et al., 2016). This knowledge leads to the development of management strategies that can ultimately control the vitality and resilience of our seas (Cormier et al., 2022; Borja et al., 2020). In the past two decades, there has been a notable shift in marine management practices, emphasising an ecosystem-based approach that considers all elements and challenges affecting the ecosystem, versus solely focusing on a specific issue, activity, or species (Breen et al., 2020; Smith et al., 2016). Policies within this domain have played a significant role in this transformation, particularly the Water Framework Directive (WFD) and the Marine Strategy Framework Directive (MSFD) (EU, 2008). Both directives use the term "pressures," and the MSFD provides detailed specifications on their nature and demands for evaluating predominant ones, including their synergistic effects, in the European marine regions (Crise et al., 2015). One of the regions is the Black Sea, located at the crossroads of Europe and Asia, serving as a critical maritime region, supporting diverse ecosystems, and playing a pivotal role in regional and global contexts (Black Sea Commission, 2007; Black Sea Commission (BSC), 2019). The pressures derive from various uses and activities, utilising different pathways, like direct discharge, atmospheric deposition, and river systems (Black Sea Commission (BSC), 2019; Slobodnik et al., 2020; Lazar et al., 2021; Strokal et al., 2023). which leads to cumulative impacts on the sea (Willsteed et al., 2017; Stelzenmüller et al., 2018a; Julius et al., 2022). These pressures include the introduction of substances, noise, litter and energy from multiple sources, overfishing, habitat destruction, climate change, and other factors that, considered together, create a more significant and often more complex impact on the sea's ecosystems and overall health. Therefore, understanding cumulative impacts is crucial for effective marine management and conservation efforts (Ban et al., 2010; Curtin and Prellezo, 2010; Katsanevakis et al., 2020; EPA, 2022).

Cumulative impacts refer to environmental alterations arising from the combined influence of historical and current human activities and natural processes (Foley et al., 2017). According to the EU, cumulative impact is defined as "the impacts (positive or negative, direct, and indirect, long-term, and short-term) arising from a series of activities in an area or region, where each effect may not be significant if taken in isolation. Cumulative impacts include a temporal dimension, as they should calculate the impact on environmental resources resulting from changes brought about by past, present and reasonably foreseeable future actions" (Clark, 1994; Ross, 1998; EU, 1999a; EU, 1999b; Piet et al., 2021). Currently, there are several initiatives in different European sea basins based on the methodology detailed above that investigate how cumulative impact assessments can be conducted and used to support the implementation of maritime policies like Adriplan Cumulative impact tool (currently called Tools4MSP), SYMPHONY - a cumulative assessment tool in Swedish Marine Spatial Planning, SIMCelt - Maritime Spatial Planning: Transboundary Cooperation in the Celtic Seas Cumulative Effects Assessment and Marine Spatial Planning, Cumulative Impact Assessment work from ESaTDOR, Med-IAMER - Interreg Med PANACeA project, Plan4Blue on the cumulative environmental impact is based on the Pressure Index and the Baltic Sea Impact Index developed by HELCOM, the SIMNORAT project - tools for cumulative impact and the ecosystem approach for maritime spatial planning in Portugal. A literature review conducted in 2016 (Korpinen and Andersen, 2016) revealed a significant gap in the Black Sea's cumulative pressures and impacts on the research landscape, where only one study encompassed the Mediterranean and Black Sea regions (Micheli et al., 2013). Notably, no studies specifically addressed only the Black Sea (Ban et al., 2010). Thus, the research in this area has laid the foundation for comprehensively understanding the pressures' dynamics in the Black Sea by developing a methodology for hierarchising pressures under different development scenarios.

Black Sea challenges and progress

In the 1980s and early 1990s, the ecological state of the Black Sea was in a severely deteriorated condition (Kideys, 2002; Oguz and Velikova, 2010; Oguz, 2012; Mee et al., 2012). The decline was primarily due to eutrophication and the invasion of the comb jelly *Mnemiopsis leidyi*, worsened by pollution and overfishing (Gomoiu, 1992; Kideys, 2002). As a result of political willingness and economic decline (Strokal and Kroeze, 2013), the sea region witnessed encouraging outcomes stemming from the implementation of specific actions by the Danube Basin's countries and those bordering the Black Sea after the ratification of the two conventions aimed at safeguarding both the Black Sea (The Convention on the Protection of the Black Sea Against Pollution – Bucharest Convention, 1992) and the Danube (International Convention for the Protection of the Danube River, 1994, ICPDR). Consequently, since the mid-1990s, mainly due to the reduction of the nutrient input (Lancelot et al., 2002; Friedland et al., 2021), both eutrophication and the *Mnemiopsis* impact have diminished (Oguz, 2005), leading to positive signs of recovery in the ecosystem. However, the recovery did not lead to the same pristine status as known in the '60s (Gomoiu, 1992; Langmead et al., 2009) but to a state dominated by jellies and opportunistic species as an alternative to the fish-dominated healthy state which could not be interpreted as a tendency of improvement and rehabilitation of the North-Western Black Sea shelf (McQuatters-Gollop et al., 2009; Oguz and Velikova, 2010). While the eutrophication status of the North-Western shelf, mainly influenced by significant European rivers (Lazar, 2021) such as the Danube, Dniester, and Dnieper, has shown gradual improvement over the past two decades (Slobodnik et al., 2020), the last assessment (2018) of Romania's Black Sea waters according to the Marine Strategy Framework Directive (EC, 2017a) (MSFD) still unveiled ecological concerns. This evaluation highlighted non-indigenous species (D2), eutrophication (D5), environmental contaminants (D8), biodiversity

issues concerning demersal fish (D1), and benthic habitats (D6) as areas of "non-good" environmental status. However, the "good" environmental status (GES) for contaminants in seafood (D9), marine litter (D10), and coastal fish (D1) was reported (Boicenco et al., 2018). This dichotomy suggests a need for targeted measures to address the identified concerns while maintaining efforts to sustain the positive aspects of the marine environment in the Romanian Black Sea waters' ecological status.

The paper aims to develop a methodology for identifying predominant marine environment pressures, underscores the importance of studying these pressures, and highlights the need for effective management scenarios in the Black Sea. In order to investigate how ecosystems in the Black Sea respond to the combined effects of increasing human pressures and climate change and to identify and explore potential management options to mitigate and adapt to these impacts, we conducted a comprehensive review of activities and identified associated indicators, assessed the complex linkages between activities and pressures, built a matrix evaluating the ecosystem components sensitivity, and created a mental map and model that integrated the correlations between activities, pressures, and habitats.

2 Material and methods

The methodology outlines a comprehensive approach to identifying the predominant pressures on the marine ecosystem components and analysing different policies under specific scenarios (Figure 1). This approach is both systematic and integrative, starting with the identification of anthropogenic pressures and culminating in strategic scenario development for future planning. Each step is crafted to build upon the previous, creating a cohesive and detailed strategy for understanding and addressing the pressures on the marine environment. The first phase is to conduct an inventory (step 1) of the different activities and uses of the marine environment to lay the foundation for further analysis. The objective is to establish a baseline understanding of how the marine environment is utilized, setting the stage for subsequent analysis. This information is then used to identify potential sources of pollution, associated indicators, and available data. This characterisation (step 2) provides a detailed overview of the different activities, uses, and pollution sources from the Romanian coastal zone aiming to identify associated indicators and compile available data illustrating the direct links between

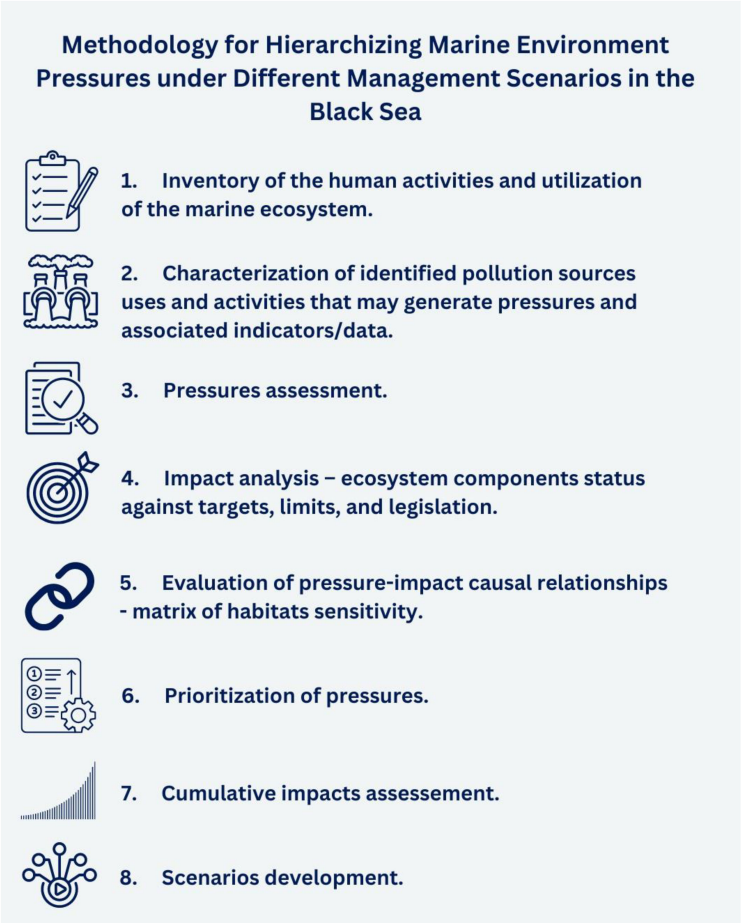

FIGURE 1
Steps of the methodology for hierarchising marine environment pressures under different management scenarios.

human activities and environmental pressures. The next phase involves assessing the pressures against existing legislation (step 3), consisting of discharges from different point sources in the Black Sea. This assessment allows the identification of potential gaps in regulations and areas where further action is needed. The impact analysis (step 4) then evaluates the status of different marine ecosystem components against targets, limits, and specific legislation to understand the impacts of identified pressures and how they alter the marine environment. The link between pressures and impact is achieved by the habitat's sensitivity matrix (step 5), built to identify the most critical areas and the most significant drivers of ecosystem change, allowing for prioritising pressures (step 6). Thus, utilizing the insights from the habitat sensitivity matrix and the impact analysis, step 6 is about prioritizing pressures based on their severity and impact. It ensures that management and mitigation efforts are directed where they are most needed. The final phase includes the cumulative pressures assessment (step 7) with the scope to understand the broader environmental challenges that arise from the interplay of various pressures, and scenario development (step 8), which evaluates potential future outcomes based on different intervention strategies and involves a detailed analysis of how various management strategies could influence the marine ecosystem under different future scenarios.

2.1 Data collection

2.1.1 The study area

The Romanian coastline along the Black Sea extends from the northern border with Ukraine to the southern border with Bulgaria, spanning a length of 244 km, representing 6% of the total Black Sea coast. The Black Sea receives a significant influx of freshwater annually from various rivers, including the Danube, Dniester, Dnieper, Don, and Bug. The Danube, Europe's second-largest river basin after the Volga, contributes the most to the Black Sea, accounting for 55% of the freshwater input. The Danube has a total river basin area of 801,463 km^2, covering approximately 33% of the Black Sea basin and traversing the territories of 19 countries ICPDR, 2005). Originating in the Black Forest Mountains of Germany, the Danube flows 2,857 km before reaching the Black Sea, with an average flow of 194 km^3/year out of the total freshwater input of 350 km^3/year ICPDR, 2005; Mee, 1992) (Panin and Jipa, 2002) This substantial contribution significantly influences the hydrography, chemistry, and biology of the entire north-western region of the Black Sea (Mee, 1992).

The continental shelf in the North-Western sector of the Black Sea has the largest expansion in the entire basin, with the 100 m isobath moving up to 180 km away from the shore. This expansion is due to the substantial sediment brought by the hydrographic network and the basin's configuration. Near the Romanian shore, the continental shelf narrows from north to south, placing the 100 m isobath at 180–200 km in the northern sector and 100–110 km in the southern sector (ESPON, 2013). Romania's maritime zones, including territorial waters, contiguous zone, and Exclusive Economic Zone, cover an area of approximately 29,600 km^2. These zones overlap with the continental shelf (0–200 m depth) by about 75%. The maximum depth in the Romanian sector reaches 1500–1700 m (Monitorul Oficial, 2023).

The ongoing study incorporated diverse data sources, including information on pressures from activities occurring on land, at sea, and offshore involving the release or emission of pollutants into the atmosphere, water, or soil. While some data sets are accessible to the public (https://sdi.eea.europa.eu/), others were acquired from the National Romanian Water Authority (Table 1; Supplementary Table 1). Discharge data were used for activity characterization (step 2) and pressure assessment (step 3).

The methodology described in Figure 1 has the following steps:

1. Inventory of the human activities and utilization of marine ecosystem - the inventory process undertaken within the Romanian Exclusive Economic Zone (EEZ) (Figure 2) consisted of identifying activities, identification of significant pressures (according to WFD) and key pressures. The process was significantly enriched by actively involving stakeholders, mainly Romanian Water Authorities. The method ensured a thorough understanding of the Romanian EEZ, laying a solid foundation for the next steps. An Excel spreadsheet that includes all existing activities (N=40) and incorporates spatial data for those with direct discharge into the Black Sea (N=8) was created. Additional information about the coastal defence and flood protection sector - beach nourishment works was collected from the National Romanian Water Authority (https://dobrogea-litoral.rowater.ro/?page_id=551). The format was designed by the project partners (National Institute for Marine Research and Development, National Water Authority, Local Water Authority and Ministry of Environment, Water and Forests throughout three virtual workshops (Zoom) held on April 6, April 29, and May 14, 2020.

2. Characterization of identified pollution sources uses and activities that may generate pressures and associated indicators/data – this step was focused on analyzing the types of emissions from identified activities. This step involved quantifying emissions to understand their impact on the marine environment ensuring each activity was accompanied by detailed emissions data, where available (Table 1; Supplementary Table 1). In the inventory, the sources of pollution are classified as potentially significant pressures (by the Local Water Authority) by applying the set of criteria presented below:

A. Point sources:

a. Human settlements > 2000 p.e. that have wastewater collection systems and/or treatment plants discharging into water resources; also, settlements < 2000 p.e. are considered potentially significant sources only if they have a centralized sewage system, as well as human settlements with a combined sewage system that are unable to collect and treat the mix of wastewater and stormwater during periods of heavy rain;

b. Industry (IED installations - including units listed in E-PRTR - water emissions, units discharging hazardous substances and/or priority substances above the limits of current legislation, units not complying with existing

TABLE 1 Activities and pathways for pressures and ecosystem components, indicators and available data – Black Sea, 2017–2018.

Activity/ Pathway	Utilisation	Activity	Type of Pressure	Pressure	Structure, functions, and processes of marine ecosystems	Indicator	Parameter (available data used in the methodology)
WWTPs with direct discharge into the Black Sea – Rompetrol, Constanta North, Constanta South, Eforie, Mangalia	Urban uses	urban wastewater treatment	Substances, litter, and energy	Input of nutrients and organic matter	–	Discharge concentration/ load of nutrients and organic matter	TN*, TP, NO_2, NO_3, NH_4, BOD_5, COD (mg/L)
				Input of other substances		Discharge concentration/ load of heavy metals	Ni, Cr, Cd, Cu, Pb (mg/L)
						Discharge concentration/ load of hydrocarbons	TPH (mg/L)
Rompetrol Refinery	Industrial uses	processing imported sulphur oil, and crude oil from Romania and obtaining a complex range of petroleum and petrochemical products		Input of nutrients and organic matter		Discharge concentration/ load of nutrients and organic matter	TN, TP, NO_2, NO_3, NH_4, BOD_5, COD (mg/L)
				Input of other substances		Discharge concentration/ load of heavy metals	Ni, Cr, Cd, Cu, Pb (mg/L)
				Input of other substances		Discharge concentration/ load of hydrocarbons	TPH (mg/L)
Thermoelectric plant		production of electricity and heat		Input of nutrients and organic matter		Discharge concentration/ load of nutrients and organic matter	TN, TP, NO_2, NO_3, NH_4, BOD_5, COD (mg/L)
				Input of other substances		Discharge concentration/ load of heavy metals	Ni, Cr, Cd, Cu, Pb (mg/L)
				Input of other substances		Discharge concentration/ load of hydrocarbons	TPH (mg/L)
Constanta Port		service activities related to water transport		Input of nutrients and organic matter		Discharge concentration/ load of nutrients and organic matter	TN, TP, NO_2, NO_3, NH_4, BOD_5, COD (mg/L)
				Input of other substances		Discharge concentration/ load of heavy metals	Ni, Cr, Cd, Cu, Pb (mg/L)

(Continued)

TABLE 1 Continued

Activity/ Pathway	Utilisation	Activity	Type of Pressure	Pressure	Structure, functions, and processes of marine ecosystems	Indicator	Parameter (available data used in the methodology)
				Input of other substances		Discharge concentration/ load of hydrocarbons	TPH (mg/L)
Oil rigs OMV Petrom		extraction of crude oil, natural gas, services related to the extraction of crude oil and natural gas, transport by submarine and land pipelines, storage, handling		Input of nutrients and organic matter		Discharge concentration/ load of nutrients and organic matter	TN, TP, NO_2, NO_3, NH_4, BOD_5, COD (mg/L)
				Input of other substances		Discharge concentration/ load of heavy metals	Ni, Cr, Cd, Cu, Pb (mg/L)
				Input of other substances		Discharge concentration/ load of hydrocarbons	TPH (mg/L)

*TN-total nitrogen, TP-total phosphorus, NO_2-nitrite, NO_3-nitrate, NH_4-ammonium, PO_4-phosphate, BOD_5-biological oxygen demand, COD-chemical oxygen demand, TPH-total petroleum hydrocarbons.

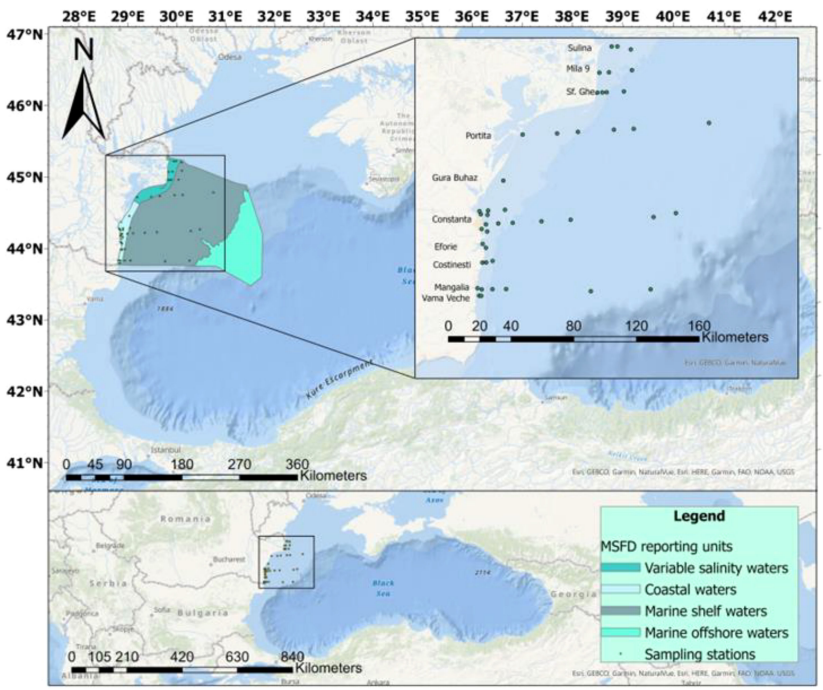

FIGURE 2
Map of sampling stations for evaluating the ecosystem components status – Romanian Black Sea, 2017–2019.

environmental water legislation, units causing accidental pollution of water resources, other units that have established a measures program);

c. Agriculture (livestock farms under the IED Directive - including units listed in E-PRTR - water emissions, farms discharging hazardous substances and/or priority substances above the limits of current legislation, other livestock units not complying with existing environmental water legislation, units causing accidental pollution of water resources, non-compliant pesticide storage, other units that have established a measures program);

d. Other point sources that do not comply with existing environmental water legislation.

B. Diffuse sources:

a. Human settlements > 2000 p.e. that do not have wastewater collection systems and/or have non-compliant municipal waste sites, human settlements (<2000 p.e.) for water bodies that do not meet environmental objectives, etc.;

b. Industry (storage of raw materials, finished products, auxiliary products, storage of non-compliant waste, units causing diffuse accidental pollution, abandoned industrial sites, etc.);

c. Agriculture (animal rearing and cultivation of agricultural lands, especially in cases where there is non-compliance with current legislation, agro-livestock farms that do not have appropriate manure storage systems, units using non-compliant pesticides, storage of non-compliant fertilizers, etc.)

C. Hydromorphological alterations (including water intakes)

3. Pressures assessment – the assessment involved comparing each discharge within the Romanian EEZ against environmental legislation and analyzing the ecological status data from the WISE Freshwater portal. This step aimed to identify discrepancies between emissions and legal standards, finding areas where activities might pose significant environmental risks. The pressures on the marine environment were classified and assessed according to Annex III (Table 2A) of Commission Directive 2017/845 (EC, 2017b).

4. Impact analysis – ecosystem components status against targets, limits, and legislation.– this step involves a detailed analysis of various components of the marine ecosystem status, both from pelagic and benthic habitats – phytoplankton, zooplankton, phytobenthos, macrozoobenthos and abiotic conditions from seawater and marine sediments. The ecosystem components were analysed according to ANNEX III Indicative lists of ecosystem elements, anthropogenic pressures and human activities relevant to the marine waters, Table 1 Structure, functions and processes of marine ecosystems of Commission Directive 2017/845 (EC, 2017b). This step is crucial for bridging the gap between recognising environmental pressures and comprehensively evaluating their actual and potential effects on marine biodiversity, habitat integrity, and ecosystem functions.

5. Evaluation of pressure – impact casual relationship - matrix of habitats sensitivity - The evaluation of the connections between pressures and the ecosystem components relies on the ecosystem components' sensitivity matrix, which provides a systematic framework for evaluating the sensitivity of various marine ecosystem components to different stressors or disturbances (Figure 3). The matrix takes the form of a table with rows designated for the pressures as outlined in Annex III (Table 2A) of Commission Directive 2017/845 (EC, 2017b) and columns corresponding to different habitat types and species from the studied area. Thus, each cell contains the product of ranks as described in (Halpern et al., 2007) (Supplementary Table 2) for features (surface, frequency of apparition, functional impact, resistance, and recovery) within each cell at the intersection of a

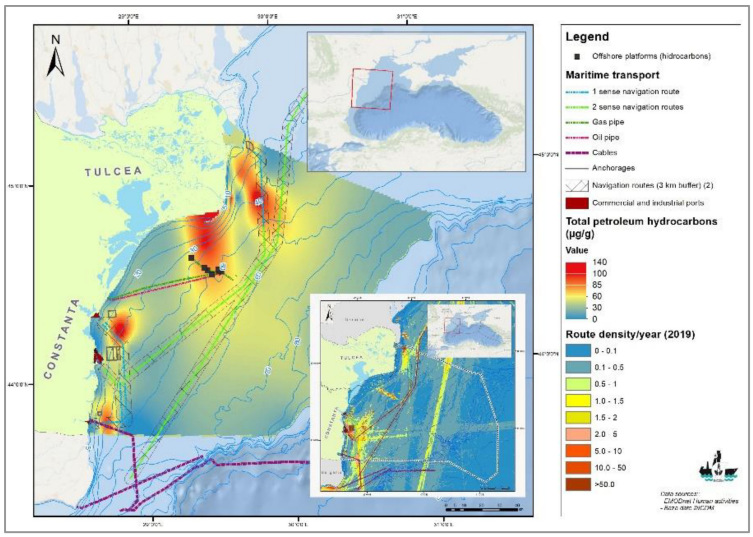

FIGURE 3
Distribution of total petroleum hydrocarbons (TPH) content in marine sediments (µg/g) and maritime traffic density – Romanian Black Sea.

specific pressure and ecosystem component (Supplementary Table 3). The values were standardised to fall within a range of 0 to 1.

6. Prioritisation of pressures - Semi-quantitative modelling was done with Mental Modeler software to obtain fuzzy cognitive maps (FCM) and metrics about the correlation between activities, pressures, and ecosystem components. Mental Modeler is a decision support software that helps experts understand the impact associated with environmental change and develop strategies to mitigate unwanted outcomes by capturing, communicating, and representing knowledge (Gray et al., 2014). Fuzzy-Logic Cognitive Mapping (FCM) represents a structured form of concept mapping that allows for the creation of qualitative fixed models, which are then transformed into partially quantitative dynamic models (Gray et al., 2013). By building the FCM, Mental Modeler allowed us to develop the semi-quantitative Activities – Pressures – Impact model that defines essential components and the strength of relationships between them and may run scenarios which determine how the system reacts under certain conditions. FCM was built by graphically representing knowledge by defining three characteristics of the system:

- -System components – human uses and activities, anthropogenic pressures and impacts on pelagic habitats, benthic habitats, fish, birds, and marine mammals.
- -Positive or negative relationships between components, according to expert judgment.
- -The degree of influence that one component can have on another, defined by qualitative weights (for example, for the causal relationship activity - pressure - the source of significant, potentially significant, or insignificant pollution), sensitivity score (for the causal relationship pressure - impact, the score obtained based on the sensitivity matrix).

Thus, weight factors were set for activity-pressure links at 0.8 for "high probabilities", 0.5 for "moderate probabilities", and 0.2 for "low probabilities". In contrast, pressure-impact links were weighted with values calculated in the habitats' sensitivity matrix.

7. Cumulative impacts assessment - The cumulative impacts assessment process involves the use of a sensitivity matrix to methodically assess the impact of various pressures on marine ecosystem components along the Romanian Black Sea coast. By summing the scores from the sensitivity matrix for each habitat, a cumulative impact score is derived, offering a comprehensive measure of how these pressures collectively affect different marine habitats.

8. Scenarios development - The Shared Socioeconomic Pathways (SSPs) encompass climate change projections outlining anticipated global socioeconomic shifts until 2100 (Riahi et al., 2017). These pathways are the foundation for formulating greenhouse gas emissions scenarios under diverse climate policies (Pinnegar et al., 2021). Utilised prominently in the IPCC Sixth Assessment Report on climate change in 2021, the SSPs offer descriptive narratives depicting alternative socioeconomic trajectories (O'Neill et al., 2020; Rozenberg et al., 2014; Nilsson et al., 2017). These storylines articulate a qualitative understanding of the logical connections among various narrative elements. Employing various Integrated Assessment Models (IAMs), the SSPs can be quantified to investigate potential future trajectories encompassing socioeconomic and climate dimensions (Kok et al., 2019; Nilsson et al., 2017). Out of the initial five scenarios, we investigated three: SSP1, known as "Taking the Green Road"; SSP2, named "Middle of the Road," and SSP5, "Taking the Highway". We defined the narratives of each scenario according to the literature. Thus, the story of SSP1, "Taking the Green Road" for the coastal Black Sea region centers on a future in which sustainable development is prioritized. In this scenario, there is a concerted effort towards environmental preservation, renewable energy adoption, and a strong focus on mitigating the impacts of climate change (Riahi et al., 2017; Nilsson et al., 2017), and stringent environmental regulations and policies to preserve the marine ecosystem. It could involve initiatives to drastic pollution reduction and protect biodiversity, and promote eco-friendly tourism practices. Coastal communities might have extended and affordable investments in renewable energy sources, such as wind or solar power, reducing reliance on fossil fuels and minimising carbon emissions. Additionally, SSP1 strongly enhances the international collaboration among Black Sea countries to actively address common environmental challenges, fostering cooperation for marine conservation and sustainable fisheries management. The narrative would likely portray a region where economic growth is balanced with environmental conservation, ensuring a resilient and thriving coastal ecosystem for future generations. The scenario looks like the Black Sea's riparian countries embrace the Green Deal initiatives – Fit for 55, European climate law, EU strategy on adaptation to climate change, EU biodiversity strategy for 2030, Farm to fork strategy, European industrial strategy, Circular economy action plan, Batteries and waste batteries, A just transition, Clean, affordable, and secure energy, EU chemicals strategy for sustainability and Forest strategy and deforestation (Ciot, 2022; Vela Almeida et al., 2023).

In the narrative of SSP2, "Middle of the Road" (Riahi et al., 2017; Nilsson et al., 2017), the Black Sea region follows a trajectory characterised by moderate changes and a balance between economic progress and environmental concerns. In this scenario, the approach to coastal development might involve a mix of sustainable practices and some degree of conventional methods. Efforts to address environmental concerns could exist, but they might not take centre stage compared to SSP1. There might be moderate regulations on industries and tourism activities along the Black Sea coastline, aiming for a balance between growth and conservation. Coastal communities may see some adoption of renewable energy sources, but the region might still rely significantly on traditional energy sources. This scenario could depict collaborative efforts among Black Sea countries, although they might not be as ambitious or comprehensive as those in SSP1. Overall, the narrative of SSP2 for the coastal Black Sea suggests a path where environmental considerations coexist with economic development, but without the same heightened emphasis on sustainability as in SSP1.

In the narrative of SSP5, "Fossil-fuelled Development" or "Taking the Highway" (Nilsson et al., 2017; Riahi et al., 2017), the coastal Black Sea region undergoes a trajectory marked by prioritising rapid economic growth and energy-intensive development, often at the expense of environmental concerns. This scenario might showcase extensive industrialisation along the Black Sea coastline, heavily relying on fossil fuels for energy generation and industrial activities. Immediate financial benefits may take precedence over environmental laws and conservation initiatives, which can result in more pollution and the deterioration of coastal habitats. Coastal communities may witness significant infrastructure development for industries and transportation, potentially impacting natural habitats and marine biodiversity. Renewable energy adoption might be limited, with the region largely dependent on conventional and less sustainable energy sources. Individual economic and territorial ambitions might overshadow collaboration among Black Sea countries, potentially leading to conflicts over resource utilisation and environmental degradation. The narrative of SSP5 could portray a future where short-term economic gains outweigh long-term sustainability, potentially posing challenges to the health and preservation of the coastal Black Sea environment.

In the context of addressing climate change across all three scenarios (SSP1, SSP2, and SSP5), consider the guiding pathway RCP2.6, aligning with the ambitious objective of limiting global warming to below 2.0°C until 2050, as set forth by the Paris Agreement (IPCC, 2014; UN, 2015).

The information about the marine ecosystem was collected through six expeditions (in 2017 – March, July, and November; in 2018 – July and September; and in 2019 – August) carried out with R/V "Steaua de Mare". During these expeditions, we conducted the sampling of water, sediment, and biota from a network comprising 45 stations located on the Romanian shelf and covering three of the marine reporting units (MRU) according to the Marine Strategy Framework Directive (MSFD) (European Union, 2008) (Figure 2). The samples were analysed within NIMRD (National Institute for Marine Research and Development) laboratories, using specific methods for each parameter.

2.2 Data analysis

Data were visualised and analysed using specialised software – MS Excel, Statistica® 14.0.1.25 (TIBCO Software Inc., Palo Alto, CA, USA) TIBCO Software, Inc, 2023, PRIMER v7.0.21 (PRIMER-E Ltd, Plymouth, UK) (Clarke and Gorley, 2015), ArcGIS Desktop 10.7 software (ESRI, 2019), Mental Modeler (Gray et al., 2013).

3 Results

3.1 The results of applying the methodology to the Black Sea context

3.1.1 Inventory of the human activities and utilization of the marine ecosystem

The pollution sources inventory analysis reveals 40 activities regarding the physical restructuring of rivers, coastline, or seabed (water management), extraction of living and non-living resources, production of energy, urban (direct discharging of wastewater from treatment plants) and industrial uses (refinery, ports, shipyards), tourism and leisure. Of these, 12 are coastal villages without sewage and wastewater treatment facilities. All sources are situated along the central-southern Romanian Black Sea coast, primarily in Constanta County. This region boasts roughly 70 kilometres of coastline, with 40 kilometres for tourism (beaches). Approximately 400,000 residents inhabit the broader coastal area covered by protected zones, attracting over 1.3 million visitors annually (Nuno, 2022).

3.1.2 Characterization of identified pollution sources uses and activities that may generate pressures and associated indicators/data

The characterisation of pollution sources relies on a dual assessment: tracking sources by emissions and categorising them as insignificant or significant in terms of their pollution potential, utilising the methodology outlined by the Water Framework Directive (WFD) (EU, 2014). Thus, in this area, there were identified as potential significant sources of pollution seven big human agglomerations (>10,000 p.e.) connected to the sewage system and four wastewater treatment plants (WWTP) with direct discharge into the Black Sea, eight human agglomerations with 2,000–10,000 p.e. from which only four are connected to the sewage system and one WWTP and five industrial sources (ports and shipyards, refinery, oil and gas exploitation rigs). Four agglomerations with 2,000–10,000 p.e. and eight with less than 2,000 p.e. with agriculture as a primary activity are not connected to any sewage system or WWTP (River Basin Management Plan 2016–2011 available at https://dobrogea-litoral.rowater.ro/?page_id=469). Additionally, temporary activities include coastal protection and beach rehabilitation, natural resource exploration (oil and gas), seasonal population increase due to intensified summer tourism (14 resorts), and, more recently, the side effects of the war in Ukraine (e.g., an increase in the number of ships in the Romanian area) (OECD, 2022). This assessment does not take into consideration the Danube's input.

3.1.3 Pressures assessment

Based on the available emissions data, the primarily monitored pressures encompass substances, litter, and energy themes. These pressures predominantly involve the introduction of nutrients and organic matter, along with releasing substances (such as heavy metals and hydrocarbons) from specific point sources. The most recent WFD assessment within the 2nd River Basin Management Plan indicated moderate to poor status in transitional and coastal waters. Specifically, according to WISE Freshwater information system for Europe, coastal waters deteriorated compared to the previous RBMP cycle).

3.1.3.1 Introduction of nutrients

The Romanian Black Sea coast witnessed a general decline in nutrient intake from wastewater treatment plants. However, 51.4% of discharged wastewater into the Black Sea remains insufficiently treated. Certain areas, particularly neighbouring the biggest WWTP

and port areas, exhibit exceedances of permissible discharge concentrations. Although port zones demand a comprehensive assessment of marine environment quality due to diverse activities, only Constanta Port's treatment plant has currently been evaluated. Neighbouring pollution land sources, Black Sea waters face risks in achieving a "good" environmental status (GES), notably in the biggest WWTP and port areas and seasonally at stations near treatment plant discharges from the southern littoral.

3.1.3.2 Introduction of organic matter

The levels of organic matter (measured as biological oxygen demand – BOD_5 and chemical oxygen demand – COD) in the released wastewater surpass the permitted limits outlined in the national legislation near Mangalia WWTP, Constanta Port, and the OMV Petrom platform, suggesting environmental compliance issues in these areas. The amount of undertreated and insufficiently treated water discharged into the Black Sea contributes to the increased load of organic matter and accumulates with the already recognised risk of failing to achieve GES for Descriptor 5 — Eutrophication.

3.1.3.3 Introduction of other substances – heavy metals and TPHs (Total Petroleum Hydrocarbons)

The annual average concentrations of heavy metals (Cu, Cd, Pb, Ni, Cr) in discharged waters notably rise around the WWTPs near Eforie Sud and Mangalia. Surprisingly, even though larger treatment plants like Constanta Sud and Constanta Nord contribute the most to annual flow, they do not show similarly elevated metal levels. The national legislation was not otherwise breached except for mercury, which exceeded the maximum permissible values in 2017 in effluents from Constanta Sud, Eforie, and Rompetrol treatment plants.

The hydrocarbon values found in wastewater discharged into the marine environment between 2017 and 2018 ranged from 0.053 mg/L to 0.049 mg/L, all well below the maximum limit of 5 mg/L set by the prevailing legislation.

3.1.4 Impact analysis – habitats status against targets, limits, and legislation

3.1.4.1 Pelagic habitat

3.1.4.1.1 Phytoplankton

Blooms (abundances surpassing one million cells/L) of five microalgae species were detected on the continental shelf. Notably, in May 2019, *Skeletonema subsalsum*, *Pseudo-nitzschia delicatissima*, and *Chaetoceros curvisetus* peaked at 2.3, 1.8, and 1.1 million cells/L, near the Danube's mouths. *Planktolyngbya circumcreta*, a cyanobacterium, achieved its maximum density (1.09 million cells/L) in July 2018 in the same area. The coccolithophore *Emiliania huxleyi* reached 1.06 million cells/L in marine waters in July 2017. However, biomass-wise, the waters from the Danube's influence area maintained GES from 2017 to 2019.

Conversely, coastal and marine waters exceeded target values, classifying them as being in non-GES. Thus, the findings underscore the impact of anthropogenic activities on the coastal zone. The recorded proliferation of phytoplankton, notably exceeding target values in coastal and marine waters, points towards ecological stress induced by human-related factors. The increase in densities and deviations from environmental targets in these areas indicate a potential disruption caused by anthropogenic influences. As such, there is a pressing need for comprehensive management strategies to mitigate the adverse effects of human activities on coastal ecosystems and safeguard their ecological integrity.

3.1.4.1.2 Zooplankton

Zooplankton exhibited a prevalent GES, particularly for mesozooplankton biomass, with high percentages in coastal and marine waters. However, the variable salinity waters, being influenced by the riverine input, faced challenges, falling short of achieving GES. In the cold season, we observed all three Marine Reporting Units (MRUs) reaching 100% GES regarding copepod biomass. As an eutrophication indicator, *Noctiluca scintillans* biomass, while indicating GES in all areas during the warm season, experienced an increase in the cold season, when only the marine waters maintaining a GES. These observations highlight different MRUs' seasonal dynamics and potential climate change implications on varying environmental statuses, emphasising the need for targeted management strategies to address specific challenges in each context.

3.1.4.2 Abiotic conditions in seawater

The Romanian waters of the Black Sea did not reach GES in the proportion of 51% (stations out of the total number), representing approximately 45% of the monitored area and approximately 27% of the Romanian waters of the Black Sea (exclusive economic zone) due to the nutrient concentrations. Transitional and marine waters in the north are the most eutrophicated. In coastal waters, GES is not reached in the larger WWTP and Constanta port areas. On the southernmost profiles, Mangalia and Vama Veche, as well as stations on the bathymetric strip 70–100m (Portita, Est Constanta and Mangalia), have predominantly a "good" and "very good" status of nutrients, a condition confirmed by biological elements status (benthic communities from that area).

The influence of discharges from the six coastal sources on the Black Sea waters, focusing on the metals Cu, Cd, Pb, Ni, and Cr, exhibits a range from potentially significant to insignificant. During the investigation of water samples from oil and gas platforms, Ni and Cr in bottom waters revealed slightly elevated levels compared to the background values for marine waters. However, they remained within the permissible limits for marine water quality. In the marine waters, the concentrations of total petroleum hydrocarbons in water samples did not exceed the maximum allowable limit of 200 µg/L as outlined by national legislation, both within the coastal zone and the continental shelf area. Therefore, the overall impact of the investigated metals and discharges on the Black Sea waters demonstrates variability, with some elements approaching significant levels but generally remaining within acceptable thresholds. Additionally, the concentrations of total petroleum hydrocarbons in the marine environment, according to regulatory standards, indicate a relatively controlled impact or too permissive standards.

3.1.4.3 Benthic habitat

3.1.4.3.1 Phytobenthos

The coastal waters had the highest quantitative proportion of opportunistic species (51.5 – 75.5%). Constanta industrialised area is mainly dominated by opportunistic species, primarily from the genera *Ulva* and *Cladophora*, which experience substantial biomass development, especially during the summer due to increased nutrient levels. Notably, in none of the water bodies did the proportion of opportunistic species biomass fall below the threshold value of 40%. Consequently, none of the three water bodies achieved GES between 2017 and 2019. Applying the "proportion of opportunistic species biomass to total biomass" indicator reveals that only 45% of the monitored coastal stations achieved a good ecological status or potential. Thus, the consistently high proportion of opportunistic species and the failure of water bodies to achieve GES highlight the substantial ecological challenges in the coastal areas, particularly in the Constanta industrialised region. This emphasises the need for targeted and proactive measures to address and mitigate the impact of opportunistic species and promote a healthier ecological balance in the coastal ecosystem. The current accepted scientific name for *Cystoseira barbata* has been updated to *Gongolaria barbata*. However, due to the widespread recognition of the species under its former name, the term *C. barbata* will be utilized throughout this document.

3.1.4.3.2 Macrozoobenthos

The M-AMBI (n) values consistently demonstrated GES for transitional waters, from the northern area, with all levels surpassing the threshold (0.61). Evaluation of the ecological status of coastal water bodies revealed a robust result, with 82% of monitoring stations indicating a good status. On the Romanian continental shelf, the ecological status of benthic macrofauna inhabiting circalittoral soft-bottom habitats revealed that 23% of stations exhibited a poor status (M-AMBI*(n) < 0.68). The M-AMBI values consistently describe good ecological conditions in transitional and coastal water bodies, indicating effective ecosystem health. While there are compartments of poor status of communities from circalittoral soft-bottom habitats, most stations on the Romanian continental shelf exhibit good ecological conditions. This suggests a general environmental state but highlights the importance of addressing specific areas to achieve comprehensive ecosystem health.

3.1.4.4 Abiotic condition in sediments

Increased accumulations of Cd and Ni were noted in marine sediments in the vicinity of industrialised areas, such as refineries and ports. In the biggest WWTP and port Constanta areas, the cumulative impact of port discharges and activities is reflected in increased concentrations of heavy metals, especially Cu, Ni and Cd. In the discharge area of the Eforie WWTP, no increased accumulations of heavy metals were recorded, except for Ni. Thus, the impact of discharges of the investigated metals (Cu, Cd, Pb, Ni, Cr), from the six pollution sources on marine sediments can be characterised as ranging between potentially significant and insignificant. In sediment samples from the oil and gas platforms area, heavy metal concentrations fell within the ranges of variation observed at the Romanian seaside. Still, the average Cu, Cd and Ni values for 2017–2018 slightly exceeded the recommended values for marine sediment quality.

Although no exceedances of total petroleum hydrocarbon levels were reported in discharged and marine waters, the maximum allowable limit (100 μg/g) in sediments was exceeded both in the coastal area, in the Constanta South area, but especially in the continental shelf area where hydrocarbon exploitation activities are carried out for a long time (Figure 3).

3.1.5 Evaluation of pressure-impact causal relationships

The matrix of the ecosystem components' sensitivity is a valuable tool for conservation, policy development, and scientific research (Figure 4). It aids in making informed decisions about the management and protection of species and habitats, ensuring the sustainability of ecosystems in the face of various environmental challenges (Goodsir et al., 2015; Korpinen et al., 2019; Quemmerais-Amice et al., 2020). Thus, by categorising habitats based on their sensitivity, the matrix helps prioritise management efforts. Consequently, the ecosystem components identified as highly sensitive may require more immediate and targeted conservation measures to prevent degradation or loss. In the development of the Matrix of the ecosystem components' sensitivity, was adopted the classifications for activities and pressures by referencing previous categorizations established in the Marine Strategy Framework Directive and by the designation of seabed conservation features, as mandated by the Habitats Directive 92/43/EEC. Scores are computed by integrating data from surveys and expert judgment, as highlighted in the degree of certainty feature (Supplementary Tables 2, 3) focusing on criteria such as the extent (surface), the functional impact, the habitat's ability to regenerate, its tolerance to alterations in environmental conditions, and the reversibility of impact. High scores indicate habitats that are highly sensitive and potentially less capable of recovering from disturbance, signifying a need for prioritized conservation efforts. Conversely, lower scores are assigned to more resilient habitats, indicating a lesser immediate need for intervention. This scoring system enables a ranked prioritization of habitats based on their sensitivity, guiding more focused and effective management and conservation strategies.

3.1.6 Prioritisation of pressures

Obtaining the semi-quantitative model and assessing as objectively as possible the causal relationships in which pressures on the marine ecosystem are involved allowed the establishment of the hierarchy of pressures based on the centrality score calculated by Mental Modeler software, considering all causal relationships (activities-pressures and pressures-impacts) and their intensity from the sensitivity matrix (Figure 5). The hierarchy of pressures was achieved by the descending order of "centrality", which represents the absolute value of the influence of pressure in the model. For calculating centrality, Mental Modeler measures the importance or influence of a node within a network by analysing its connections, pathways, and relationships with other nodes, aiding in understanding their impact or prominence in the overall system (Figure 6). Thus, the higher this value, the greater the importance of

Pressures \ Habitats	1	2	3	4	5	6	7	8	9	10	11	12	13
Introduction of non-indigenous species	0.125	0	0	0	0	0.083	0	0.069	0.014	0	0	0	0
Disturbance of species		0									0.028	0	0
Extraction of wild species	0.007	0				0.083		0.028	0.005		0	0.083	0.167
Physical disturbance of seabed				0				0.005	0.005				
Physical loss		0	0.333	0.333	1	0.375	0.625						0
Input of nutrients	0.063	0.007	0	0	0	0	0.009		0	0	0	0	0
Input of organic matter	0.021	0	0	0	0	0.002	0			0	0	0	0
Input of substances	0.063	0.028	0.003	0.003	0.021	0.010	0.042		0.007	0.014	0	0.007	0.007
Input of litter	0.028	0	0	0.010	0.010	0.005	0.005		0.021	0.007	0.002	0.014	0.007

1. Pelagic; 2. Macrophytes; 3. Littoral rock (0-1m); 4. Littoral sediment (0-1m); 5. Mediolittoral coarse or medium clean sand with *Donacilla cornea* (and *Ophelia bicornis)* (0-1m); 6. Infralittoral rock (1-18m); 7. Upper-infralittoral rock dominated by *Cystoseira barbata* (3-10m); 8. Infralittoral coarse, mixed, sand, mud sediment (1-20m); 9. Mussel beds of *Mytilus galloprovincialis* on circalittoral mud and mixed sediments (30-60m); 10. Deep circalittoral shelly mud with *Modiolula phaseolin*a (60-120m); 11. Birds; 12. Mammals; 13. Fish.

FIGURE 4
Matrix of the ecosystem components sensitivity to pressures – Black Sea, 2017–2019.

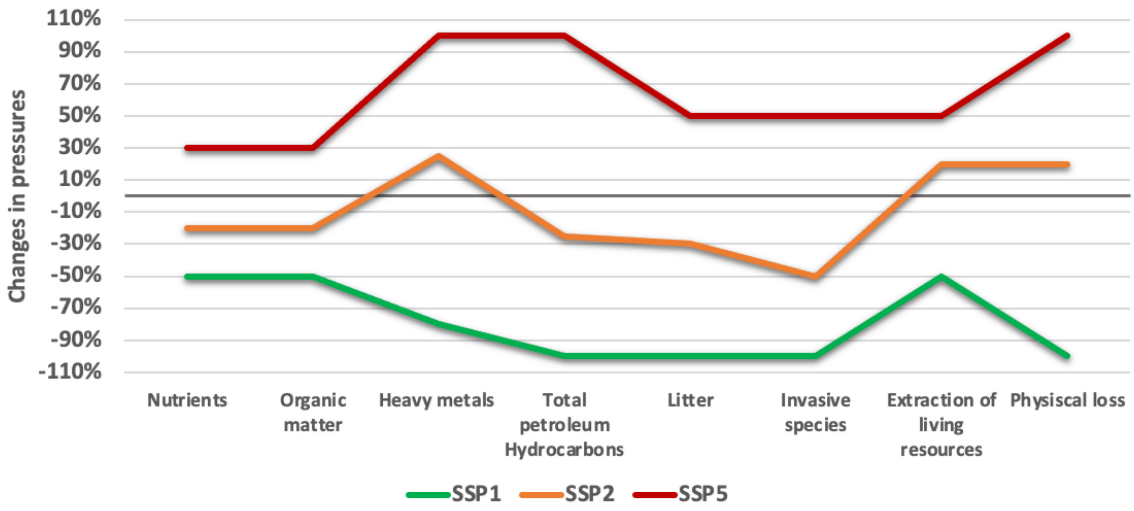

FIGURE 5
Changes in components according to each scenario narrative (negative values stand for decreasing and positive for pressure increasing).

pressure in the model. The model has 29 components – 7 drivers, 13 receivers, 9 ordinary connections, and 64 total connections with a density of 0.08, representing 2.21 connections/components (Supplementary Figure 1).

3.1.7 Cumulative impacts

The pelagic ecosystem is influenced by multiple pressures, with the introduction of invasive planktonic species constituting a 40.7% influence. Nutrient loading and the addition of other substances each have a 20.5% impact. The accumulation of litter and organic debris further exacerbates contamination levels, indicating a significant threat of biological invasions. Macrophytes face substantial threats from the addition of substances (80%) and nutrients (20%). Coastal environments, including the littoral rock (0–1m), littoral sediment (0–1m), mediolittoral coarse or medium clean sand (0–1m), and upper infralittoral rock (3–10m) habitats, experience pronounced effects (99%, 96%, 97%, and 92% respectively) from physical loss due to beach nourishment activities. The infralittoral rock habitat accumulates impacts from various stressors, predominantly from physical loss (67.2%), followed by the introduction of non-native species (14.9%) and impacts from bottom trawling fisheries (14.9%). These fisheries also affect the infralittoral coarse, mixed, sand, and mud sediment (1–20m) habitats, where they contribute to a 27.5% impact, alongside

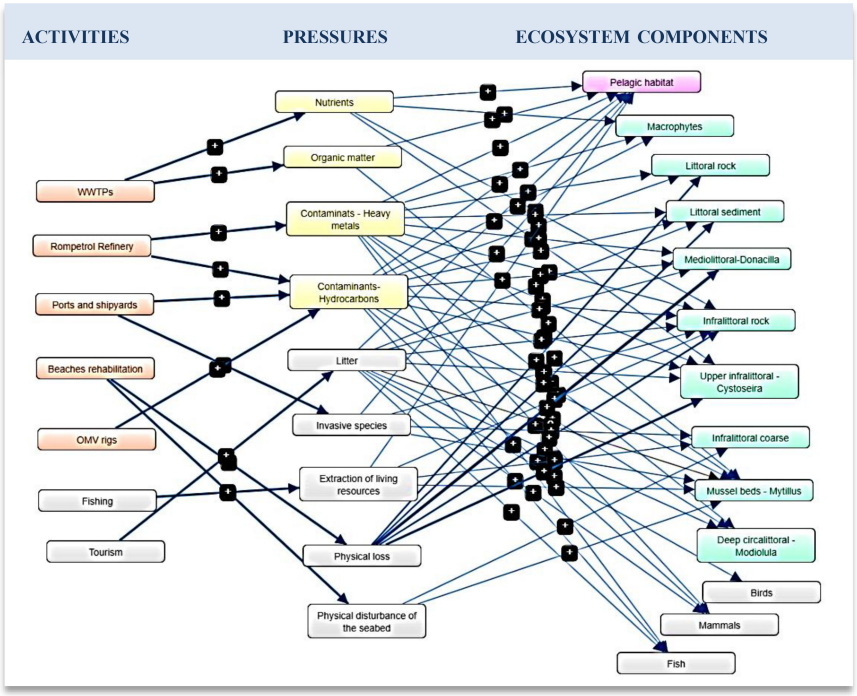

FIGURE 6
Fuzzy Cognitive Map (FCM) of activities (orange)-pressures (yellow) -impacts on the ecosystem components (magenta – pelagic habitat consisting of phytoplankton and zooplankton; green – benthic habitats; grey – species, assessed only by expert judgement-.

physical seabed disturbances (4.9%) and a significant threat of physical loss (67.6%). In the *Mytilus galloprovincialis* beds located in circalittoral mud and mixed sediments (30–60m), a combination of pressures significantly impacts the environment. Here, substance input is the predominant issue (35.6%), followed by the introduction of the non-indigenous Rapana whelk (23.7%), and equal inputs of litter and organic matter (11.9% each). Although the intensity of bottom trawling decreases offshore, its impact, including the extraction of wild species (8.5%) and physical seabed disturbances (8.5%), remains notable. The deep circalittoral shelly mud habitat, inhabited by *Modiolula phaseolina* (60–120m), primarily suffers from substance input (66.7%) and litter (33.3%). Bird populations are predominantly disturbed (93.3%) by various anthropogenic activities, which disrupt natural behaviours, coupled with a 6.67% impact from litter. Mammals are notably affected by accidental captures in fisheries (79.8%), along with substance input (6.7%) and litter (13.5%), highlighting the consequences of human exploitation and incidental harm. Similarly, fish populations are significantly impacted by direct extractions or mortality/injury (92.3%), with additional pressures from litter (3.3%) and substance input (3.3%), indicating the extent of anthropogenic stressors on these species (Figure 7).

3.1.8 Scenarios development

Knowing the sources, pressures and impacts on prevalent ecosystem components and their cumulative effect facilitates the development of scenarios, allowing researchers and policymakers to assess potential future outcomes based on different intervention strategies according to each narrative (OECD, 2016). This foresight is crucial for informed decision-making and long-term planning. In response to these scenarios, we have identified specific variables for each respective Key Performance Indicator (KPIs), which serve as guiding metrics to assess and track environmental impact and sustainability within each scenario (Table 2). The percentage values associated with each scenario typically reflect the likelihood or desirability of that future pathway based on narratives, expert judgment and Romania's profile (https://ssp-extensions.apps.ece.iiasa.ac.at/profile/Romania/development). Thus, KPIs in SSP1 are strongly reduced based on concerted efforts toward environmental preservation and climate change mitigation, alongside stringent policies, drive significant pollution reduction and biodiversity protection in the marine ecosystem. KPIs in SSP2 reflect a scenario where environmental considerations and economic development proceed together, though without the intense focus on sustainability found in SSP1. Finally, for SSP5, KPIs are aligned with prioritizing short-term economic gains over long-term sustainability, which could challenge the health and conservation of the coastal Black Sea environment.

Changes were made individually to each pressure (Table 2) (Figure 5), and the Mental Modeler produced corresponding values (Figure 8) based on the initial model. The Mental Modeler scenario interface (Supplementary Figures 2, 4) shows the relative change in the components included in the model, influenced by the defined relationships in the FCM for each selected scenario. Running scenarios involve changing variables from −1 (significant negative

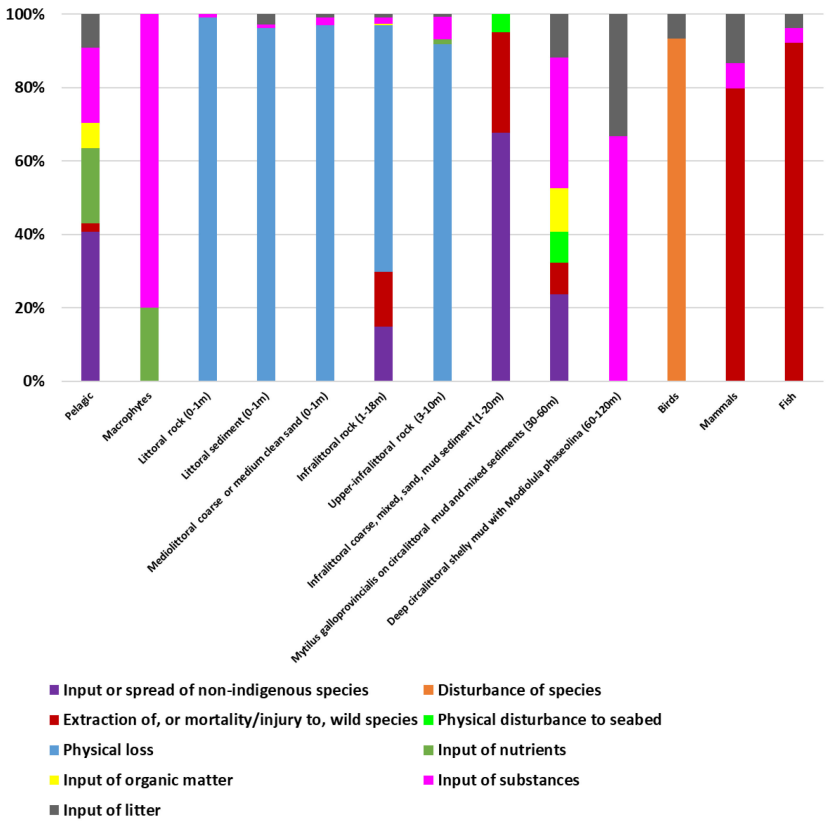

FIGURE 7
Cumulative impacts of different pressures on the Black Sea habitats.

TABLE 2 Pressure variability (associated activities) according to SSPs and estimated associated Key Performance indicators (KPI).

	Pressure	KPI	SSP1 Taking the green road	SSP2 Middle of the road	SSP5 Taking the highway	Activity
1	Introduction of nutrients	Concentration of nutrients in seawater	-50%	-20%	+30%	Urbanisation (WWTPs)
2	Introduction of organic matter	Concentration of organic matter (BOD_5 and COD) in seawater				
3	Introduction of substances (hydrocarbons)	Concentrations of Total Petroleum Hydrocarbons (TPH) in seawater	-80%	-50%	+100%	Ports and shipyards
4	Introduction of non-indigenous species	Number of newly introduced invasive species	-100%	-50%	+50%	
5	Introduction of substances (hydrocarbons)	Concentrations of Total Petroleum Hydrocarbons (TPH) in seawater	-20%	0%	+50%	Rompetrol Refinery
6	Introduction of substances (hydrocarbons and heavy metals)	Concentrations of Total Petroleum Hydrocarbons (TPH) in seawater Concentrations of Heavy Metals in seawater	-80%	+25%	+100%	OMV rigs & gas exploitation
7	Physical loss	Surface	-100%	+20%	+50%	Beaches nourishment
8	Introduction of litter	Beach Litter quantities	-100%	-30%	+50%	Tourism
9	Extraction of living resources	Captures	-50%	+20%	+100%	Fishing

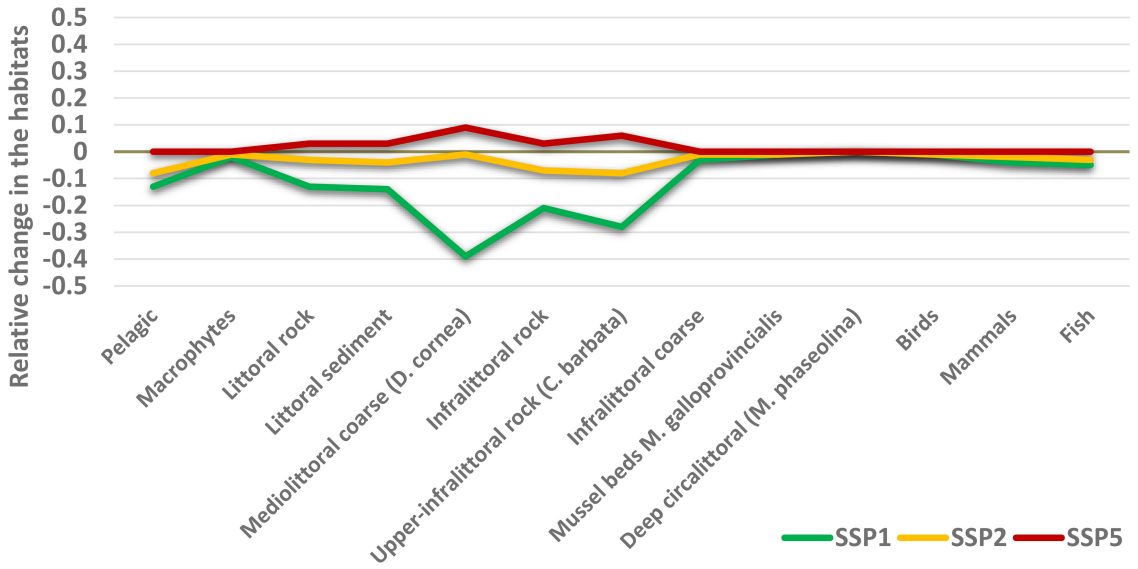

FIGURE 8
Relative changes in the ecosystem components in three scenarios (negative values stand for improvement and positive for degradation) (SSP1 – Taking the green road, SSP2-Middle of the road, SSP5-Taking the highway).

change) to +1 (significant positive change). As a result, a bar graph visually represented the relative system change, displaying how components could respond within the specified scenario (Supplementary Figures 2, 4) (Gray et al., 2013).

4 Discussion

The application of the methodology revealed that the primary pressure is physical loss, with subsequent pressures including the introduction of hydrocarbons and non-indigenous species (Figure 9). The activities associated with these pressures include beach nourishment, maritime transport, port infrastructure, and oil exploitation in the Romanian Black Sea. It is noteworthy to observe that traditional pressures in the region, such as nutrient introduction and fishing (Oguz and Velikova, 2010; Oguz, 2017), have been surpassed by recent beach nourishment projects, maritime transport and infrastructure and oil and gas exploitations. The need for prompt mitigation measures is urgent, as these activities can severely disrupt the marine ecosystem. Additionally, the ongoing conflict in Ukraine, which has increased maritime traffic and opened new corridors for grain exports, together with climate change-induced alterations such as changes in river hydrology, elevated surface temperatures, and altered wave, wind, and current patterns, could further destabilize the ecosystem.

Significant habitat loss has been observed in areas with mediolittoral coarse or medium clean sand, particularly impacting species like *Donacilla cornea*, which only recently reappeared (Micu and Micu, 2006), after nearing extinction between the 1970s and 1980s. Despite attempts at species relocation in 2022 (AON S.R.L, 2022), adverse weather conditions led to poor outcomes. The upper-infralittoral rock habitats dominated by *Cystoseira barbata* have also been heavily impacted by beach rehabilitation works. The habitat of *Cystoseira barbata* is linked to zoobenthos communities characterised by a well-organised structure, diversity, and productivity (Filimon et al., 2016). The loss of these habitats risks

FIGURE 9
Pressures hierarchy according to their centrality (FCM) – Black Sea, 2017–2019.

the complex balance of marine life and could result in irreversible ecological damages, as these species play critical roles in maintaining ecosystem stability (Duffy, 2006).

The introduction of hydrocarbons from port activities and oil and gas exploitation poses significant threats to pelagic habitats, potentially disrupting ecological balances and affecting species distribution and abundance (Perhar and Arhonditsis, 2014). Therefore, it is essential to enforce strict regulations on hydrocarbon discharges to maintain environmental standards and apply penalties for non-compliance.

Marine ecosystems, once significantly impacted, are often difficult to restore even after reducing pressures due to their complex dynamics and variable resilience. Hence, pressure assessments need to be dynamic and straightforward to aid decision-makers (Sinclair et al., 2017). Employing different management scenarios against a baseline provides a practical approach for ecosystem-based management.

Management decisions must aim for substantial reductions in pollutants and stressors, aligning with the "Taking the Green Road" narrative. Achieving a 50% reduction in nutrients and organic matter requires strong political will, stringent legislation, and strict enforcement of regulations against agricultural runoff and industrial discharge. This involves mitigating nutrient pollution, encouraging sustainable farming, investing in advanced wastewater treatment, and monitoring industrial processes to prevent heavy metal discharge. Moreover, a 25% reduction in hydrocarbons and a 50% reduction in heavy metals necessitate comprehensive strategies including strict industrial emissions controls and proper waste disposal. Such measures are crucial to protecting the marine environment, requiring a concerted effort to monitor and regulate industrial activities. While stringent environmental policies can enhance certain habitats and improve ecosystem services, they may also pose challenges to industries and communities reliant on these areas, potentially affecting economic activities and coastal erosion management. On the other hand, the level of awareness and education is remarkably high, and people follow the rules without too much constraint. In this case (SSP1), due to the policy implementation, the most significant decrease in pressure is experienced in the habitat of Mediolittoral coarse or medium clean sand with *Donacilla cornea* (and *Ophelia bicornis*) (0–1m), mainly because the decision to forego beach nourishment and other activities resulting in no more physical loss. Similarly, implementing a strict environmental protection policy could bring improvement in the Upper-infralittoral rock dominated by *Cystoseira barbata* (3–10m) and the Infralittoral rock (1–18m) habitats, leading to ecosystem services improvement by enhanced biodiversity and ecosystem health, carbon sequestration, nutrient cycling, or bioremediation (Farghali et al., 2023) of the coastal waters. However, there might also be negative consequences or challenges associated with these actions. Halting beach nourishment efforts might affect coastal erosion control or impact certain human activities that depend on wider beaches. Additionally, while the strict environmental policy can provide significant advantages for particular habitats, it might pose challenges for industries or communities reliant on these areas for economic activities. Overall, while there are positive aspects to these decisions regarding habitat preservation and environmental protection, there might also be trade-offs or challenges that need to be addressed for a comprehensive understanding of their impacts.

In a moderate scenario (SSP2), management strategies will balance economic growth with environmental protection, imposing moderate restrictions on pollutants and development. This approach aims to reduce nutrient levels, control non-indigenous species, and decrease marine litter, though less effectively than more stringent policies. Encouraging a shift towards renewable energy while maintaining some reliance on traditional sources is also part of this strategy. Moderate increases in habitat disruption from beach rehabilitation and fishing highlight the need for habitat restoration and sustainable land-use to mitigate adverse impacts and promote long-term ecological resilience. Notably, there is no observed reduction in total petroleum hydrocarbons in seawater due to industrial activities, and the contribution from oil and gas development projects is on the rise. Moderate increases have been noted in physical loss from beach rehabilitation efforts and fishing activities (Table 2). In this instance, there is still a positive trend in the condition of the pelagic habitat, along with enhancements observed in habitats like the Infralittoral rock and Upper-infralittoral rock dominated by *Cystoseira barbata*. The pelagic environment also undergoes improvement due to the reduction in nutrient input, although to a lesser extent than in SSP1. The already significant physical loss of habitats should be addressed through various measures, including habitat restoration initiatives, conservation efforts, and sustainable land-use planning. These measures should aim to counteract the adverse impacts of habitat loss by restoring degraded areas, establishing protected zones, and implementing practices that promote ecosystem resilience. Additionally, community involvement, education, and the promotion of responsible resource management plays crucial roles in mitigating habitat loss and fostering long-term ecological sustainability.

Conversely, a rapid growth-focused scenario (SSP5) prioritizes economic expansion over stringent environmental regulations, allowing increased pollution and reliance on fossil fuels. This approach leads to extensive infrastructure development along the coastline, potentially harming natural habitats and biodiversity. A lack of coordinated action may worsen environmental challenges across borders, emphasizing the need for collaborative strategies to address transboundary issues.

The main limitations of the methodology are linked to lack of data and exclusion of socioeconomic data. Addressing these limitations involves a combination of improving data quality, integrating socioeconomic considerations, acknowledging and managing uncertainties, and adopting a more dynamic approach to accommodate temporal variability. These enhancements will contribute to a more robust and applicable methodology for assessing and hierarchising pressures on marine ecosystems for policy-makers decisions.

5 Conclusion

This methodology offers a structured framework to assess and prioritize the impacts of various pressures on the marine environment, aiding decision-makers in developing targeted

strategies. It highlights the complex nature of environmental pressures in the Romanian Black Sea, primarily driven by human activities such as beach nourishment, maritime transport, and oil and gas exploitation. The re-emergence and subsequent threat to species like *Donacilla cornea* illustrate the delicate balance of marine ecosystems and the significant impact of human activities.

The adaptability of this approach under various scenarios enhances its utility in resource allocation and promoting sustainable marine practices. It evaluates potential impacts across different development trajectories, aiding in informed policy-making and sustainable development. Scenarios ranging from strong environmental focus (SSP1) to economic prioritization (SSP5) provide insights into potential future ecosystem management outcomes.

Improving the methodology for hierarchising marine environment pressures involves systematically refining and enhancing its effectiveness by considering diverse perspectives to ensure a comprehensive understanding of the marine environment and its related pressures through stakeholder engagement. The results of the methodology should be included in the dynamic modelling capabilities that account for temporal and spatial variations of marine pressures. Scenario-based modelling integrating socioeconomic issues to capture the complex interactions influencing marine pressures should be implemented to predict potential future impacts under different conditions

Future enhancements should include refining the methodology by incorporating diverse stakeholder perspectives and improving dynamic modelling to account for temporal and spatial variations. This could involve advanced modelling techniques like Ecopat with Ecosim (EwE) to simulate ecological dynamics more accurately, offering a comprehensive view of marine ecosystem pressures and facilitating effective management and cooperation among Black Sea countries.

Data availability statement

The data analyzed in this study is subject to the following licenses/restrictions: Data from sources were directly supplied by the Romanian Water Authority as a partner of the project. The data from marine cruises are restricted under different projects policies. Requests to access these datasets should be directed to https://www.nodc.ro/.

Author contributions

LL: Conceptualization, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. AS: Resources, Writing – review & editing, Writing – original draft. LB: Resources, Writing – original draft, Writing – review & editing. AO: Resources, Writing – review & editing, Writing – original draft. ND: Resources, Writing – original draft, Writing – review & editing. EB: Resources, Writing – review & editing, Writing – original draft. VA: Resources, Writing – original draft, Writing – review & editing. AF: Resources, Writing – review & editing, Writing – original draft. GH: Resources, Writing – original draft, Writing – review & editing. OM: Resources, Writing – review & editing, Writing – original draft. EP: Resources, Writing – original draft, Writing – review & editing. FT: Resources, Writing – original draft, Writing – review & editing. OV: Resources, Writing – review & editing, Writing – original draft. SK: Supervision, Writing – review & editing, Writing – original draft.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1388877/full#supplementary-material

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Impact chains for the deep seafloor: assessing pressures footprint under limited knowledge and uncertainty

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Pressures on the marine environment threaten biodiversity, ecosystem functions and services. Current marine environmental policies, such as the European Marine Strategy Framework Directive, require the assessment of combined effects and the application of ecosystem-based management approaches to maintain or achieve Good Environmental Status (GES) of marine ecosystems. We mapped the major activities and pressures affecting deep-sea benthic habitats in the mainland component of the Portuguese EEZ to assess their combined effects and support decision-making on management and conservation. Activities related to marine traffic, fisheries, and climate change processes are among the most prevalent in the study area. As a data-poor case study, most of the pressure layers were only partially mapped due to a lack of information or the inadequacy of the available data on activities to derive suitable proxies of pressure intensity. Pressures related to chemical changes, chemicals and other pollutants were the most widespread, while abrasion and damage were the most geographically limited. Endogenic pressures dominate in bathyal benthic habitats and decrease their prevalence with depth, while exogenic pressures are more widespread in the abyss than in the bathyal area. Benthic habitats in the bathyal zone, closer to the 200-meter bathymetric contour, consistently exhibited higher combined effect scores, suggesting higher risk of potential impacts on these ecosystem components. Research directed towards these areas is required to assess the state of these habitats and develop conservation and restoration measures, if necessary, to achieve GES. A continuous support for open-access databases containing high-quality, standardized, and harmonized marine data is crucial for future assessments of the combined effects of human pressures on deep-sea ecosystems.

KEYWORDS

combined effect assessment, human activities, climate change, data-poor, deep sea, benthic habitats

1 Introduction

Marine ecosystems are increasingly affected by human activities (Borja et al., 2024), and the deep sea is no exception (Jouffray et al., 2020; Ramirez-Llodra, 2020). The largest biome on Earth is located in the ocean's aphotic zone, below 200 meters depth, and covers approximately 65% of the planet's surface. However, the remoteness of deep sea does not protect this environment from anthropogenic impacts (Benn et al., 2010). Human activities such as fishing and the introduction of pollutants contribute to a multitude of pressures in the deep sea, including physical disturbances, litter concentration, and climate change effects such as ocean acidification and warming (Glover and Smith, 2003; Sweetman et al., 2017). However, our understanding of the deep sea and impacts of anthropogenic activities remains limited because of sampling/observing/monitoring constrains, both technical and logistical, arising from deep sea remoteness and vastness (Paulus, 2021). Nevertheless, it is already acknowledged that the deep sea harbors a rich variety of lifeforms and supports various ecosystem functions and services [e.g., habitat provision, nutrients regeneration, carbon storage (Thurber et al., 2014; Hilmi et al., 2023; La Bianca et al., 2023)].

International organizations and national governments are developing marine environmental policies and adopting mechanisms to address the protection of marine ecosystems while ensure the sustainable use of the ocean [e.g., ecosystem-based management - EBM, maritime spatial planning - MSP (Fraschetti et al., 2018; O'Hagan, 2020)]. At the European level, the Marine Strategy Framework Directive (MSFD) (European Commission, 2008) establishes a framework for EU member states to develop and implement individual marine strategies to achieve or maintain "Good Environmental Status" (GES) in their marine waters. The implementation of the MSFD requires the application of an ecosystem-based approach to the management of human activities, enabling a sustainable use of marine goods and services. For this purpose, comprehensive and consistent information on human activities is needed, as well as information on the resulting pressures and consequent state changes of ecosystem components (Smith et al., 2016; Borgwardt et al., 2019).

The concept of activities and pressures is central to environmental impact assessment and marine management. Activities refer to human actions within the system to be managed, whereas pressures are the mechanisms resulting from activities that directly impact the environment (Elliott et al., 2017). Pressures can be classified as endogenic, if generated within the system under study, or exogenic, if they result from outside the system (e.g., due to climate change or seismic activity) (Elliott, 2011). While endogenic pressures can be locally manageable, exogenic pressures are not and management decisions can only respond to their effects (Elliott, 2011). Another key aspect of the assessment of the impact of human activities and derived pressures is the identification of the ecosystem components (EC) potentially affected (Eastwood et al., 2007). In addition to our limited understanding of the impacts resulting from human activities on the deep sea, our knowledge of the distribution of deep-sea ecosystem components is also basic. The European Nature Information System (EUNIS) developed a comprehensive and hierarchical classification system for benthic habitats considering environmental factors that impact biological communities (Galparsoro et al., 2012). Although the EUNIS classification for deep-sea habitats has been improved (Howell, 2010; Galparsoro et al., 2012), its application in the European broad-scale seabed habitat map (EUSeaMap 2023; Vasquez et al., 2021) still relies solely on depth and substrate information (EUNIS 2019 - level 3), mostly due to a generalized lack of knowledge of the distribution of biological communities at deeper environments to support habitat mapping with higher resolution. The scarcity of readily accessible, long-term, and spatially extensive datasets on human activities and pressures coupled with limited representation of the heterogeneity of the deep-sea benthic habitats, significantly challenges the assessment of the human impacts on marine ecosystems (Smith et al., 2016). Moreover, the absence of reference or other baseline conditions hinders the identification of state changes in ecological indicators.

Several approaches have been developed to support the EBM of marine ecosystems. Spatial explicitly Cumulative Impact Assessment/Combined Effects Assessment (CIA/CEA) approaches, enable the quantification of the combined effects of multiple pressures on the marine environment and guidance to targeted management action [e.g., Halpern et al. (2008)]. These approaches incorporate spatial information on the intensity of human pressures, the distribution of ecosystem components, and the vulnerability of ecosystem components to pressures affecting them. However, applying this approach is not trivial, especially for the deep sea, due to the limited availability of data on anthropogenic activities and pressures affecting this environment, as well as how ecosystem components respond to these pressures (Howell et al., 2020). This makes any attempt to conduct a CEA in a deep-sea area a typical case study characterized by poor data availability (e.g., Rodrigues et al., 2023). Spatial Cumulative Assessment of Impact Risk for Management (SCAIRM) is another CEA approach that calculates Impact Risk (IR) by integrating expert judgment and quantitative methods into a single framework (Piet et al., 2023). Because it allows the integration of qualitative and quantitative information into a single approach, this method is more easily applied in data-poor areas. SCAIRM relies on a linkage framework consisting of impact chains that connect activities to pressures, and pressures to ecosystem components. To calculate the IR, this approach incorporates estimates of Exposure (i.e., the spatial overlap of an EC with a given pressure) and Effect Potential (i.e., the degree to which an EC is likely to be affected by a pressure). However, CEA approaches typically make several assumptions (Halpern and Fujita, 2013) and therefore, the results might be subject to high uncertainty. Hence, assessing the uncertainty of model results is a crucial component of CEA, directly relevant to the management process of ecosystem components (Stelzenmüller et al., 2018; Murphy et al., 2024).

Located within the Northeast Atlantic Ocean, the Portuguese maritime space holds significant potential for natural resources and cultural heritage (Fernandes et al., 2017). The Exclusive Economic Zone (EEZ) of Portugal extends over 1.7 million km² and is divided

into three sub-areas: the Azores, Madeira, and Mainland Portugal. The Mainland component extends from the continental shelf to the abyssal plain, encompassing several topographic features such as submarine canyons and seamounts. The narrow continental shelf is followed by a steep continental slope, which reduces the extent of the seabed within the 200-2000 m depth bands, culminating in large abyssal plains (Stratoudakis et al., 2019). Two Ecologically or Biologically Significant Areas (EBSAs), considered essential for key ecological functions and processes by the Convention on Biological Diversity (Dunn et al., 2014), are included within the Mainland Portugal EEZ: the West Iberian Canyons and the Banks and Madeira-Tore. These areas are marine hotspots with diverse benthic communities, characterized by enhanced productivity compared to adjacent areas and supporting important spawning grounds for various species. Among deep-sea environments, the Mainland Portugal EEZ hosts vulnerable marine ecosystems (VMEs) indicators and habitat types, such as cold-water corals, sponge aggregations, and cold seeps (e.g., mud volcanoes) (ICES, 2020). Marine Protected Areas (MPAs) have been recognized as key elements in the suite of measures designed to attain GES under the MSFD (European Commission, 2008). Portugal has proposed and/or designated (sensu Grorud-Colvert et al., 2021) over 140 MPAs, encompassing various protection levels and habitats, but fully protected marine reserves are still limited in number and area covered (Stratoudakis et al., 2019). At present, there are no fully protected MPAs in the Mainland Portugal EEZ encompassing deep-sea ecosystems.

Previous studies aiming to assess the combined effect of human activities within the Mainland Portugal EEZ focused essentially within the limits of territorial waters (12 nautical miles) (Batista et al., 2014; Fernandes et al., 2017). Currently, there is no clear picture of the mains activities affecting deep-sea ecosystems within the Mainland Portugal EEZ and resulting impact chains. With this study we aim to (i) map activities affecting the deep-sea areas within the Mainland Portugal EEZ, (ii) determine how these activities generate pressures on deep-sea ecosystems and set a baseline of the pressures effects, and (iii) identify areas with high levels of human impacts that might require conservation and management measures to mitigate negative effects on marine ecosystems.

2 Materials and methods

The study area encompasses the seabed below the 200 meters depth, within the Portuguese EEZ sub-area Mainland Portugal. It includes four MPAs, either proposed or designated, that cover deep-sea regions: the Nazaré Canyon, Gorringe Bank, Amperè - Coral Patch and Mud Volcanoes. The Amperè - Coral Patch MPA partially encompass areas within the Extended Continental Shelf claimed under the United Nations Convention on the Law of the Sea, as well as of the EEZ of the Madeira Archipelago (Figure 1). The data sources about the geographical limits and bathymetric information are identified in Table 1. The coordinate reference system used in this study is the ETRS89-extended/LAEA Europe (EPSG:3035), and the resolution adopted for the data layers is 3 x 3 km.

The CEA was limited to the seabed ecosystem components (i.e., benthic habitats) because the available data on human activities would not provide the depth ranges at which activities occurred for most of the datasets, requiring a different approach to discriminate the effects of the associated pressures across the different pelagic habitats. The list of human activities and pressures occurring or potentially occurring within the study area was derived from a subset of an existing database adapted from Borgwardt et al. (2019).

Data processing and analysis were conducted using QGIS 3.34 (QGIS.org, 2023) and the packages raster (Hijmans, 2024) and sf (Pebesma, 2018) for R (R Core Team, 2024). Data visualization was produced using the R packages ggplot2 (Wickham, 2016), ggOceanMaps (Vihtakari, 2024), ggalluvial (Brunson, 2020) and ggrepel (Slowikowski, 2024).

2.1 Ecosystem component

Ecosystem component data layers were generated from the most updated version of EMODnet broad-scale seabed habitat map for Europe (version 2023). Habitat descriptions were derived from the EUNIS 2022 full description, or from other unpublished classifications where EUNIS 2022 was not applicable as specified in Mickaël et al. (2023). We rasterized the EC spatial data into a 3 x 3 km grid, calculating the proportion of EC coverage area (ranging from 0 to 1) within each grid cell for all ECs present in the cell. This means that within the same area (i.e., grid cell) information for multiple ECs can be available, although it is separated in different data layers, one for each ecosystem component.

2.2 Human activities

Data on human activities were compiled using multiple data sources (Supplementary Table S1) drawing on the best available open-access information. When information of human activities was available for more than one year, we calculated the average across the entire time range, except for climate change. We should also mention here that this study considered the recent past to select data for mapping only "current" activities. However, the term "recent past" encompasses a broad timeframe, especially considering the slow dynamics of deep-sea environments and the poor temporal resolution of the information available. Original datasets were processed into a raster format with 3 x 3 km resolution prior to CEA analysis as detailed in the sub-sections below. A summary of processing steps is listed in Table 2. Due to the lack of detailed information to differentiate between specific primary activities (e.g., general vs. operational), the same indicator of activity intensity (e.g., average annual fishing hours) was used for each grouped primary activity (e.g., fishing).

2.2.1 Fishing

To assess the fishing activities footprint, we used data from Global Fishing Watch, which is based on AIS-derived fishing effort and vessel presence datasets (Souza et al., 2016; Kroodsma et al.,

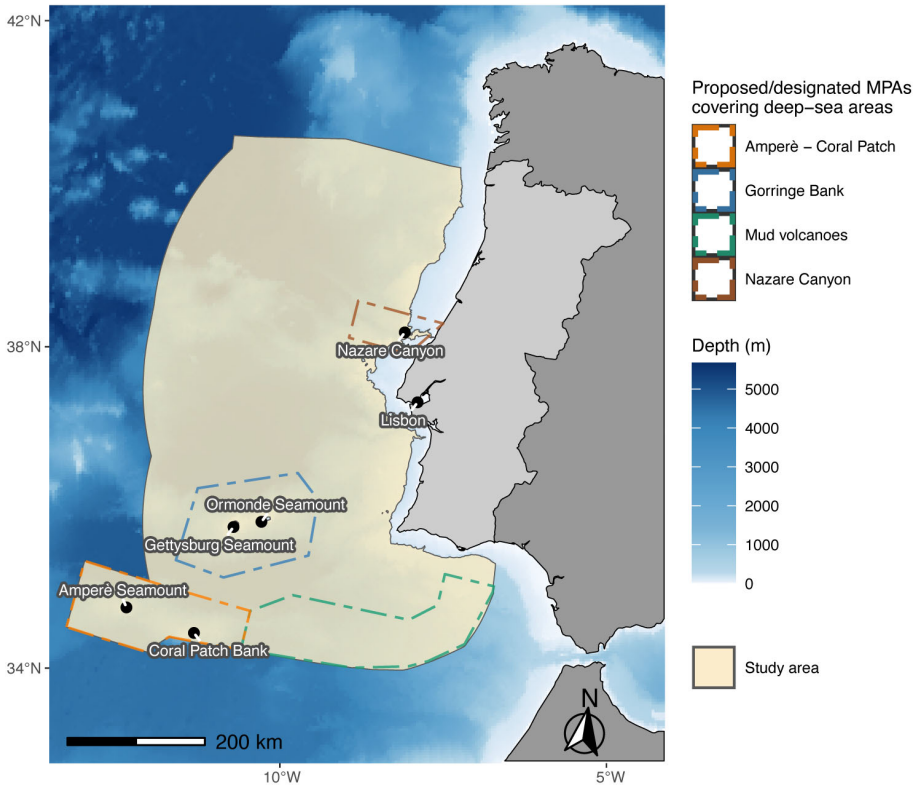

FIGURE 1
Map of the study area, encompassing the Mainland component of the Portuguese Exclusive Economic Zone (EEZ) beyond the 200-meter depth. Dashed lines indicate the spatial limits of four proposed or designated MPAs which include deep-sea areas: Amperè-Coral Patch (including portions of the Madeira Archipelago's EEZ and the claimed Portuguese Extended Continental Shelf), Mud Volcanoes, Gorringe Bank, and the Nazare Canyon.

2018). These datasets cover the period from 2012 to 2020 and allowed to estimate fishing intensity for various fleets: net and fixed gear (including purse seines, set longlines, gillnets, and fixed gear), as well as pelagic longlines and benthic trawlers. We assumed the available data on trawling fishing effort from the Global Fishing Watch database corresponds to benthic trawls within the study area. This decision was based on the locations with identified fishing activity and the composition of the current Portuguese fishing fleet (Campos et al., 2021). The original datasets are provided at a 0.01-degree grid resolution and represent the hours of fishing effort by gear type for each year. We aggregated this data into a 3 x 3 km resolution data layer based on fishing gear and year, and then calculated the fishing intensity for each gear type by averaging the available information across years. Finally, this information was summed whenever more than one gear type contributed to a specific primary activity to produce a single data layer of the activity intensity (e.g., Nets – fixed/set/gillnets/other nets/lines, Supplementary Table S1).

TABLE 1 Data sources for the spatial and political boundaries of the Portuguese Exclusive Economic Zone, proposed deep-sea marine protected areas (MPAs), and bathymetry considered in this study.

Description	Source	Link
Economic Exclusive Zone limits	Marine Regions	www.marineregions.org
Proposed deep-sea MPAs	Directorate-General for Natural Resources, Safety and Maritime Services - DGRM	https://webgis.dgrm.mm.gov.pt/portal/apps/webappviewer/index.html?id=df8accb510bc4f33963d9b03bf3674b8
Bathymetry	European Marine Observation and Data Network - EMODnet	https://emodnet.ec.europa.eu/geoviewer/

2.2.2 Non-renewable energy - oil and gas

Information on the intensity of oil and gas activities was obtained from the Directorate-General for Energy and Geology (DGEG), namely data on seismic survey, piston core samples, and survey/drilling operations. Given the absence of current hydrocarbon exploitation activities within the study area, only proxies for the intensity of oil and gas exploration activity were generated. Due to the absence of data regarding sound propagation resulting from 2D seismic surveys, important for CEA (Carroll et al., 2017), this information was not considered when generating the data layer representing the intensity of oil and gas exploration.

2.2.3 Research

To estimate the intensity of the Research activities in the study area data was sourced from SeaDataNet - Pan-European

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TABLE 2 List of data layers on human activities considered in the study and indicators of activity intensity, along with details on the data processing to generate the respective activity layer.

Primary activity type	Grouped Primary Activity	Specific Primary Activity	Indicator of the activity intensity	Data processing
Exogenous/ Unmanaged (e.g. due to climate change)	Climate Change	Climate Change	Weekly average values of pH, temperature and salinity	Weekly average values were calculated from daily average values
Fishing	Fishing: Benthic trawling and suction/ hydraulic dredges	Benthic trawls and dredges - general (anti-fouling, ballast water, litter, lost gear)	Average annual fishing hours	The original dataset was converted from text files (.csv) with spatial information to a raster format with a spatial resolution of 3 x 3 km. For each gear type, average data for the years 2012 to 2020 were calculated and then summed within the same specific primary activity (e.g., fishing effort of purse seines, other purse seines, set longlines, set gillnets, and fixed gear within the activity "Nets – fixed/set/gillnets/other nets/lines")
		Benthic trawls and dredges - operations (interaction with seafloor, catch, bycatch, waste products)	Average annual fishing hours	
	Fishing: Pelagic trawls and long-line pelagic (including steaming, operations, mooring/anchoring)	Long-line pelagic - general (anti-fouling, ballast water, litter, lost gear, waste products)	Average annual fishing hours	
		Long-line pelagic - operations (catch, bycatch, waste products)	Average annual fishing hours	
	Fishing: Nets, potting/ creeling (set up/ recovery, operations)	Nets (fixed/set/gillnets/other nets/ lines) - general (litter, lost gear, antifoulants, steaming, waste products)	Average annual fishing hours	
		Nets (fixed/set/gillnets/other nets/ lines) - operational (catch, bycatch, waste products)	Average annual fishing hours	
		Nets (fixed/set/gillnets/other nets/ lines) - set up/recovery (interaction with seafloor, atmospheric emissions)	Average annual fishing hours	
Non-Renewable Energy	Oil and Gas	Oil and Gas - exploration (seismic surveys, exploratory drilling and anchoring, oil spills)	Number of sites reported	Geographic position
Research	Research	Research: Operations (specific to activity but can include interaction with seafloor, catch, bycatch)	Geographic position for boreholes, geophysical and multibeam surveys. For fish trawl surveys, activity intensity was determined by calculating the annual average cumulative swept area.	The fish trawl trajectories were estimated from haul initial and final locations. The total number of transects within a grid cell of 3 x 3 km was determined by overlapping the midpoints of the transects with the grid cells. The average swept area was calculated by dividing the total swept area by the number of surveys transects within a grid cell
Services	Military	Military: General (anti-fouling, ballast water exchange, litter)	Average density of vessels expressed as hours per square kilometer per year	Average vessel density from 2017 to 2022 and extrapolated to each grid cell
			Presence or absence defined by delimited areas of military use	Geographic position
		Military: Operations (specific to activity but can include seismic activities, sonar)	Average density of vessels expressed as hours per square kilometer per year	Average vessel density from 2017 to 2022 and extrapolated to each grid cell
			Presence or absence defined by delimited areas of military use	Geographic position
	Shipping	Shipping: Accidents, sinking of wrecks	Number of sites reported	Geographic position
				Average vessel density from 2017 to 2022 and extrapolated to each grid cell

(Continued)

TABLE 2 Continued

Primary activity type	Grouped Primary Activity	Specific Primary Activity	Indicator of the activity intensity	Data processing
		Shipping: General (anti-fouling, ballast water exchange, litter, Mooring)	Average route density expressed number of routs per square kilometer per year	
	Telecoms and Electricity	Telecoms and Electricity: Communication and electric cables - active operational (localized electro-magnetic changes)	Cable routes	Geographic position
Tourism/Recreation and Non-Commercial Harvesting		Cruise ships	Average route density expressed number of routs per square kilometer per year	Average vessel density from 2017 to 2022 and extrapolated to each grid cell

Infrastructure for Ocean and Marine Data Management (Schaap and Lowry, 2010), EMODnet - European Marine Observation and Data Network and DATRAS, the online database of trawl surveys of the International Council for the Exploration of the Sea (ICES). From SeaDataNet, we extracted information available for the years between 2014 and 2023, licensed under Creative Commons Attribution 4.0 International, and directed toward the deep-sea floor sampling or mapping, which included only data for multibeam surveys. The data extracted from EMODnet included information on boreholes and geophysical survey lines. As with 2D seismic surveys for oil and gas exploration, no data was available on sound propagation for the geophysical and multibeam survey, therefore this information was not included in the data layer generated to represent the intensity of the Research activity. For the data extracted from DATRAS, since exact trajectories were unavailable, estimated survey trajectories were determined using the start and end locations of the hauls. As swept area values are provided by transect, the midpoint of each transect was used to calculate the activity intensity of fishing trawlers within the intersected 3 x 3 km grid cell. When multiple transects intersected the same grid cell, the cumulative swept area was estimated and divided by the total number of transects. The Research activity intensity layer was constructed by determining the total area affected within each grid cell, after merging potential overlapping areas.

2.2.4 Services

Human activities related to Services identified in the study area include Shipping, Telecommunications and Energy activities, and Military operations. Shipping activity intensity was calculated by summing the routes density of tankers and cargo ships. The original routes density datasets, derived from AIS data, were extracted from the EMODnet database for the years 2019 to 2023 at a 1 km resolution. These data were subsequently aggregated to a 3 x 3 km resolution and expressed as a yearly average of vessel routes per square kilometer. Information for shipwrecks location was also available. Information regarding Telecommunications and Energy activities was obtained by combining data from schematic and actual submarine cable routes. When actual route information was available, it replaced the closest schematic route. The area of coverage in each grid cell was used to encode the intensity of the impacts resulting from this activity. For Military activities, data layers were derived from polygons delineating military areas. Given the intermittent nature of activities within these areas, the derived data layer was encoded as presence-absence information with low confidence. Additionally, information on vessel density related to military and law enforcement vessels extracted from EMODnet was aggregated into a 3 x 3 km grid data layer and encoded as the annual average number of hours per square kilometer.

2.2.5 Tourism - commercial cruises

As for Shipping activities, data on Commercial cruises were obtained from EMODnet. The intensity of related activities was assessed by calculating the routes density of vessel of passenger ships. This density was determined by calculating the average routes density for the years 2019 to 2023, measured as total number per square kilometer per year, and aggregated into a 3 x 3 km resolution data layer.

2.2.6 Climate change

Climate change was the only exogenous activity assessed for its pressures in this study. Data on daily average ocean conditions for seawater temperature, salinity and pH were extracted from the Copernicus Marine Environment Monitoring Service (CMEMS, Supplementary Table S1) for the period between 1993 and 2021. The data include information for 50 unevenly distributed depth layers, ranging from near the sea surface to a depth of 5698 meters. We then calculated weekly averages from this data to derive the pressure layers (see section 2.3.5).

2.3 Pressures

Pressures were broadly categorized into five groups: Physical Change, Biological Disturbance, Chemical Changes, Chemical and Other Pollution, Energy and Exogenous/Unmanaged Processes (Supplementary Table S2). They can originate from single or multiple activities and there is often lack of information to accurately measure pressure magnitude or spatial distribution, leaving little alternative but to use human activity information as proxies of pressures. In this study, pressure layers were estimated

from single or multiple datasets on human activities, each capturing distinct aspects of the same pressure, while some activities could contribute to more than one pressure layer. Moreover, the datasets available within each activity were included in the data aggregation process to generate the pressure indicator layer only if deemed adequate for estimating pressure intensity. Similarly to the activities, the derived layers for pressures reflect the recent past pressures footprint (generally from 2012 onwards), i.e., pressures that are no longer acting or stopped long time ago (e.g., associated deployment stage of a given activity such as cables) were not considered.

To estimate the pressure intensity resulting from activities where only geographic location was available (e.g., point data, cable routes), buffers were applied to estimate the area potentially affected. For piston core samples and survey/drilling operations associated with Oil and Gas exploration, buffers of 10 centimeters and 25 meters (Eastwood et al., 2007) were defined, respectively. For each borehole related to Research activities, a 12.5 cm buffer was defined to estimate the potential impact area (Todd, 2017). The pressures exerted by Telecommunications and Energy activities in the study area were estimated by defining a buffer area of 1.5 meters around the cable locations (HELCOM, 2023). For the shipwrecks we used a 1000 m buffer area around wreck locations to determine the affected area (Lonsdale et al., 2020). Finally, to account for the uncertainty level in the spatial prevalence of the military activity resulting from the dataset defining military areas, the contribution of this dataset to pressure layers was weighted by a factor of 0.5 (Andersen et al., 2013).

All pressure data layers were normalized before use in the CEA analysis to ensure consistent comparability across layers on a 0-1 scale. The normalized pressure layers represent the relative spatial distribution of pressure within the study area. For pressure layers influenced by activities quantified using different metrics, we normalized the individual activity data layers before aggregation, then summed them and renormalized to obtain the final pressure layer (Halpern et al., 2009). Pressure layers were not log-transformed prior to normalization as in Halpern et al. (2008), to avoid enhancing the relative impact of low-intensity pressures (Hammar et al., 2020). Activities with negligible contribution within the study area for a given pressure were omitted from the data aggregation process to produce the pressure data layers (Supplementary Table S2).

2.3.1 Pressure inducing physical change

To generate the pressure layer 'Abrasion/damage', data on trawling fishing and research activity intensity was used. For the pressure layer 'Artificialization of habitat', datasets for submarine cables and shipwrecks were considered. Datasets contributing to each of these pressure layers were merged to avoid spatial overlap and then intersected with a 3 x 3 km grid to calculate the affected area within each cell. Finally, the pressure layers generated for "Changes in Siltation", and "Smothering" were originated from activities with intensities measured using different metrics (Supplementary Table S2). Therefore, each dataset was normalized, and the layers were subsequently summed and renormalized to create the final pressure layer. No pressure layer was generated for 'Barriers to species movement,' 'Death or Injury by Collision,' or 'Selective Extraction of Non-Living Resources: Substrate (e.g., gravel, mineral resources)' due to their lack of relevance for benthic habitats, insufficient data, or the minor scale of impact in the study area, given the spatial resolution of this study.

2.3.2 Chemical changes, chemicals and other pollutants

The impacts resulting from "Changes in input of organic matter" were estimated based primarily in fishing specific primary activities. Fish discards and the deleterious effects of fishing gear on benthic communities, including injury and mortality, can lead to localized organic enrichment of the seabed (Clark et al., 2016). Data on the operations of benthic trawls, longline pelagic gear, and nets/fixed gears were aggregated to estimate the change in organic matter input resulting from these activities. For this pressure, information from research operations resulting from fishing surveys was also considered. The sources of "Introduction of Synthetic Compounds" and "Introduction of Non-Synthetic Compounds" in the deep sea are multiple (e.g., fishing, maritime traffic, waste disposal, and accidental spillage). For these pressure layers, information from multiple activities was considered, namely fishing activities, shipping and military operations. The pressure layer "Litter" resulted from the aggregation of activities from fisheries, military operations, shipping and commercial cruises. Given their nature and the spatial resolution of this study, the contribution of activities with available data that could result in the "Introduction of Radionuclides" and "N&P Enrichment" was assumed to be negligible.

2.3.3 Energy

Operational power and telecommunication cables equipped with power relays, generate electromagnetic changes in their surroundings. Localized electric and magnetic fields can influence the behavior and migration patterns of species such as elasmobranchs, potentially affecting actions like attraction, repulsion, feeding, and orientation (Hermans et al., 2024). However, the available information for the study area only reports the cables as communication cables, without specifying any energy transmission. Consequently, we did not consider the pressure 'electromagnetic changes' in our analysis. Likewise, the pressure resulting from 'Noise (Underwater and Other)' was omitted from the analysis due to the lack of publicly available data on noise propagation. Sound propagation in water is not linear, instead sound waves are subject to reflection, refraction, and diffraction, altering their trajectory (Erbe et al., 2022). While vessel routes density can provide information on noise energy emission, this data is inadequate for assessing the impacts of underwater noise at the seabed. Nonetheless, increasing levels of underwater noise generated by human activities have negative consequences for marine life. Noise disrupts critical behaviors such as communication, navigation, and feeding, and induce high levels of stress in organisms including whales, dolphins, fish, and invertebrates (Duarte et al., 2021).

2.3.4 Biological disturbance

The pressure layers for "Extraction of flora and/or fauna" and "Translocations of species (native or non-native)" were derived from aggregated data on benthic trawling, fisheries utilizing nets and fixed gears, and fishing surveys conducted in the context of research. For the pressure layer "Introduction of Microbial Pathogens," information was aggregated from benthic trawling, fisheries using nets and fixed gears, and longline fisheries as a result of gear loss and discharge. Additionally, fishing surveys and information on military activity were also included. The "Introduction of non-indigenous species" into the marine environment is facilitated primarily by maritime traffic (Katsanevakis et al., 2023), through ships' ballast water tanks and hull biofouling. Given that this study focuses on the pressures impact on the seafloor below 200 meters depth resulting from human activities, the impact of the introduction of non-indigenous species was considered negligible.

2.3.5 Exogenous/unmanaged processes: temperature, salinity and pH changes

Changes in sea water conditions due to climate change were determined following the method described in Halpern et al., 2008 to calculate a metric of change. To establish a baseline for seawater temperature and salinity levels, we calculated the long-term weekly average for each grid cell within each depth layer using data spanning 1993 to 2021 (i.e., 1515 weeks). We then determined the number of weeks where the anomaly in each variable (i.e., the difference between the weekly average and the long-term weekly average) exceeded the standard deviation for each location (i.e., grid cell) and week of the year. To quantify change over time, we then compared the frequency of positive anomalies between the recent period (2016-2021, 315 weeks) and the early period (1993-1998, 315 weeks). For pH, we employed a similar approach but compared the frequency of negative anomalies (decrease of pH level) between the two periods. Finally, for each variable, data were extrapolated onto the study area's bathymetry at a 3 x 3 km resolution by matching cell grid depths to the closest available depth layer within the variable's dataset, resulting in a continuous representation of near-seafloor conditions.

2.4 Overall impact risk for the study area

The interplay among human activities (A), pressures (P), and ecosystem components (EC) has typically been conceptualized within linkage-based frameworks, facilitating the identification and analysis of impact chains (Knights et al., 2013, 2015). For the activities and pressures with available data, we weighted each APEC chain following the SCAIRM approach (Piet et al., 2023) to estimate the overall Impact Risk by EC. The spatial extent of a pressure was determined by the relative overlap of an activity with the total area of each ecosystem component within the study area. Frequency was estimated as the average number of events per year co-occurring with each EC (e.g., average number of trawl passages/fishing sets per year), using the indicator of the pressure intensity and information from literature (Supplementary Table S3). Magnitude was calculated based on the average pressure intensity within the EC. The value used to define the highest magnitude of a pressure (maximum), necessary to standardize the parameter for calculating the IR, was determined based on the pressure indicator. For indicators based on areas, we used the average area impacted in the EC divided by the total area of the EC. For pressures measured in hours, we used the total number of hours in a year to standardize the magnitude value. For exogenous pressures, we average by the total number of weeks in a 6-years period. For vessels/routes density, we used the maximum density recorded in each EC over the analysis period. Finally, for the military area, defined as presence or absence, we set the magnitude as low to account for the uncertainty of the pressure proxy (magnitude set at 0.01; adverse effects expected but ≤ 1% of maximum).

Dispersal, hazard, behavior, and recovery time were defined using information estimated by expert judgment for the North Sea (Piet et al., 2023). Some degree of interchangeability in the values of these parameters can be expected between regions for the same pressures and ecosystem components, although some differences may exist. The impact risk score (0-1) represents the likelihood that an ecosystem component status or function will decrease by a certain proportion because of a pressure. In this work, the impact risk score was not spatially explicit determined, therefore it does not account for the spatial variability within ecosystem components identified in the study area. This risk score is presented as a complimentary information to the spatially explicit CEA (next section).

2.5 Spatial distribution of combined effects

For the CEA we applied the algorithm developed by Halpern et al. (2008), considering additive effects of multiple pressures. A vulnerability score was used to weight the potential impact of the pressure on a given ecosystem component (Supplementary Table S4). The vulnerability scores represent the relative impact of anthropogenic activities on an ecosystem component when both are present and were selected from Halpern et al. (2007). Considering that, the classification of ecosystem components differed from the original source of the vulnerability scores, we adopted the closest available classification. This correspondence was established based on the bathymetric distribution and substrate type of the EC. For example, "Atlantic upper bathyal rock" was classified as equivalent to 'Hard slope' in the original source of the vulnerability scores. For ECs classified as 'seabed' in the EUNIS, we assumed they were dominated by soft substrate due to their location (e.g., abyssal plains). Similarly, for pressures, we selected the vulnerability scores that most closely matched the related pressure. For example, for changes in salinity levels, we used the vulnerability scores for "thermal change", while for litter, we adopted the scores estimated for "Pollution input: trash, urban runoff". When multiple activities contributed to a single pressure, the vulnerability scores were averaged within each ecosystem component to obtain a single vulnerability value to that particular pressure.

The combined effect in each grid cell was calculated by multiplying the intensity of each pressure by the proportion of the ecosystem component's coverage area (ranging from 0 to 1) and the vulnerability of the respective EC to the pressure being analyzed. We then sum the individual pressure impact scores for each grid cell to obtain the combined effect score.

2.5.1 Uncertainty and sensitivity analyses

To quantify the uncertainty in the estimates of the spatial combined effect assessment and the sensitivity of the model to various settings, we used the open-source software EcoImpactMapper (Stock, 2016). These analyses were based on seven factors related to modelling assumptions and user options: (1) missing data, (2) vulnerability score errors, (3) multiple pressure effect model: additive, antagonistic, dominant, (4) mean or sum over habitats, (5) reduced spatial resolution, (6) improved pressure resolution, and (7) ecological thresholds instead of linear responses of EC to increasing pressure. Uncertainty analysis was conducted using Monte Carlo simulations with 2500 interactions by randomly varying the seven factors. The output of this analysis estimates for each EC and pressure the percentage of simulation runs where each term was among the largest and smallest contributors to overall combined effect scores. Moreover, the simulations help identify areas consistently classified with high and low combined effect scores, using this information to recognize 'hot spots' and 'cold spots' of combined effect (e.g., Murphy et al., 2024). Finally, a sensitivity analysis was conducted to identify the factors that most influence the combined effect model outputs. The sensitivity analysis was based on the elementary effects method (Morris, 1991), as adapted by Stock and Micheli, 2016. A total of 1000 runs with random factor starting points were conducted. The absolute values of the elementary effects from these runs were then averaged for ecosystem components and for pressures to calculate the metric 'mu*', where higher mu* values indicate greater importance of the factor on the estimate of the combined effect model.

3 Results

The study area (i.e., the seafloor below the 200 m depth) includes 92% of the seabed area of the Mainland Portugal EEZ. The combined effect of endo- and exogenic pressures was assessed for a total of 15 benthic ECs (Supplementary Figure S1). Abyssal benthic habitats were the most representative ECs, accounting for 85% of the total area (Table 3), followed by Atlantic lower bathyal seabed (approximately 7%). The remaining ECs together occupy less than 8% of the study area.

TABLE 3 Total area of each ecosystem component identified within the study area, below 200 meters depth.

Ecosystem component	Total area (km^2)	Percentage of coverage
Atlantic lower abyssal seabed	135966.7	45.0%
Atlantic mid abyssal seabed	87119.9	28.9%
Atlantic upper abyssal seabed	33249.4	11.0%
Atlantic lower bathyal seabed	21964.6	7.3%
Atlanto-Mediterranean mid bathyal seabed	14454.2	4.8%
ME62: Atlantic upper bathyal mud	4509.5	1.5%
Atlantic upper bathyal seabed	2522.8	0.8%
Atlanto-Mediterranean mid bathyal mud	999.5	0.3%
ME52: Atlantic upper bathyal sand	668.5	0.2%
ME12: Atlantic upper bathyal rock	215.3	0.1%
Atlanto-Mediterranean mid bathyal sand	130.0	<0.1%
MF62: Atlantic lower bathyal mud	49.4	<0.1%
Atlanto-Mediterranean mid bathyal rock	39.9	<0.1%
ME42: Atlantic upper bathyal mixed sediment	9.4	<0.1%
ME32: Atlantic upper bathyal coarse sediment	0.6	<0.1%

3.1 Activities

From a total of 47 specific primary activities identified as occurring or potentially occurring within the study area, we were able to compile information for 16 (Supplementary Figures S2–S8). The temporal coverage of the datasets used varied depending on the data source. The oldest data refers to 1969 while the most recent records extend to 2023. The oldest records included in the study concerns to seismic survey and boreholes related to oil and gas exploration and research activities. Nevertheless, most of the information is related to the period from 2000 onwards. The most widespread activities in the study area, based on the number of affected cells, are marine traffic (with shipping virtually present everywhere – in 100% of the grid cells – followed by tourism cruises recorded in 81.2% of the study area) and longline fishing (83.7%). The least dispersed activities are shipwrecks (0.4%) and fish surveys (0.4%).

Fishing intensity varied across gear types. Benthic trawls and dredges had the highest fishing intensity (up to approximately 975 average annual hours per km² per year), predominantly in the southern part of mainland Portugal, followed by nets and fixed gears (up to 300 average annual hours per km² per year), concentrated more in the center-northeast of the study area. Pelagic longlines had the lowest fishing intensity recorded (up to around 55 hours, Supplementary Figure S2); however, this fishery is more dispersed across the study area. The most intense pelagic longline fishing activity occurred around the Gettysburg and Ormonde seamounts (Gorringe Bank) and the Ampère Seamount within the Ampère-Coral Patch MPA.

Oil and gas exploration operations concentrated along the continental slope while research activity was more spread throughout the study area. Regarding oil and gas exploration, 61 piston cores and survey operations were identified, affecting less than 0.008 km² of the study area. Additionally, information about six transects of 3D seismic surveys covering approximately 8532 km² (about 3% of the study area) was compiled as well as data about 1047 transects of 2D seismic surveys. However, the total affected area for the 2D surveys could not be estimated. The negligible area affected by these operations or the unsuitable format of the available information to derive adequate proxies of pressures caused by these activities led to the exclusion of information about oil and gas exploration from the estimation of activity intensity and associated pressures and consequently from the CEA. This limitation was also observed for some of the datasets related to research operations. Information about 686 boreholes, representing an affected area smaller than 0.001 km², 23 geophysical survey lines and seven multibeam surveys was collected but not considered in the CEA. The exception was the data from fishing trawling surveys, which was used to estimate the intensity of research operations in the study area. On average, around 19 km² was swept annually.

Within the activities identified for Services and Tourism, shipping and commercial cruises have maximum route densities of 4059 and 76 per km² per year, respectively. These activities were mostly concentrated along the continental slope and more offshore areas along the western coast of mainland Portugal, while in the southern part of the study area, shipping and cruise traffic began to diverge towards the Strait of Gibraltar. For military activity, the vessel density follows a similar spatial pattern to shipping, although at lower densities (maximum density 0.06 average hours per km² per year) and more concentrated in areas closer to territorial waters. Finally, the submarine cable routes cross the study area in various directions, converging in the region closer to Lisbon and Setúbal.

Regarding climate change, the overall variation in average seafloor conditions for salinity and temperature (°C) in the study area was greater during the early period (1993-1998) compared to the recent period (2016-2021, Figure 2). When comparing the two periods for areas where anomalies were detected (Supplementary Figure S9), there is no clear trend in the salinity and temperature weekly averages over time, with differences observed between periods ranging from -0.014 to 0.033, and -0.082 to 0.131, respectively (Figure 2). Conversely, a clear decreasing trend in average pH was observed over time, becoming more pronounced when comparing the two periods, with differences between weekly averages ranging from 0.003 to 0.008. If considering the overall spatial variation for the entire study area, then more clear trends are detected for the three parameters. When analyzing the variation of each variable at the grid cell scale, the differences in the mean weekly averages between the two periods become more pronounced. Salinity and pH present an overall decreasing trend, varying respectively from -1.840 to 0.423, and from -0.082 to 0.019 (Figures 3A, B), while temperature shows increasing trends, with differences ranging from -3.880 to 5.320°C (Figure 3C). During the early period (1993-1998), 45.6% of grid cells displayed at least one week with a positive salinity anomaly that exceeded the standard deviation for a given week of the year. This proportion increased slightly to 48.4% in the recent period (2016-2021). For temperature, 52.9% of cells exhibited at least one week with a positive anomaly exceeding the standard deviation in the early period, decreasing slightly to 51.0% in the period between 2016 and 2021. With respect to pH, the frequency of cells with at least one week with a negative anomaly exceeding the standard deviation increased from 43.9% in the early period to 52.9% in the recent period.

3.2 Pressures

Pressure layers were generated for 14 out of the 27 pressures identified as occurring or potentially occurring within the study area (Figure 4; Supplementary Figures S9–S12). Based on the linkage framework of activities-pressures-ecosystem components, only the pressures related to changes in salinity, temperature and pH were fully represented, encompassing contributions from all the relevant specific primary activities that lead to them. For other pressures, data on contributing activities was either partly available or not used due to result in an inadequate proxy for pressure intensity. Hence, the overall characterization of pressures distribution and intensity in the study area is underestimated and only partially mapped.

The most widespread pressures in the study area, based on the number of affected grid cells, were related to chemical changes, chemicals and other pollutants: litter affects virtually the entire study area (100%), followed by the introduction of synthetic (88.2%) and non-synthetic compounds (87.9%). Additionally, the introduction of microbial pathogens (biological disturbances) was also considerably widespread, impacting 87.9% of the study area. Conversely, the less widespread pressures identified were abrasion and damage (6.2%; physical disturbance) and salinity changes (9.8%; climate change).

3.3 Combined effect assessment

3.3.1 Overall impact risk for the study area

The overall IR calculated using SCAIRM for the study area identified activities related to fisheries, military operations, shipping, and climate change as the main sources of impact (Figure 5). Impact Risk from endogenic pressures decreases with depth, whereas IR from exogenous pressures tends to increase with depth, representing the pressures contributing most to the IR at the abyssal level. Activities related to military operations and shipping, which are the main pressures contributing to the IR at the bathyal level (Supplementary Figure S13), primarily cause chemical changes, pollutants, and other contaminants. These are followed by benthic trawling and dredging operations, where their contribution to the IR results largely from the abrasion and damage of ECs. On the other hand, the exogenous pressure contributing most to the IR in the ECs results from changes in pH. Excluding climate change, the primary activity type

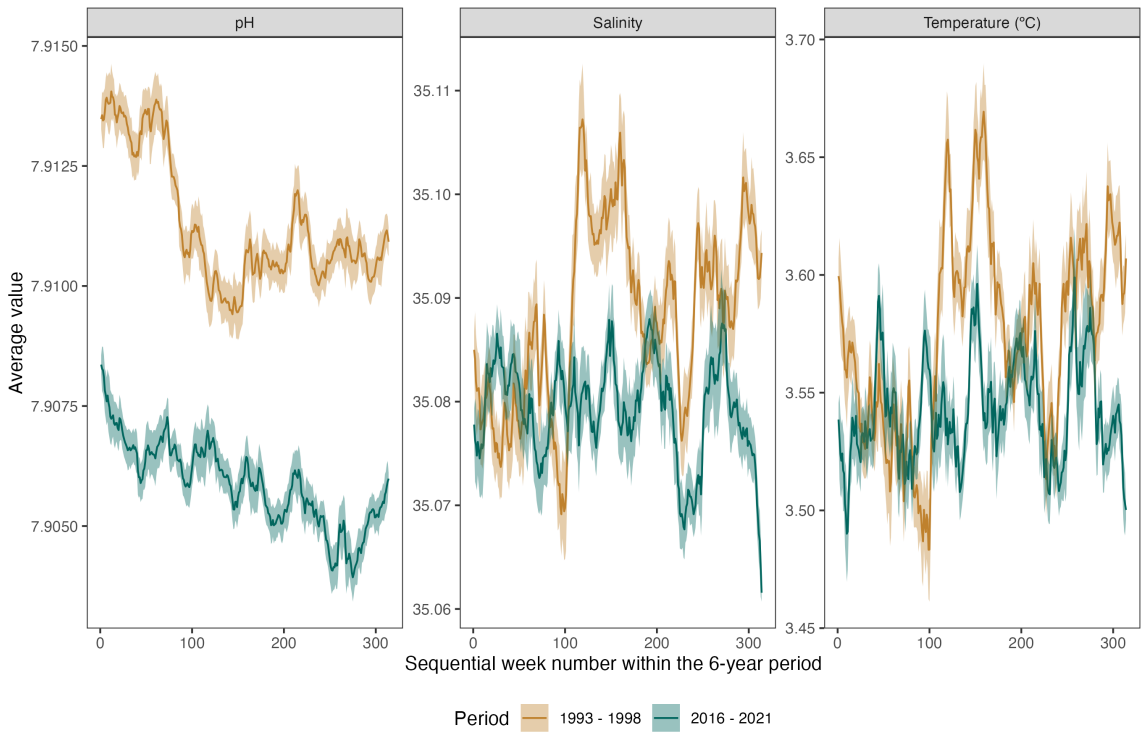

FIGURE 2
Average pH, salinity, and temperature (°C) at near seafloor conditions for the early (1993-1998, brown line) and recent (2016-2021, green line) periods. This analysis was based on grid cells where anomalies – positive for salinity and temperature, negative for pH – exceed one standard deviation at least once in the analysed period. The shaded areas indicate the standard deviation from the mean.

contributors to the overall IR in the study area are Services (55.7%) and fisheries (13.9%). The top three pressures affecting the study area in terms of aggregated IR are litter (44.1%), changes in pH (29.4%), and introduction of non-synthetic compounds (9.2%). The pressures of less concern include salinity changes due to climate change, translocation of species and artificialization of habitat. The average value of IR aggregated by ecosystem components was 0.424 ± 0.266 (mean ± standard deviation). The ecosystem component under the highest IR is the ME32 - Atlantic upper bathyal coarse sediment (0.966), particularly due to risk of impact resulting from litter and introduction of non-synthetic compounds while the least impacted is the Atlantic mid abyssal seabed (0.097), primarily affected by changes in pH level.

3.3.2 Spatial explicit assessment of combined effect

When analyzing the combined effects on the scale of grid cells, changes in pH levels were again identified as among the most important pressures affecting the study area (Supplementary Table S5). Pressures related to chemical changes, chemicals, and other pollutants were also identified as a major pressure class affecting deep-sea ecosystems, with litter assuming the position of the second most relevant pressure. The physical disturbance resulting from changes in siltation was identified as the third most relevant. Changes in salinity levels and artificialization were once again identified as among the least relevant pressures impacting the study area.

The combined effect score (CES) in the study area varied from nearly zero to 15.20 (1.09 ± 1.13, mean ± standard). High-intensity effects were mostly found on the edges of the continental shelf, especially in the south areas located closer to the mainland (Figure 6A). Based on the third quartile of distribution of the CES, the combined effect score was generally below 2.5 (Supplementary Figure S14). When standardized by the area covered by benthic habitats, the ecosystem component with the highest average effect score identified was the Atlantic upper bathyal mixed sediment (CES = 3.12), while the Atlantic mid abyssal seabed had the lowest (CES = 0.06). The shallower benthic habitats were consistently ranked among the most impacted in the study area, in all tested scenarios of the uncertainty analysis (Figure 6B), namely the Atlantic upper bathyal coarse sediment, mixed sediment and rock (>77% of Monte Carlo simulation runs, Supplementary Table S6). Conversely, the more remote Atlantic mid and upper abyssal seabed were among the least impacted ECs (>98% of Monte Carlo simulation runs) with a substantial area defined within the proposed deep-sea MPAs (Figure 6B). When vulnerability of the ecosystem components is ignored in the calculation of the combined effect score, the overall spatial pattern remains consistent (Figure 6C). However, the change in the magnitude of the CES could approach 50%, with larger differences observed in the shallower ECs (Figure 6D). Overall, the combined effect on benthic habitat results from multiple pressures with relatively balanced contributions (Figure 7). However, as depth increases, the number of these pressures decreases, while the contribution of

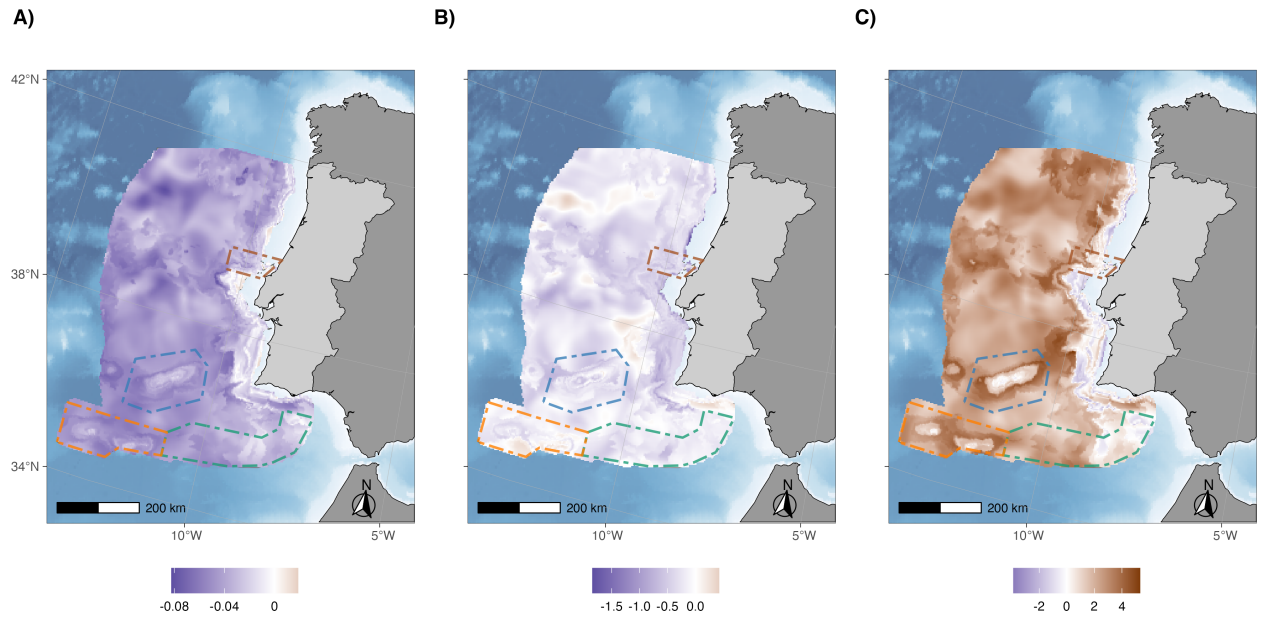

FIGURE 3
Spatialised differences in the mean weekly average (n = 315 weeks per cell) seafloor conditions for **(A)** pH, **(B)** salinity, and **(C)** temperature (°C) between the two 6-year periods: 2016-2021 vs. 1993-1998. Greater differences between means are represented by darker shades.

pressures related to climate change and chemical changes, chemicals and other pollutants gains more influence.

The sensitivity analysis averaged over all ecosystem components and pressures highlighted that, of all the factors tested, the output of the CEA is less influenced by the type of aggregation process chosen (i.e., using the sum of impacts on all ecosystem components in a grid cell or the mean of impacts, Figure 8). Factors such as the use of finer resolution of the pressures data, the type of cumulative model applied (i.e., additive or antagonistic), or the omission of pressures from the model, showed greater influence on the CEA output. However, their influence was lower compared to the impact of assuming linear responses of ecosystem components to increasing pressures rather than ecological thresholds. For the ECs, sigma* values were higher than mu* values, indicating that the effects of these factors on CEA output depended on the values of other factors and the stochastic elements of the model.

4 Discussion

Our understanding of deep-sea ecosystems and their response to anthropogenic pressures remains limited. However, the extensive coverage of deep-sea ecosystems within the European EEZs requires a comprehensive assessment of threats to mitigate pressures and achieve an environmental status aligned with the objectives of the EU Marine Strategy. We mapped multiple pressures occurring in deep-sea areas of the Mainland Portuguese EEZ to identify where they are most pronounced. This information indicates where protection and pressure mitigation measures are most needed and where the ecosystems components are under higher risk of being in poorer conditions.

In the study area, fisheries (i.e., trawling, nets and fixed gear, longlines), shipping, and military operations dominate the bathyal level, contributing primarily to physical disturbances on deep-sea benthic habitats and chemical changes and pollution. Trawling is a well-known threat to benthic habitats. Despite being less prevalent in terms of area coverage in the study area compared to other activities, its negative effects on the benthic ecosystem can be severe. In heavily fished areas, it can lead to the loss of up to 95% of large sessile fauna in heavily fished areas compared to unfished areas (Koslow et al., 2000), reshaping the seabed and provoking sedimentological changes (Durán et al., 2023). These disturbances affect not only the seabed integrity but also the ecosystems functioning (Ramalho et al., 2020) with significant consequences for the GES of the ecosystems (Ramalho et al., 2017; Paradis et al., 2021). Longlines, nets, and traps are less harmful fishing methods for deep-water habitats. However, the amount of lost fishing gear, especially gillnets, is a major problem as they can continue to kill for extended periods. Fisheries were also determined as the primary source of marine litter, for instance, in seamounts present in the study area (Vieira et al., 2015). The amount of litter produced is reportedly different across fishing gear types (Richardson et al., 2022). For instance, according to Eurostat, between 2012 and 2019, the average number of vessels operating trawls in Portugal Mainland was 127. Assuming an average loss of fishing gear of 2120.98 m^2 for bottom trawls annually per vessel (Richardson et al., 2022), the estimated amount of marine litter resulting solely from this activity in all study area would be 0.27 km^2. However, as the number of vessels operating in the area within the remaining gear types (i.e., fixed-nets and long-lines) could not be established, fishing hours per cell was the common indicator available across gear types used as proxy for litter pressure derived from fishing

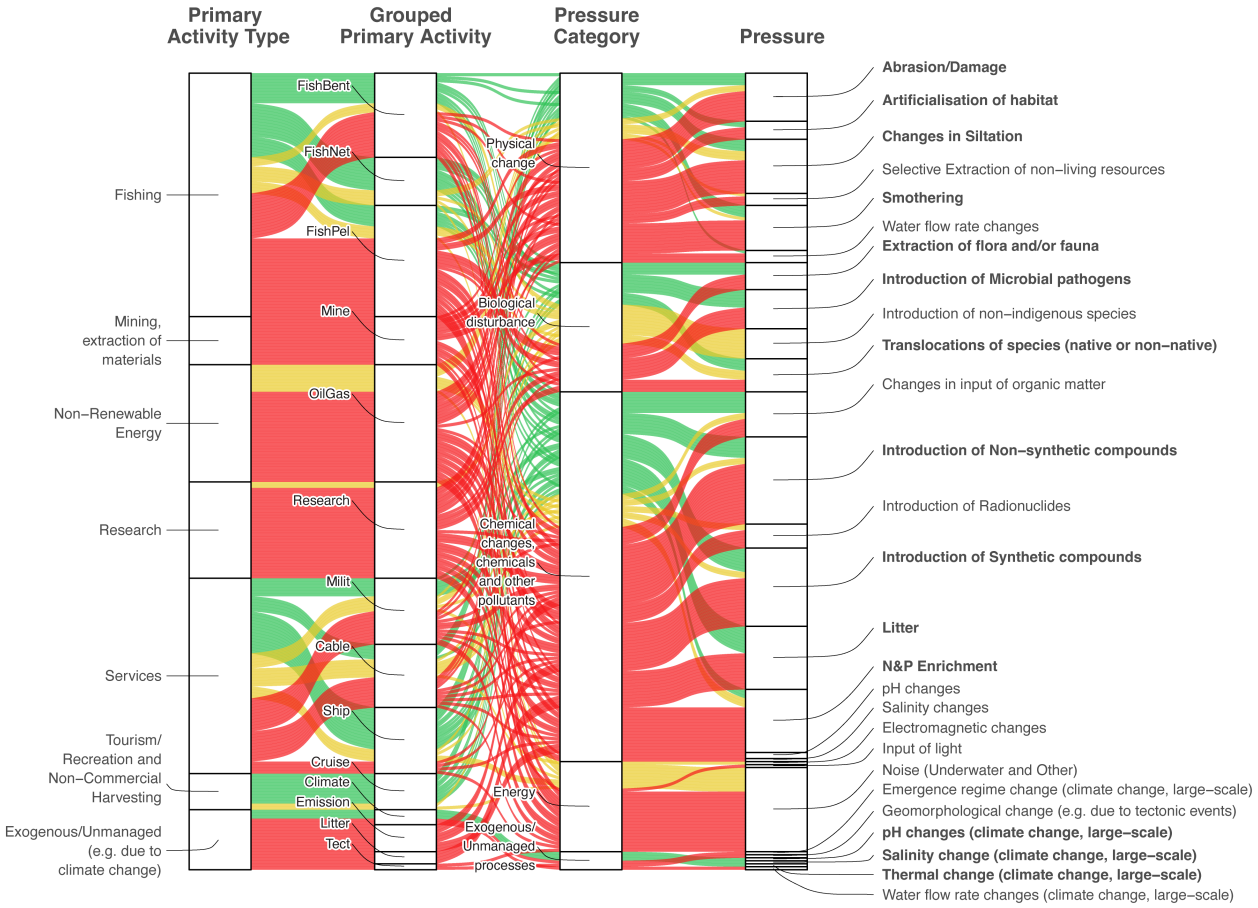

FIGURE 4
Sankey diagram representing the linkage framework of activities occurring or with potential to occur within the study area and resulting pressures. The height of the strata (white boxes) indicates the number of activities represented within each activity/pressure category. Red flows represent activities for which there is no information available. Yellow flows represent linkages with available information on activities but considered inappropriate proxies for estimating the resulting pressures or deemed negligible within the study area. Green flows indicate linkages included in the combined effect assessment. Pressure names in bold indicate the pressures for which data layers were generated. FishBent, Benthic trawls and dredges; FishNet, Nets (fixed/set/gillnets/other nets/lines); FishPel, Long-line pelagic; Milit, Military; Tect, Tectonics events.

activities. Future attempts to generate pressure layers, integrating literature-based information, will enhance future CAE by more accurately representing pressure intensity and combined effects. In addition, when selected indicators reflect more accurately the amount of pressure (e.g., litter) produced by each of the specific activities, they will also support a more efficient evaluation of the impact of the measures implemented to reduce that pressure in the marine environment.

In abyssal areas, exogenous/unmanaged processes related to climate change are the most widespread. These processes led to changes in pH over large areas and, to a lesser extent, changes in water temperature and salinity. Climate change is recognized as one of the top pressures on deep water habitats in regions like the Scotian Shelf in Atlantic Canada and the area influenced by the California Current, due to the widespread distribution and high vulnerability of many ecosystems (Halpern et al., 2009; Murphy et al., 2024). Changes in water conditions near the seafloor, including temperature and pH, can directly impact deep-sea organisms by altering their metabolism and body structure (Sweetman et al., 2017), which can hinder the recovery of ecosystem components from pressures like physical damage. The observed decreasing trend in pH levels in the study area aligns with predictions that by 2100, the North Atlantic Ocean's seafloor below 500 meters may experience a reduction in pH levels greater than 0.2 units (Gehlen et al., 2014). This decrease in pH causes a rise of the carbonate compensation depth (CCD) submerging important geomorphological features, such as canyons and seamounts, below the CCD (Harris et al., 2023). In our study area several of these features are included in proposed or designated MPAs that will not be effective in protecting from climate change, but may minimize the compounded effects with other pressures. In this study, we examined positive salinity anomalies under the assumption that increased salinity poses a higher risk to biological communities. However, the limited understanding of deep-sea ecosystems constrains our ability to accurately assess the impacts of salinity changes (Röthig et al., 2023). Given the overall decreasing trend in this parameter in the study area over time, future assessments may also consider negative anomalies in their analysis.

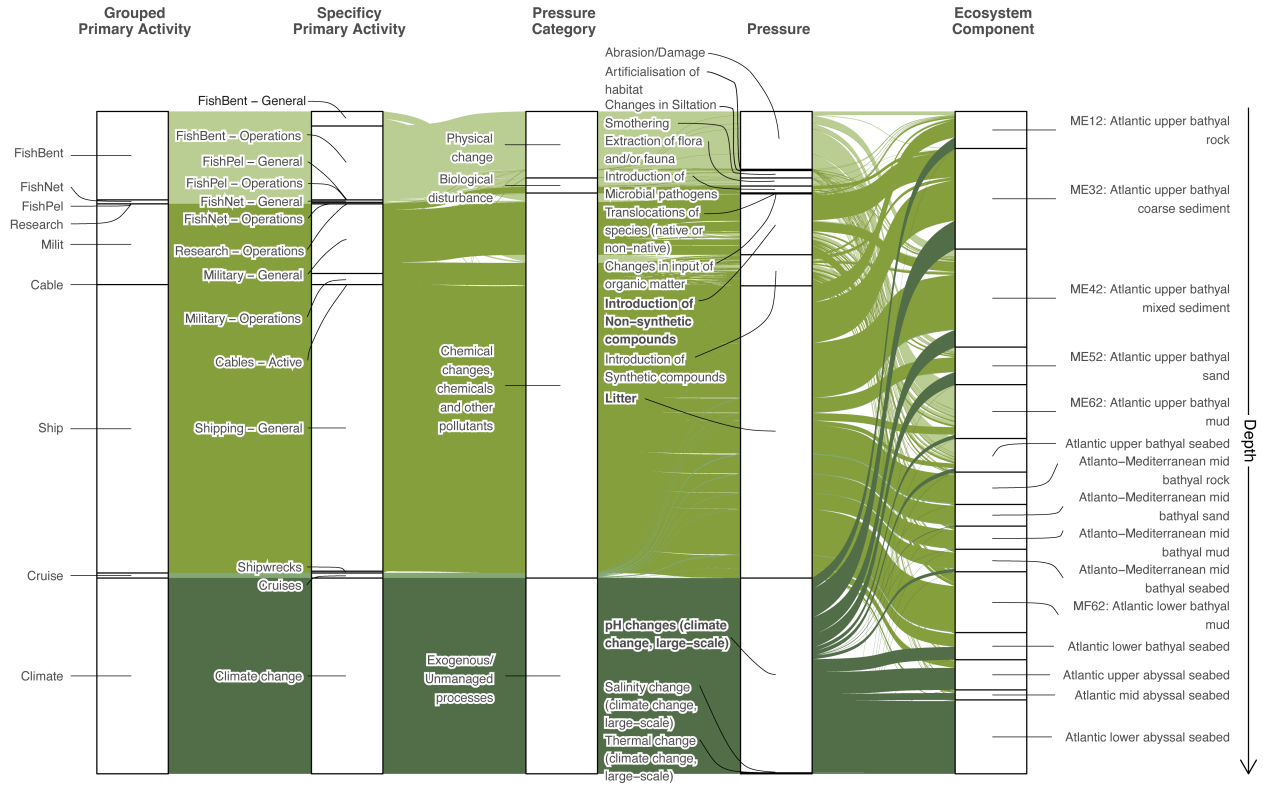

FIGURE 5
Sankey diagram representing the impact chains of activities, resulting pressures and ecosystems components affected weighted according to the Impact Risk (IR) calculated using SCAIRM. The different shades of green group impact chains within the same group of primary activities. The height of the strata (white boxes) corresponds to the value of the aggregated IR. The top three pressures, based on aggregated IR, are highlighted in bold. FishBent, Benthic trawls and dredges; FishNet, Nets (fixed/set/gillnets/other nets/lines); FishPel, Long-line pelagic; Milit, Military.

Although mapped, some activities were only partially represented in this study due to a lack of data or their low frequency. In this study, research activities are one of those examples although a large fraction of the study area remains essentially unexplored (Stratoudakis et al., 2019). Moreover, except for fisheries-related research, research activities generally cause localized impacts of a few square meters (Benn et al., 2010). Other activities that might result in considerable impacts on deep-sea benthic habitats are related to oil and gas operations. Currently, no exploitation rights have been granted in Portugal due to uncertainties related to the economic viability of the operations and public opposition to these activities. No changes on this situation are foreseen (DGEG; Pinto and Castro, 2021) consequently, it is not anticipated that this activity will pose a threat to the benthic ecosystem within the study area in the future. Conversely, the exploitation of mineral resources on the deep seafloor has received increased attention worldwide in recent years (Levin et al., 2020). In the mainland component of the Portuguese EEZ, the presence of Fe-Mn crusts rich in cobalt are reported from seamounts and polymetallic nodules in abyssal areas, although the latter have not been explored for this purpose (Madureira and Ribeiro, 2023). The Portuguese authorities have called for a moratorium on mining in the Area (the seabed and ocean floor and subsoil thereof, beyond the limits of national jurisdiction) but no clear position was yet taken regarding exploiting mineral resources in the seafloor under national jurisdiction. Consequently, potential pressures resulting from these activities, currently absent in the study area, could become threats in the future.

4.1 Combined effect assessment

Overall, the results of the CEA for the entire study area were comparable to the assessment of combined effect at the grid cell scale. However, some differences arise regarding the ecosystem components potentially under higher threat. SCAIRM identifies examples both of bathyal and abyssal ECs among the most impacted, while when using the combined effect score at the grid cell scale, the habitats potentially more impacted are located at the bathyal area. These differences arise from the method used to calculate pressure effects on ecosystem components. The SCAIRM approach we applied estimates the IR for the total area of the EC. For ecosystem components in the bathyal zone with relatively large areas but activities concentrated in specific locations (e.g., benthic trawling), SCAIRM reduces the estimated overall effect of related pressures and tends to attribute more weight to pressures that are widespread.

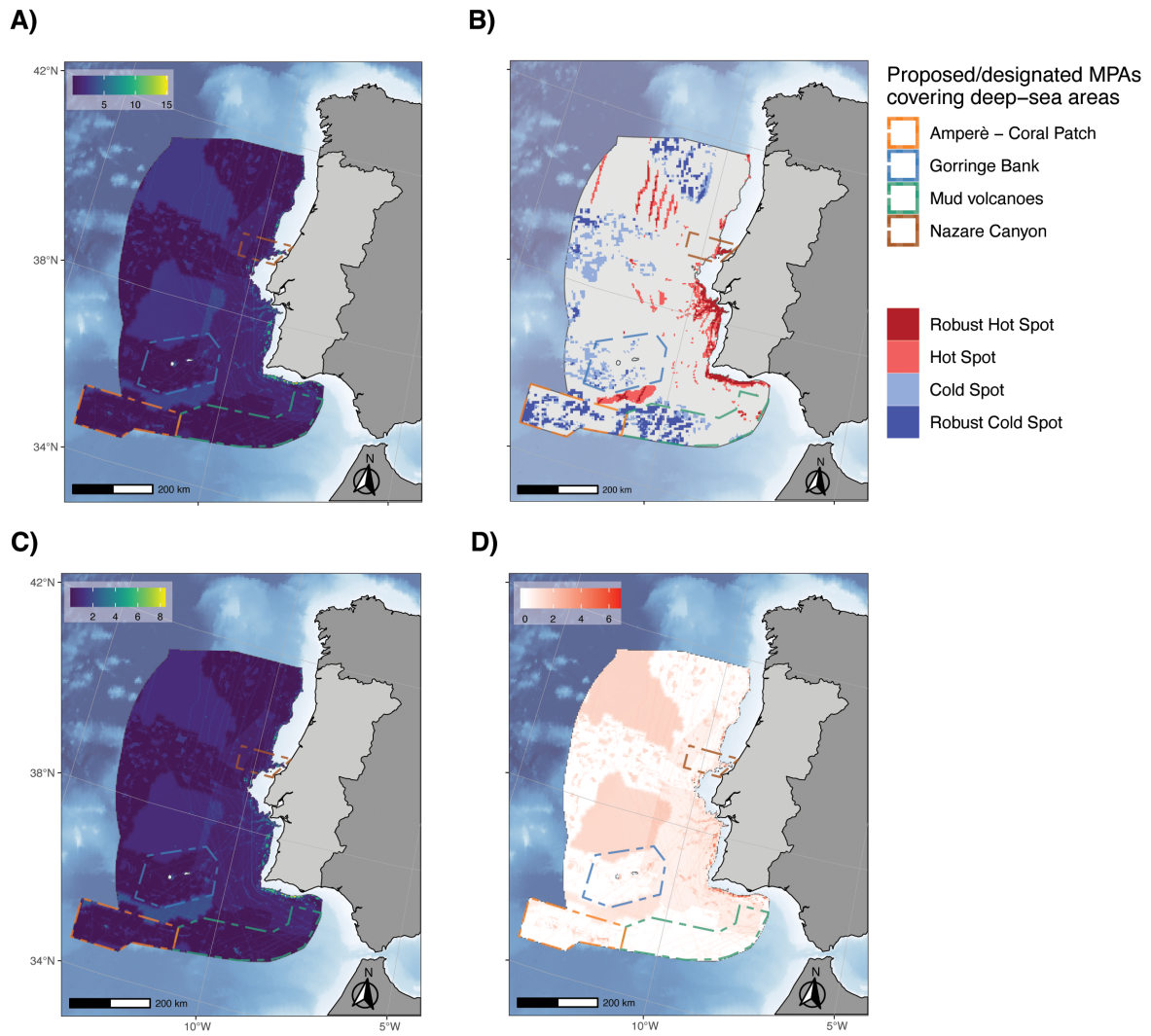

FIGURE 6
(A) Distribution of combined effects across the study area, with warmer colours indicating higher combined effects. **(B)** Hot and cold spots areas of combined effects (CE): hot spots (red shades) represent regions in the combined effect map with CE scores in the top 25th percentile of the combined effects and were identified in at least 75% of 1000 Monte Carlo simulations. Robust hot spots are those consistently appearing in the top 25th percentile in at least 90% of simulations. Cold spots (blue shades) represent areas in the bottom 25th percentile of CE scores, also detected in at least 75% of simulations, while robust cold spots are consistently identified in the bottom 25th percentile in at least 90% of simulations. **(C)** Distribution of combined effects ignoring the vulnerability of ecosystem components to pressures. **(D)** Map showing differences in CE scores between CEA outputs, with and without accounting for ecosystem vulnerability to pressures.

The spatially explicit CEA identified areas in the bathyal zone, closer to the 200 m bathymetric contour and extending from the Lisbon region to the south, as the most impacted. These areas are near shallower waters where a higher concentration of human activities occurs along Mainland Portugal's EEZ (Fernandes et al., 2017). All the three categories of endogenic pressures considered are present in this area (i.e., physical change, biological disturbance, chemical changes, chemical and other pollution). Notably, for most bathyal habitats, no single pressure truly stands out from the others. This could result from multiple factors, including the clustered distribution of human activities, limitations due to poor habitat mapping and the partial availability of information on activities contributing to each pressure. As we move deeper, some pressures gain relevance, particularly those related to physical disturbances (e.g., changes in siltation, smothering) and chemical changes and pollution (e.g., introduction of synthetic compounds and litter). For abyssal benthic habitats, the dominance of some pressures is more evident, particularly the change in pH levels, and again litter and introduction of synthetic compounds. The reduction or absence of the effects of other pressures at abyssal depths can be explained by the distance of these habitats (hundreds of kilometers) from where most human activities take place. However, and despite that this CEA focused on the benthic components of the deep-sea, we cannot disregard the cascade effects from pressures harassing the pelagic environment, particularly those capable of disrupting benthic-pelagic coupling of critical processes such as e.g., nutrient cycling or energy transfer across food webs (Graf, 1989; Griffiths et al., 2017). Such pressures may have indirect implications to the deep

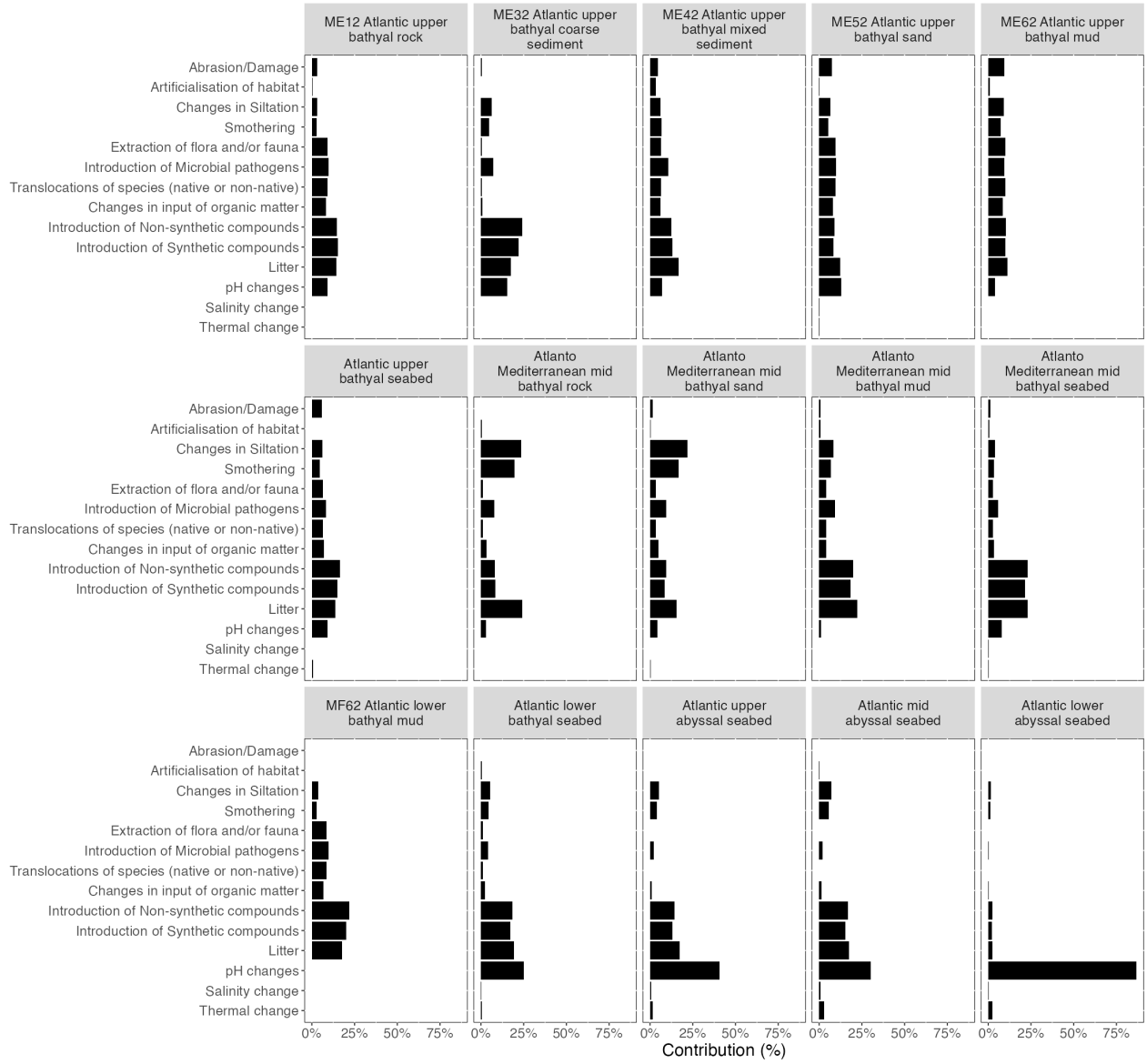

FIGURE 7
Relative contribution of pressures (measured by the number of grid cells affected within the total number of cells impacted) to the combined effect by ecosystem component.

seafloor components (Zhulay et al., 2023; Wurz et al., 2024), through impacts on the water column biotopes or pelagic processes and should be integrated in future assessments.

In addition to the distribution of pressures, the spatial variation in combined effects is also largely influenced by the distribution and relative vulnerability of marine ecosystems (Halpern et al., 2009). The most sensitive ECs occur in the bathyal zone, where the pressure intensity is also higher. Ecosystem components already affected by multiple endogenic pressures face an increased risk of further negative impacts from climate change (Levin, 2019). However, in the study area, the overlap between endogenic and exogenic pressures seems limited so far and synergistic effects have not been considered in this assessment. Vulnerability of the ecosystems to pressures is an important component of the approaches applied here, the SCAIRM (Piet et al., 2023) and the CEA using the Halpern et al. (2008) method. Both methods rely on expert judgement-based criteria to distinguish between degrees of vulnerability as characterized by complimentary elements (e.g., hazard - negligible to highly lethal, behavioral - likelihood of interaction based on avoidance response, time to recovery (ranging, from example from up to a year to over a century). Grasping how hazardous a pressure can be, its functional impact and how resistant are deep-sea communities or creating expectations about behavioral responses of yet unknow species and entire ecosystems let alone their recovery times, calls for highly conservative and precautionary use of vulnerability or sensitivity scores in deep-sea CEA studies (Smith et al., 2020). The poor resolution of global deep-sea environments habitat

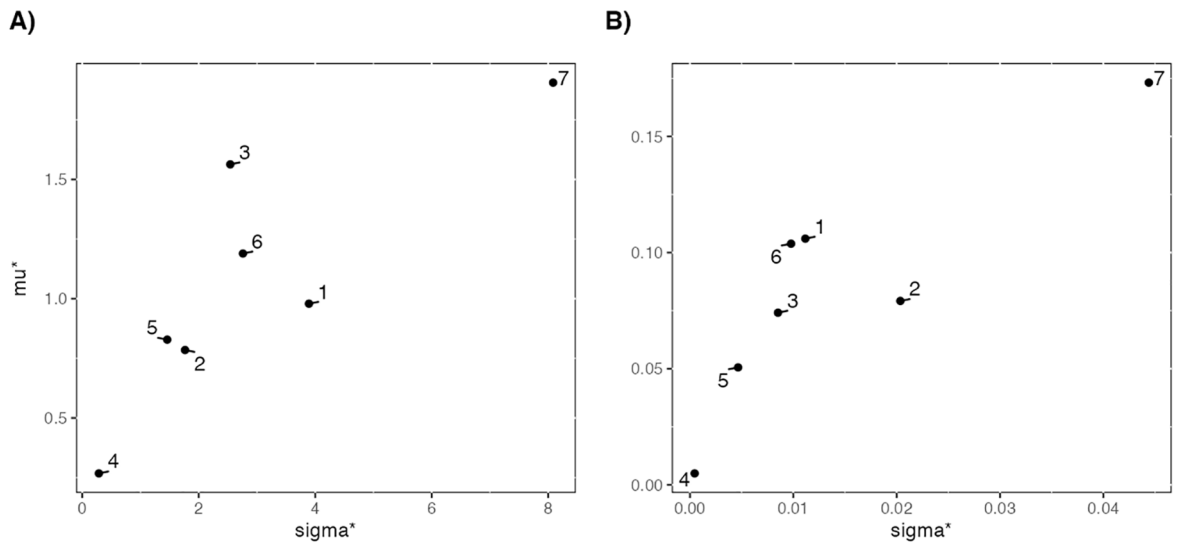

FIGURE 8
The most influential factor for the ranks of **(A)** ecosystem components and **(B)** pressures from most to least impacted according to the sensitivity analysis based on the adjusted elementary effects method. Comparison of the mean elementary effect (mu*, a measure of a factor's overall effect on a model output) and the sigma*, a measure of how much the factor's effect depends on interactions with other factors and random components in the model. 1, missing data; 2, vulnerability score errors; 3, multiple pressure effect model: additive, antagonistic, dominant; 4, mean or sum over habitats; 5, reduced spatial resolution; 6, improved pressure resolution; 7, ecological thresholds.

mapping, which this study so well illustrates, reflects the poor knowledge of deep-sea communities' composition and distribution, and in this context, discriminating and prioritizing based on ecosystems' vulnerability becomes even more challenging.

4.2 Implications for policy

Ensuring the sustainable use of the deep sea is a complex endeavor, given the uncertainty surrounding how deep-sea ecosystems will respond to exo- and endogenic pressures and the consequent implications for the ecosystem services and functions they provide (Armstrong et al., 2019). Achieving this objective is even more challenging when confronted with potentially competing business and policy objectives. Our results provide a snapshot of the recent impacts of multiple pressures, excluding older historical effects and omitting human activities for which data were insufficient, lacking or their presence is limited in space. This baseline serves as a reference point for comparing future combined effect assessments in the study area. As new data become available, these results must be continuously refined to reflect the evolving state of the ecosystem components and address the objectives of the MSFD. The areas identified with higher combined effects should be considered as priority locations for additional research and may require conservation/restoration actions. For instance, the area between 200 and 500 meters depth from the Lisbon region to the south of mainland Portugal is among the most intensively fished in European waters by trawling fleets (Bueno-Pardo et al., 2017; Eigaard et al., 2017). Currently, measures like the European Council EC Regulation 2016/2336, which prohibits bottom trawling below 800 meters for vessels targeting deep-sea fish species, do not protect these highly impacted locations. On the other hand, the decreasing trend in the intensity of human activities and resulting pressures as depth increases suggests that remote areas are potentially in better condition than those closer to the mainland, as observed for deep-sea areas in contiguous Spanish waters (Kazanidis et al., 2020). However, is important to note that the comparison of the combined effects is relative within the study area and not necessary reflect the real state of the ecosystem component (Micheli et al., 2013).

The results presented herein might also contribute to achieve the Aichi and the Kunming-Montreal Global Biodiversity Framework targets of the Convention on Biological Diversity by supporting targeted conservation measures. Of the four proposed or designated deep-sea MPAs, three are consistently classified as cold spots of combined effects. Additionally, these areas experience relatively low levels of exogenic pressures, which are particularly challenging to mitigate, compared to other pressures in the study region. These results indicate that these areas may be among the most suitable for effectively protecting deep-sea benthic habitats in the Portuguese Mainland EEZ. The Nazaré Canyon MPA, however, in its portion that is closer to the shore, is consistently classified as hot spot of combined effects. Considering the role of submarine canyons as transport pathways of litter and chemical pollution from the shelf to the deep-sea, this process deserves especial attention in the next steps of the implementation of this MPA. Similar hot spots of combined effects have been detected in the areas of Cascais, Lisbon and Setúbal canyons. As recognized by the designation of the West Iberian Canyons EBSA (CBD, 2019), these are important areas for the maintenance of biological diversity and ecosystem processes. EBSAs do not confer management obligations, but they do highlight areas where additional management measures may be

appropriate. Our results contribute to prioritizing precautionary efforts and to the design of activity-specific management zones, both within and outside MPAs. Nevertheless, several other points need to be considered when defining Area-Based Management Tools, including MPAs, such as ensuring the representativeness of geomorphic features and benthic habitats (Fischer et al., 2019). The current resolution of deep-sea benthic habitat poorly represents the study area's habitat diversity (e.g., occurrences of cold-water coral and sponge aggregations), due to the lack of biological and ecological data. Addressing this gap is crucial to support the conservation of deep-sea habitats and enhance future CEAs.

4.3 Sources of uncertainty

The reliability of CEA results heavily depends on the quality and accuracy of the underlying data (Halpern and Fujita, 2013; Stock and Micheli, 2016; Korpinen et al., 2021). Data on the distribution of human activities and ecosystem components at appropriate spatiotemporal scales is a fundamental requirement (Solaun et al., 2021). This study is a case study constrained by data limitations. While some data is available, it may not be sufficient to fully characterize all activities and pressures identified or with potential to occur within the study area. Also, ecosystem components within the study area are poorly mapped. The largest proportion of the study area has been classified solely based on bathymetry to distinguish between EC, while the substrate classification has been simplified to 'seabed'. Vulnerable marine ecosystems like habitat-forming species are not identified in the study area using the most recently available EUSeaMap, despite the known presence of VMEs indicators such as deep-sea sponge aggregations, cold-water corals (ICES, 2020). Hence, the low spatial resolution of deep-sea benthic habitat mapping limits our ability to accurately identify and assess the risk of pressure effects. This gap can be partially overcome in the future with more survey effort and ecological modeling techniques (e.g., Morato et al., 2020). Regarding human activities, the AIS data, for example, are a valuable source for mapping the potential fishing footprint, but they may not fully capture the total extent of the activity or all shifts in fishing locations over time (Morgan and Baco, 2021). The same issues apply to pressures; for instance, in addition to the intensity of various human activities (e.g., maritime traffic, fishing), topography (e.g., the presence of submarine canyons) and oceanography determine the concentration of litter in the deep sea (Mordecai et al., 2011; Mecho et al., 2020). Nevertheless, the estimated spatial distribution of combined effects on benthic habitats is expected to accurately represent the actual conditions. Human activities should generally be more concentrated in the shallowest areas and become more diffuse as they extend into deeper regions.

In this study, the overlap of human activities with ecosystem components was used as the baseline to define a proxy for pressures. To reduce the uncertainty of this type of proxies, future studies might also include dispersal/diffusion models to better estimate the pressure extension and intensity in the study area (Loiseau et al., 2021). The sensitivity analysis identified the omission of pressures from the model as a major factor influencing the CEA output. The omission of pressures from the CEA may lead to the misrepresentation of key drivers, resulting in the underestimation of the overall effect score and limiting the effectiveness of mitigation measures. One pressure considered important in marine ecosystems is underwater noise. However, it was not possible to include this pressure in this assessment due to the lack of studies on underwater noise propagation. Nevertheless, despite the potential for widespread underwater noise pollution along major shipping routes, the impact on deep-sea benthic organisms may be limited (Glover and Smith, 2003). Vulnerability scores are a fundamental part of the CEA approach. Evaluating potential negative impacts of multiple human-induced pressures on deep-sea ecosystems depend primary on expert knowledge (e.g., Teck et al., 2010). Nevertheless, expert knowledge is also subject to uncertainty when estimating the sensitivity of ECs to a given pressure. This uncertainty should be considered during the CEA and can be addressed by estimating score ranges based on different sensitivity scenarios to improve the reliability of assessment results and their use for management (e.g., Jones et al., 2018). However, the sensitivity of CEA results to different vulnerability scores was not a major influence in this study. Finally, because pressures often impact ecosystem components in non-linear ways causing cascading effects within ecosystems, approaches based linear models may oversimplify or underestimate the consequences of such impacts (Griffiths et al., 2024). We tested the effect of changing the nature of the pressure effect (i.e., additive, antagonistic, dominant) on the CEA results. The sensitivity analysis identified this factor as the second most influential for the ranking of the ECs. Assuming the interactions among pressures as solely additive may lead, for instance, to an underestimation of combined effects compared to synergistic interactions, potentially resulting in misleading management decisions and increasing risks to ecosystems. Although accounting for the nature of interactions between pressures is crucial to estimate their effect on EC, its implementation remains difficult (Hodgson et al., 2019). Methods based on tipping point detection could help overcome this limitation. However, their application, especially in the deep sea, is hindered by the scarcity of long-term datasets (Orejas et al., 2020). These datasets are essential for comparing current conditions to baseline data and identifying trends over time.

4.4 The way forward

Addressing the multiple pressures on the deep sea requires effective conservation and management measures. However, significant knowledge gaps and governance challenges hinder our ability to adequately manage these pressures and ensure GES of deep-sea ecosystems (Johnson et al., 2018). We identified the improvement of benthic habitat mapping as a primary need to enhance the assessment of cumulative effects in deep-sea ecosystems. The characteristics of deep-sea benthic habitats, such as their low resilience to impact, combined with the absence of baseline information (i.e., habitat distribution, vulnerability and

ecosystem responses to pressure effects) and the lack of long-term data series to evaluate trends, hampers the effective assessment of the environmental status of the deep sea. Enhancing international scientific collaboration through global initiatives like Challenger 150 (Howell et al., 2020) and fostering industry partnerships is therefore essential to address this limitation through monitoring, evaluation and adaptative management. Another important limitation to the application of the methodology followed in this study originates from the availability and quality of data related to activities and pressures, which affect, for instance, the development of more suitable pressure proxies. The continued provision of open-access databases with quality-assured, standardized, and harmonized marine data (e.g., EMODnet, European Atlas of the Seas) is crucial for future attempts to assess the combined effect of human activities and the ecological status of deep-sea ecosystems. Also, the development and increasing availability of global numerical ocean models with high temporal resolution provide valuable hindcast information to estimate climate change trends for various dynamic ocean variables, including those not covered in this study but having a significant impact on marine ecosystems (e.g., dissolved oxygen). This approach is not limited to open ocean areas but can also be applied to coastal marine ecosystems where regional ocean models are available. These models typically offer higher spatial resolution and better representations of ocean conditions, enabling the assessment of combined effects derived from climate change on shallow marine ecosystems. The spatial resolution used in CEA is ultimately determined by the quality of the available data and its relevance to the geographical scope of the assessment. Nevertheless, integration with spatial scales of higher or lower spatial resolution is technically feasible, supporting its application in localized assessments (e.g., management plans for specific Marine Protected Areas) or regional frameworks, such as within the scope of the OSPAR Regional Sea Convention and the North-East Atlantic Ocean marine region under the MSFD.

Data availability statement

The pressures dataset presented in this study is available in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.5281/zenodo.14941432. The original data underlying the pressures dataset were provided by multiple sources cited in the manuscript, including the SeaDataNet Pan-European infrastructure for ocean and marine data management (https://www.seadatanet.org), EMODnet (http://emodnet.ec.europa.eu) and Copernicus Marine Services (https://data.marine.copernicus.eu/products).

Author contributions

FM: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. AH: Conceptualization, Formal Analysis, Funding acquisition, Investigation, Project administration, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. HT: Conceptualization, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Supplementary material

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Risk assessment to Barents Sea ecosystem services: an expert-based approach

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This study aims to investigate the risks posed by climate change and anthropogenic activities on ecosystem services in the Barents Sea, Norway. Using an expert assessment approach, we identify which ecosystem services are at high risk and the human activities and pressures contributing to these risks. The findings indicate that risks vary across ecosystem services, activities, and pressures; however, most are categorized as medium or low. Biodiversity, as a cultural service, and fish/shellfish, as a provisioning service, are identified as the two most threatened ecosystem services. In contrast, educational services are perceived as the least impacted. Temperature change is found to have the greatest impact on the services. Experts are generally uncertain about the risk levels; however, fish/shellfish and biodiversity are the two services associated with the least uncertainty. The results highlight the limited knowledge regarding risks to ecosystem services in the Barents Sea. The study emphasizes the need for future research to address these knowledge gaps and discusses where management efforts should be focused.

KEYWORDS

Barents Sea, certainty, ecosystem services, expert, risk assessment

1 Introduction

Reducing risks to ecosystems from climate change and anthropogenic activities is one of the major challenges of the twenty-first century. The risks posed by climate change to species and ecosystems have cascading effects on aquatic production and on social and cultural systems closely linked to the aquatic environments (Cooley et al., 2022; Campbell et al., 2016). In addition, severe impacts of anthropogenic activities on marine ecosystems have also been detected (Helle et al., 2020; Halpern et al., 2019; O'Hara et al., 2021), which, in combination, may have severe consequences for human communities. Ecosystem-based management (EBM) is advocated as a holistic approach to managing human interactions with ecosystems, with risk assessment being a crucial component to evaluate trade-offs and prioritize issues for management.

Risk assessments have broad applications across various fields. In marine resource management, they can assist in evaluating the risks associated with climate change (e.g., Hare et al., 2016) and other human drivers (e.g., Armstrong et al., 2019), and inform management to avoid critical stock levels (e.g., Patrick et al., 2010). The concept of risk assessment has evolved from understanding how individual risks affect ecosystems to more recent efforts to understand the impact of multiple stressors on a regional to global scale (Halpern et al., 2008; Gissi et al., 2021).

While risk assessments related to ecosystems are becoming more common, very few have been carried out in relation to marine ecosystem services (Armstrong et al., 2019; Gissi et al., 2021; Cooley et al., 2022). Although the demand for ecosystem service input into marine spatial planning is increasing (Ntona and Morgera, 2018), there remains a knowledge gap regarding ecosystem services. This gap is partly due to the concept being relatively young (MEA, 2005) and the lack of clarity around who qualifies as experts to assess these services. An important question is how this increased demand can be met, especially on a blue planet increasingly affected by anthropogenic pressures and resource extraction (Jouffray et al., 2020).

It is also important to note that many risk assessments often overlook crucial elements, such as the assessment of certainty. This omission weakens their reliability and may undermine the "science-based" decisions they are intended to inform. A substantial body of literature has raised concerns about the robustness of risk assessments, particularly in the context of ecosystem services, and emphasized the need to address the issue of certainty (Schägner et al., 2013; Gissi et al., 2021; Jones et al., 2018). Seppelt et al. (2011) pointed out that only one-third of the assessments studied considered certainty, even in the most basic manner. This suggests that certainty assessments remain inadequately addressed in the field of ecosystem services.

This study aims to identify the human activities, pressures, and ecosystem services connected to risk in the Barents Sea. Specifically, we consulted scientific and management expertise related to the Barents Sea to assess the activities and pressures at risk, as well as the ecosystem services affected. Additionally, we examined certainty to determine whether a lack of understanding regarding likelihood and effect results from insufficient knowledge or from a well-understood probabilistic process. Risk assessments can be conducted using various approaches, including qualitative (e.g., Fletcher, 2005; Doubleday et al., 2013), semiquantitative (e.g., Allison et al., 2009), quantitative (e.g., Okey et al., 2015), or a combination of these methods. Holsman et al. (2017) provided an overview of the diverse analytical frameworks used for ecosystem risk assessment. While the quantitative method can generalize whether the risks are statistically significant, the qualitative approach, which primarily relies on expert opinion, enables a deeper analysis of the potential quantitative results.

In this study, we adopt a mixed-method approach. Specifically, qualitative analysis is used to assess risks based on expert judgments regarding various human activities and pressures in the Barents Sea. In addition, quantitative analysis tests the significance of risk ranking differences between services, activities, and pressures. The results show that the risks differ across ecosystem services, pressures, and activities, though most are classified as medium or low. The most threatened ecosystem services are fish/shellfish, as a provisioning service, and biodiversity, as a cultural service. Temperature change has the most significant impact on these ecosystem services. The study also discusses which combinations of risk and certainty levels should be prioritized in management strategies, e.g., focusing on services with high risk and high certainty, or high risk and low certainty.

2 Materials and methods

2.1 Identification of ecosystem services, human activities, and pressures—conceptual framework

To identify human activities, pressures, and ecosystem services relevant to risk assessment, we proposed the Driver–Activities–Pressures–State–Impact (Welfare)–Response (Measure) (DAPSI(W)R(M)) framework alongside the UN Common International Classification of Ecosystem Services (CICES) framework. The DAPSI(W)R(M) framework provides a basis for selecting pressures and activities, and for establishing causal links between these activities, pressures, and the ecosystem studied. In contrast, the CICES framework helps classify the ecosystem services impacted by these activities and pressures.

The DAPSI(W)R(M) framework is a recent and widely recommended conceptual model for marine EBM (Elliott et al., 2017). It refines the Driver–Pressure–State–Impact–Response (DPSIR) approach by addressing key limitations, enabling the identification of more holistic management strategies that can address the linkages between various environmental problems and their associated drivers and pressures (Cooper et al., 2013; Atkins et al., 2011). Within the DAPSI(W)R(M) framework, drivers refer to societal drivers that are related to basic human needs, such as food, energy, and security. These drivers lead to activities (A)—human intervention—that generate pressures, which are the mechanisms of change. These pressures, in turn, cause alterations in the state (S) of the natural system, resulting in certain impacts (I) (on welfare) on the social system that prompt various responses (measures), such as prevention, mitigation, compensation, or other initiatives. Examples of pressures in a marine context include pollution, climate change, and invasive species. The I (on welfare) are measured here as the risk associated with changes in the state of the environment affecting both biotic and abiotic ecosystem services. For the pragmatic application of DAPSI(W)R(M) in this study, we made some simplifications. First, we defined the overall health of the marine ecosystem as the sole indicator of the state. Second, we focused on identifying human activities and natural pressures that can be clearly observed and are indisputable, rather than considering all societal needs of drivers, which may be disputable. Third, we prioritized negative impacts in this study, as these are often highlighted and receive significant attention due to their urgency and the need for intervention. In contrast, positive impacts may be uncertain or difficult to quantify, which presents challenges in establishing causation and thus falls outside the scope of this study.

Ecosystem services were first broadly introduced by the Millennium Ecosystem Assessment (MEA) and defined as "the benefits that people obtain from ecosystems", both natural and managed (MEA, 2005). These services are categorized into provisioning, regulating, cultural, and supporting services. The first three categories have a direct impact on human well-being, while the latter has an indirect impact by supporting provisioning, regulating, and cultural services. Since its release, the MEA has served as a conceptual framework identifying, classifying, and quantifying ecosystem services (ESs) (Armstrong et al., 2012; Costanza et al., 2017; Fisher et al., 2009). Other more recent frameworks, including The Economics of Ecosystems and Biodiversity (TEEB) (TEEB, 2010), the CICES (CICES, 2013), and the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) (IPBES, 2017), have been developed to differentiate, structure, and provide the basis for evaluating ecosystem services (Thurber et al., 2014). To some degree, these frameworks critique the MEA framework, particularly with regard to the inclusion of both direct and indirect services, which may create the potential for double counting values.

We applied the CICES framework (Haines-Young, 2023) because it represents an important step forward compared to earlier classifications provided by MEA (MEA, 2005) and TEEB (TEEB, 2010). First, in CICES, ESs are defined as the contributions ecosystems make to human well-being, distinct from the goods and benefits people derive from them. This framework emphasizes identifying both the purposes and uses people have for the different kinds of ESs. Second, supporting services are excluded from the classification to avoid the issue of "double counting" when linking ecosystem and economic accounts. Third, CICES distinguishes between ESs that depend on living systems (i.e., biophysical ecosystem outputs) and those that involve nonliving (abiotic) parts of ecosystems, which also contribute to human well-being (geophysical ecosystem outputs). The framework also facilitates a clearer identification of the different service categories and their coverage. For this study, we defined and classified all the biotic and abiotic services examined, focusing on the class level of the CICES framework.

2.2 Risk and certainty assessment

Risk matrices are widely adopted structures for risk assessment in marine ecosystem-based management (Cox, 2008). They are commonly used to provide a ranking framework for visualizing and prioritizing risks, guiding resource allocations in a convenient and efficient manner. Different concepts of risk have been discussed in recent years to address the complex interactions and uncertainties associated with climate change and human activities (Oppenheimer et al., 2015; Field et al., 2012; Hobday et al., 2011). In the most common definition, risk is the product of likelihood and effect. Specifically, risk is typically seen as the product of (1) the likelihood that an event will occur, and (2) the effect that event may have. However, recent literature emphasizes the potential pitfalls of the risk matrix, such as risk rating, limitations in resolution, and the possibility of errors (Cox, 2008). Additionally, the risk matrix establishment process often fails to account for the risk attitudes of decision-makers (Ruan et al., 2015; Kaya et al., 2019). Therefore, risk should be viewed as a multivariate construct rather than a scalar. Furthermore, to evaluate risk in a more comprehensive manner, it is recommended that it be viewed in a way that integrates risk attitudes based on utility theory (Ruan et al., 2015).

In this study, we have nonetheless chosen to use the risk matrix method for several reasons. First, despite its limitations, this approach is still widely applied in many fields (Cox, 2008; Duijm, 2015). Second, assessing risk based on utility theory may also be problematic due to what is commonly known as the Allais paradox (Allais, 1953). For instance, people may not always make rational decisions, i.e., based on their utility, but may instead be influenced by cognitive biases that affect their perception of risk (Zhang et al., 2022). This is due to social and cultural relationships, meaning that the opinions of others can influence one's choices (Nick et al., 2019).

We designed the risk matrix based on the principles of weak consistency, betweenness, and consistent coloring, as recommended in more recent literature (e.g., Cox, 2008; Li et al., 2018). Solutions for addressing limitations such as poor resolution, range compression, and ranking reversal errors, which aim to minimize their impacts, are also considered (Figure 1). In addition, we ensure that all risk values

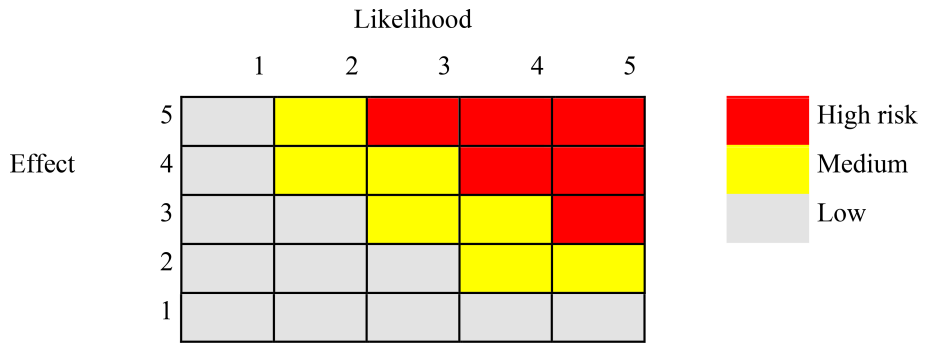

FIGURE 1
Risk matrix.

associated with higher-rated cells are quantitatively greater than those in lower-rated cells. To avoid the issue of scalar risks, we present risk as a graphical combination of likelihood and effect, offering a more comprehensive understanding of the risks involved.

In recent years, there has been increased emphasis on uncertainties concerning risk assessment and management (Brown and Cox, 2011; Aven and Zio, 2011). Criticisms have been directed at the traditional probabilistic approach to risk assessment and management due to its limited scope in addressing risk and handling uncertainties. As proposed by Aven (2017), the general framework for risk description should encompass three components: effect (E), likelihood (L), and background knowledge (K), upon which both E and L are based. This approach to describe risk allows for all types of uncertainty representations and could serve as a basis for a unified perspective on uncertainties within the context of risk assessment.

Following this recommendation, we conduct a certainty assessment in addition to the risk assessment for the study. This allows us to examine whether the lack of effect and likelihood arises from insufficient knowledge (uncertainty) or from a well-understood probabilistic process (risk). Certainty is assessed in the same manner as the risk assessment, i.e., based on experts' judgment using a Likert scale ranging from very uncertain (1) to very certain (5) for all the drivers and ecosystem services.

Despite the growing recognition of the importance of describing uncertainty in risk assessment, there remains a scarcity of practical proposals for assessing uncertainty in relation to risk. One alternative qualitative approach is visualizing uncertainty in risk diagrams, which includes concepts such as the family of risk curves (e.g., Kaplan and Garrick, 1981), uncertainty boxes in probability-consequence diagrams (e.g., Duijm, 2015), and bubble diagrams (e.g., Abrahamsen and Aven, 2011). Recent recommendations favor the use the three-dimensional PCD-PISEA visualization (probability-consequence diagrams with prediction intervals and strength-of-evidence assessments). This method incorporates three dimensions: (i) the assigned likelihood for event occurrence (L), (ii) a prediction for the effect given the occurrence of events (E), and (iii) a measure of the strength of evidence upon which the likelihood and effect assignments are based (K). Here, we propose a three-dimensional visualization using a spider web diagram for judgment. Furthermore, we investigate whether certainty levels for ranking risk between services and between drivers differ significantly from each other. To do this, we perform a pairwise Wilcoxon signed-rank test with two types of correction for multiple testing: Bonferroni correction and False Discovery Rate (FDR). While Bonferroni's correction is conservative, FDR helps avoid false-positive outcomes. This approach is appropriate because the assumption of a normal distribution is not met for the data.

2.3 Barents sea region

The Barents Sea region is a high-latitude shelf ecosystem situated north of Norway and Russia (Figure 2). It covers an area of approximately 1.6 million km^2 and has an average depth of around 230 m. The region hosts a wealth of resources, including oil and gas, minerals, and some of the largest fish stocks in the world. With 5.1 million people living around the Barents Sea and extensive international trade and tourism, a broad range of human activities take place in this region.

The management plan for the Barents Sea was first presented as a white paper titled *Integrated Management of the Marine Environment of the Barents Sea and the Sea Areas off the Lofoten*

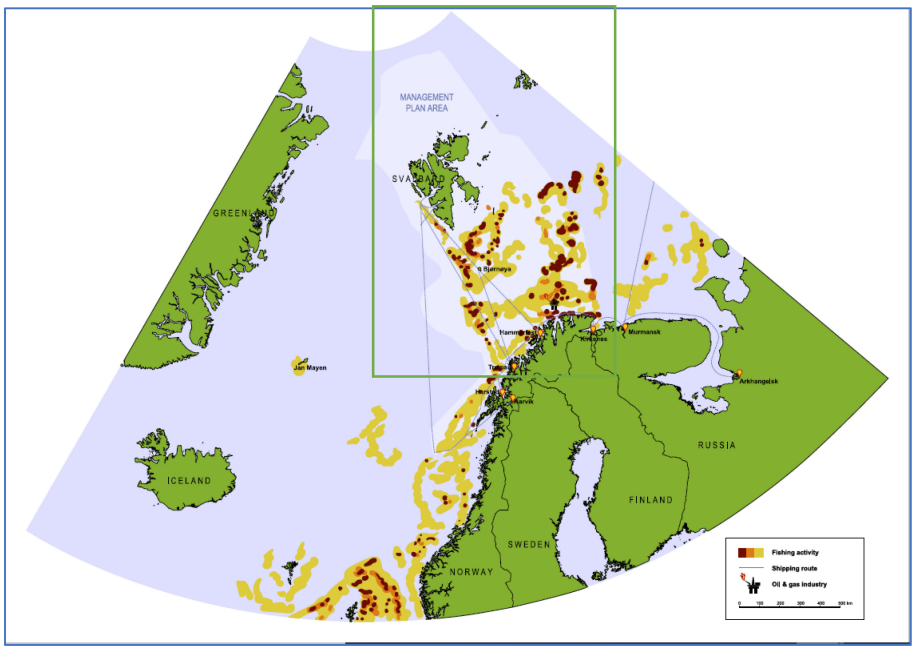

FIGURE 2
Barents Sea region (the green square).

Islands (Report No. 8 (2005–2006) to the Storting) (The Royal Norwegian Ministry of the Environment, 2006). This plan has since been revised, with the most recent update in 2011, in the white paper *First update of the Integrated Management Plan for the Marine Environment of the Barents Sea–Lofoten Area* (Meld. St. 10 (2010–2011) Report to the Storting) (Norwegian Ministry of the Government (2012)). The plan consolidates existing and new knowledge about the main activities, pressures, ecosystems, and services, as well as trends in regional risks. The main activities and pressures in the Barents Sea were also summarized in The Professional Forum for Norwegian Marine Areas (2023).

Accordingly, primary activities in the Barents Sea include fishing, tourism, oil and gas, and shipping. The region is regarded as one of the most productive fishing areas in the world, home to major commercial species such as cod, haddock, and capelin. It is also rich in hydrocarbons, leading to increased oil and gas exploration and extraction activities. This includes drilling operations, seismic surveys, and the establishment of offshore platforms, all of which have raised environmental concerns due to increased pollution, noise, and the risk of accidental spills. As climate change reduces ice coverage, the Barents Sea is becoming more accessible for both petroleum activities and shipping routes. Increased shipping traffic, including cargo vessels and cruise ships, poses potential risks to marine ecosystems (e.g., pollution, vessel noise, accidental spills) and safety. Invasive species, such as the king crab and snow crab, have also been recognized in the region (Husa et al., 2022).

The Barents Sea provides numerous ecosystem services, including the supply of seafood and oil and gas resources, which are vital for local and regional economies. The region plays an important role in climate regulation, carbon sequestration, and water purification (Rogge et al., 2023; Smedsrud et al., 2013). It is also significant for cultural identity, both locally and nationally, and supports educational and research opportunities that enhance public awareness of marine conservation.

However, the region is also impacted by global stressors, such as climate change and long-range pollution. Climate change is evident in the Barents Sea through rising sea temperatures, which alter the distribution, growth rates, and reproductive cycles of marine species. Shrinking ice cover affects habitat availability for ice-dependent species, leading to shifts in food webs and ecological dynamics (Cooley et al., 2022; Mikkelsen et al., 2023). Pollutants, including heavy metals, microplastics, and organic contaminants, are increasingly entering the Barents Sea due to local activities and long-range atmospheric transport. These pollutants threaten marine life and can accumulate in the food chain, posing health risks for humans who depend on marine resources (Frantzen et al., 2022).

2.4 The survey

The survey was conducted by collecting experts' opinions to identify relevant human activities, pressures, and ecosystem services at risk in the Barents Sea, followed by an evaluation of the risks posed by these different pressures and activities on the ecosystem services. The survey was developed specifically for this case, though it was based on a previous Atlantic Ocean deep-sea ES risk assessment (Armstrong et al., 2019).

2.4.1 Step 1: Identification of human activities, pressures, and ESs in the Barents Sea

Scientists involved in this task within the BarentsRISK project (Grant Number: RCN #288192), drawing on the literature review, their knowledge, and expertise, compiled a list of relevant human activities, pressures, and ESs in the Barents Sea, using the DAPSI (W)R(M) framework as the foundation. The following documents were particularly important when identifying the list: the management plan of the Barents Sea presented in the white paper submitted to the Norwegian government in 2006 (The Royal Norwegian Ministry of the Environment, 2006), the summary report on main activities and pressures in the Barents Sea by The Professional Forum for Norwegian Marine Areas (2023), and the recently published article on stakeholders' perspectives concerning the Barents Sea ecosystem (Mikkelsen et al., 2023). This list was then presented to all the experts in the BarentsRISK project consortium during a face-to-face workshop. At the workshop, the concepts of ecosystem services, human activities, and pressures were introduced for reference. The participants then reviewed and discussed the list of ongoing activities, pressures, and ESs that apply to the Barents Sea. Reaching a consensus on the activities and pressures was relatively straightforward. This may be attributed to the fact that most participants were natural scientists working in the Barents Sea, with expertise in studying issues related to pressures and activities. Additionally, the management plan for the Barents Sea, presented as a white paper to the Norwegian parliament, provided valuable guidance. In contrast, achieving consensus on ecosystem services was more challenging, as several ecosystem service concepts are more familiar to social scientists than to natural scientists. Ultimately, we did not reach a definitive conclusion on the number of ecosystem services identified. Instead, we compiled a list of the main potential ecosystem services that most participants agreed upon and introduced a category labeled "Others" for participants to fill out, accommodating differing viewpoints.

Tables 1, 2 present a summary of the activities, pressures, and ESs identified for the Barents Sea, as agreed upon by the stakeholders involved in the workshops. A total of three human activities, three pressures, and 11 ESs were identified.

The identified human activities are fisheries, oil and gas, and shipping, while the three pressures are pollution, invasive species, and temperature change. Fisheries encompass various forms of commercial fishing conducted in the Barents Sea. Oil and gas activities refer to operations related to the exploration,

TABLE 1 Human activities and pressures identified in the Barents Sea region.

Human activities	Pressures
Shipping	Temperature change
Fisheries	Invasive species
Oil and gas	Pollution

TABLE 2 Biotic and abiotic services impacted by human activities and pressures in the Barents Sea region (abbreviations in parentheses), based on the CICES framework.

Services	Biotic/abiotic	CICES code (5.2 version)	Definition
Provisioning			
Fish/shellfish (FS)	Biotic	1.1.1.1	Biomass for nutritional purposes for direct use or processing
Raw material (RM)	Biotic	1.1.1.2	Biomass for materials for direct use or processing
Oil and gas energy (OGE)	Abiotic	4.2.X.X	Geosystem outputs for energy
Waste disposal sites (WD)	Abiotic	5.1.1.4	Geological structures and deposits for storage of anthropogenic wastes
Regulation and maintenance			
Climate regulation (CR)	Biotic	2.2.5.2	Regulation of the chemical condition of salt waters by living processes
		2.2.6.1	Regulation of the chemical composition of the atmosphere and oceans
		2.2.6.2	Regulation of air temperature and humidity
Waste absorption/ detoxification (WA)	Biotic	2.1.1.1	Biotic remediation of waste or toxic substances of anthropogenic origin by living processes
Carbon sequestration/ absorption (CSA)	Biotic	2.1.1.2	Biotic filtration, sequestration, and storage of waste
		2.3.6.1	
Biological control (BC)	Biotic	2.2.2.3	Maintaining or regulating nursery populations and habitats
		2.2.3.1	Pest control
		2.2.3.2	Disease control
Cultural			
Educational (Edu)	Biotic	3.2.1.1	Scientific investigation, education, and training interactions with nature
Existence/bequest (EB)	Biotic	3.2.2.1	Characteristics or features of living systems that have an existence value, or an option or bequest value
		3.2.2.2	
Biodiversity (Bio)	Biotic	3.2.1.3	Elements of living systems that resonate with or support a culture of heritage and aesthetic experiences, hold symbolic meaning, and capture the distinctiveness of settings or their sense of place.
		3.4.1.1	
		3.4.1.2	

X.X, CICES' approach to new or emerging services that are not specifically classified.

exploitation, and installation of associated infrastructure and carbon sequestration storage. Shipping includes the movement of vessels at sea, including the transport of people, goods, and freight within the marine environment. Temperature change could be due to climate change, thermal discharge, or thermal construction affecting water flow (OSPAR, 2022). Pollution arises from various sources, including organic (substances) or inorganic (the compounds of inorganic by-products). There are also a number of different invasive species in the Barents Sea. While only three pressures and three human activities are listed here, these are broad concepts that cover a range of specific activities and pressures. The generality of the pressures and activities reflects both the survey development process and the need for simplification due to the complexity of the risk elicitation.

The study focuses solely on existing, observable, and indisputable human activities for several reasons. First, this approach minimizes respondent fatigue due to the complexity of the risk elicitation. Second, evaluating existing activities provides insights that can inform assessments of potential impacts from emerging sectors. Understanding the effects of existing activities also lays the groundwork for future risk assessments, allowing these insights to be applied to evaluate new activities.

Consequently, activities that have not yet been undertaken in the Barents Sea or are not addressed in the management plan—such as ocean-based aquaculture, deep-sea mining, and offshore renewable energy—are excluded from consideration. Currently, there are no governmental plans for ocean-based aquaculture. Although the government has opened mining opportunities, these are limited to the Norwegian Sea and Greenland Sea, not the Barents Sea. Offshore wind is currently identified in the southern Barents Sea; however, its development is still far in the future, and the specific areas were not yet defined at the time of our assessment. Although marine biotechnology is occasionally mentioned, it is not seen as a critical issue for the marine environments of the Barents Sea, as *in-situ* collection is minimal due to the central role of synthetization in producing commercially viable compounds.

The ESs are classified into three main service types: provisioning, regulation and maintenance, and cultural services. Provisioning

services include four ESs: fish/shellfish, oil and gas/energy, waste disposal sites, and raw materials. Regulation and maintenance services, which play vital roles in regulating ecological processes and maintaining ecosystem balance, consist of climate regulation, waste absorption, carbon sequestration, and biological control. The cultural services are linked to cultural heritage, including educational services, existence/bequest, and cultural aspects of biodiversity. In CICES, each service is identified by a four-digit code with a hierarchical structure. The first digit identifies the "section" (e.g., provisioning), the second the "division" within this "section" (e.g., biomass), the third the "group" within this "division" (e.g., wild plants for nutrition, materials or energy), and the last the "class" within this "group" (e.g., fibers and other materials from wild plants for direct use or processing), as shown in Table 2. It is highlighted that, although we discussed during the workshops what these services could be in relation to the Barents Sea, we did not explicitly define them in the questionnaire. Our intention was to allow respondents—who are experts in the field—to exercise their own judgment in this regard.

2.4.2 Step 2: Score risks

After the list of activities, pressures, and ESs was established, an Excel sheet survey was developed, in which basic, anonymous information about the respondents was collected (e.g., workplace, expertise, years of work/study). This was followed by a matrix in which assessments of the effect and likelihood of all identified pressures and activities in relation to ecosystem services were filled in. The respondents were asked to base their assessments on a 30-year period leading up to 2050. We also asked respondents to rate their level of certainty regarding each driver and service on a scale from 1 to 5, with 1 representing very uncertain and 5 being very certain. To utilize experts' knowledge and minimize bias, we designed an "Other" category under each ES type in the survey, allowing participants to add additional ESs if they had perspectives that differed from the group consensus (see the survey in Appendix 1).

To facilitate experts in scoring risks, we conducted six workshops to introduce the concepts of services, pressures, and activities, provided guidance on scoring during the workshops, and offered additional support afterward if respondents had any questions. Some experts filled in the survey during the workshops, while others submitted it later. Additionally, some sent further queries before submitting the surveys. In total, 25 surveys were submitted after the six workshops.

The experts gathered in the workshops included both natural and social scientists, with the majority being natural scientists who possessed extensive experience working in the Barents Sea. In particular, 21 experts had natural science backgrounds, while the remainder had social science backgrounds, The natural scientists had an average of 12 years of work experience in the field, while the social scientists had an average of 7 years. Seventeen experts were from research institutions, six from universities, and two from management.

The external experts were identified using the snowball sampling method, which begins with one or more study participants and continues through referrals from those participants. This method is particularly useful for reaching hard-to-access populations, such as experts with knowledge related to the Barents Sea, particularly those working in management bodies. In total, eight experts were from the project consortium, while 17 were external. Among the external experts, two had a social science background, and 15 had a natural science background (see Table 3). The two managers, both natural scientists, were also from this external group. Although the data may appear unbalanced due to the small number of social scientists, the majority of participants were external to the BarentsRISK consortium. Furthermore, there is a balance in the number of social scientists across both internal and external expert groups, with two in each group. Although the percentage representation differs, with social scientists comprising 25% of the internal group and 11.8% of the external group, this numerical balance was prioritized to facilitate interdisciplinary integration. This approach overcomes, to some extent, the relatively small size of the social science group compared to the natural science group while also leveraging opportunities to involve more social scientists in the survey process. Some services, pressures, and activities were marked as "nonapplicable". These were given 0 values for both effect and likelihood. Since the lowest effect (1 value-effect) and lowest likelihood (1 value-likelihood) represent very low effect and very low likelihood, it is reasonable to assume a 0 value for both effect and likelihood in nonapplicable cases. Similarly, when a service, pressure, or activity is not applicable, the equivalent certainty may not be identified and is given a 0 value, as the lowest Likert scale measure (1) is defined as very uncertain. For the most part, however, certainty measures were provided by respondents, as these encompass all ESs for each activity and pressure, as well as all activities and pressures for each ES.

3 Results

3.1 Knowledge of respondents

As already mentioned, the data are limited, and there is significant variance in the number of responses for each activity, pressure, and service, making it challenging to compare their likelihood, effect, and consequently, risk levels. We have therefore attempted to assess the lack of response, i.e., the "holes" (or the zero values) in the dataset, to illustrate the differences in knowledge among the respondents across services, activities, and pressures. This is illustrated in Figure 3, which shows a greater number of scored values for the services fish/shellfish and biodiversity, while educational services have more "nonapplicable" values. We also observe that invasives and shipping are marked as "nonapplicable"

TABLE 3 Overview of experts who participated in the survey.

	Total	Natural scientists	Social scientists
Experts within the consortium	8	6	2
External experts	17	15	2
Total	25	21	4

Unit: persons.

for most ESs, whereas pollution and temperature change are on the opposite end of the scale.

3.2 Risk to ecosystem services

In the following, we present the results from two forms of risk associated with pressures and anthropogenic activities identified in the Barents Sea: (1) the risk associated with each activity and each pressure (Figure 4) and (2) the risk resulting from each ES (Figure 5). In Figure 4, the general impression is that all pressures and activities generate risks. Although the levels of risk varied among the pressures and activities depending on the ES being assessed, all risks were medium or low. However, some distinct results emerge. For instance, shipping has the lowest variance in risks, whereas temperature change shows the greatest variance overall. Although temperature change is recognized as a medium-risk pressure, changes in temperature poses higher risk levels to a greater number of ESs than other pressures. Meanwhile, pollution poses a medium risk to most ESs and, in some cases, a low risk. The same situation applies to fisheries and oil and gas activities. Shipping is the only activity that places all ESs at a low-risk level.

Figure 5 focuses on the services, illustrating that all are at risk of impact from a broad spectrum of activities and pressures; however, the risk levels vary among them. Notably, fish/shellfish and biodiversity services are ranked as the highest-risk services under most activities and pressures. To a lesser degree, biological control, climate regulation, and existence/bequest are also highly ranked, while educational services appear to be much less at risk. Interestingly, perceived risk levels for fish/shellfish from, e.g., pollution are higher than those from fisheries, suggesting that the respondents may have high confidence in fisheries management. However, the difference in risk to fish/shellfish between pollution and fisheries is not statistically significant.

3.3 Certainty of risk assessment

As seen in Figure 6, we observe that all services, pressures, and human activities are perceived at medium certainty on average, with somewhat less certainty associated with ESs compared to the pressures and activities. The mean values differ slightly from the median values in some services/pressures and activities. For instance, all ESs, pressures, and activities have the same certainty mean of 2, with a standard deviation of ± 0.9 for ecosystem services, ± 1.3 for activities, and ± 1.1 for pressures. Meanwhile, the median certainty for ES is 2, while it is 3 for pressures and activities. This is as expected, given that the data are not normally distributed.

Among the identified pressures, temperature change is ranked as having the highest certainty levels, while invasives exhibit the lowest. Experts are also fairly certain about pollution, although this certainty is somewhat lower than that associated with temperature change. Regarding activities, fisheries are perceived to have the highest certainty levels, whereas shipping is associated with significantly lower certainty.

With respect to ecosystem services, certainty varies between the services, and its variance is generally high. The highest certainty levels are assigned to fish/shellfish, followed by climate regulation and biodiversity. The certainty levels for oil and gas/energy, raw materials, waste absorption, and carbon sequestration/absorption are also significantly different from most of the services identified in the Barents Sea.

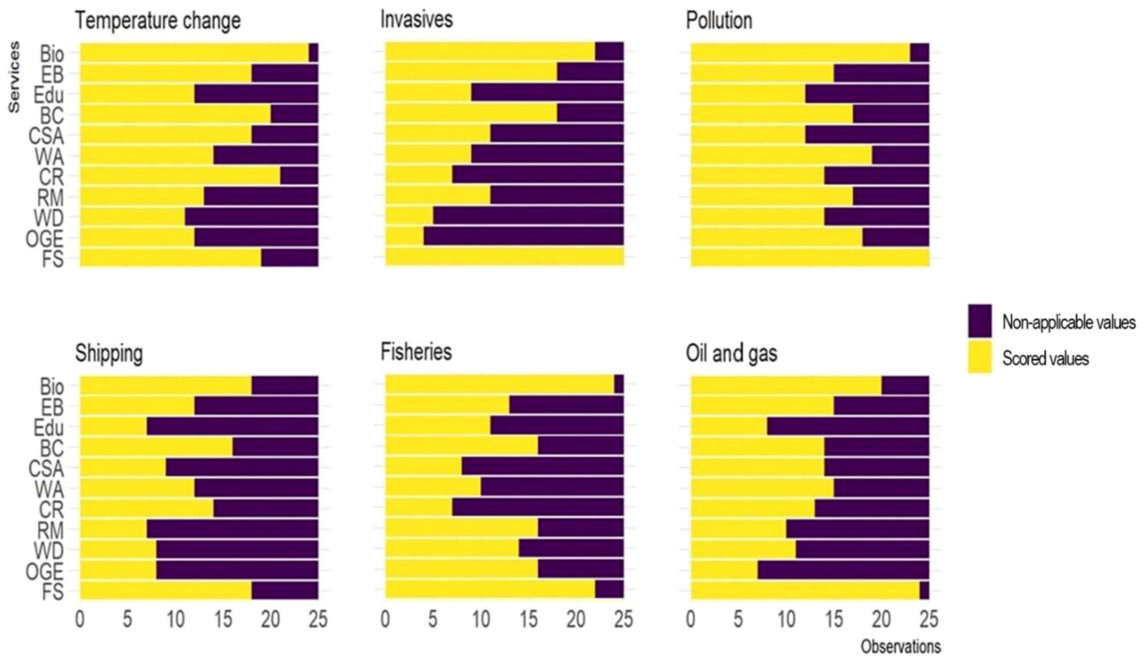

FIGURE 3
Observations with "nonapplicable" values and scored values.

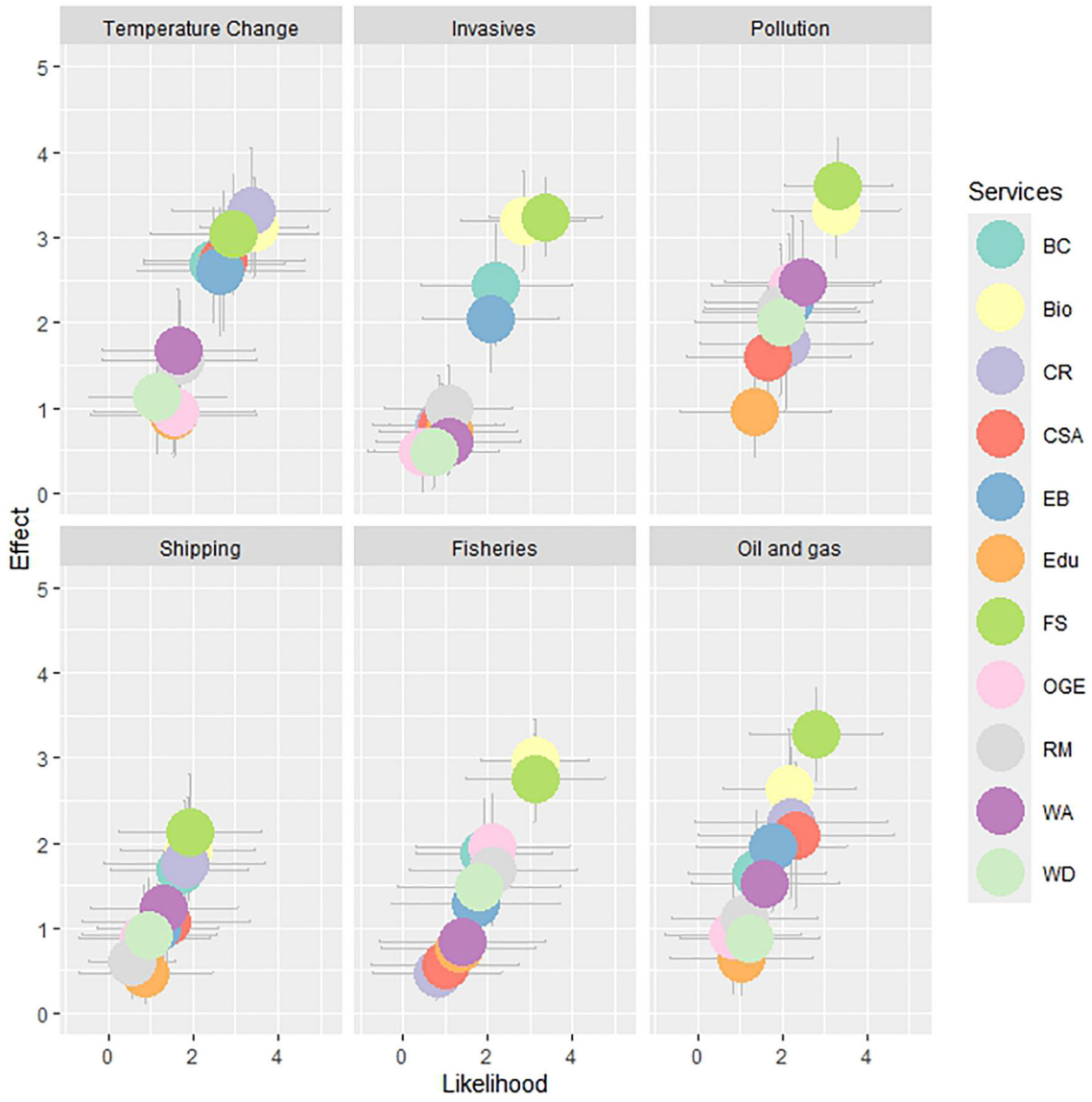

FIGURE 4
Risks posed by human activities and their pressures on various ecosystem services. The *y*-axis represents the severity of the effect, ranging from 1 (low severity) to 5 (high severity). The *x*-axis represents the likelihood of the effect, ranging from 1 (low likelihood) to 5 (high likelihood). The plots display mean values (the median values of effects and likelihoods of all ecosystem services and drivers, along with their corresponding 25th and 75th percentiles, are presented in Appendices 2, 3) with standard deviations.

The statistical results (*p*-values) of the Wilcoxon test to determine significant differences in the levels of certainty between the pressures, human activities, and services are presented in Tables 4, 5. Two methods to avoid multiple comparison problems, Bonferroni correction and FDR, are applied to detect significant differences in certainty levels (when scoring risk) between services/pressures and activities. The certainty levels of temperature change and fisheries are similar but significantly different from the certainty levels of oil and gas, shipping, and invasives. While the certainty level of pollution is similar to those of temperature change and fisheries, it is not significantly different from the level of oil and gas. For services, those significant *p*-values support that the certainty levels of WD, Edu, EB, CSA, and BC are similar to those of FS, OGE, CR, and Bio, as seen in Figure 6. The level and quantile ranges of WA appear similar to those of RM in plots, but the *p*-value indicates a significant difference. The results may be due to a number of outliers.

3.4 Risk in relation to certainty

Figures 7, 8 present risks in relation to certainty for services, pressures, and activities using radar charts. While the certainty levels are assumed to be the same for all pressures and activities in each ES (Figure 7) and for all services in each pressure or activity (Figure 8), the likelihood and effect vary accordingly. As seen in Figure 7, the likelihood, effect, and certainty scores for fish/shellfish and biodiversity are the greatest, suggesting these are the most

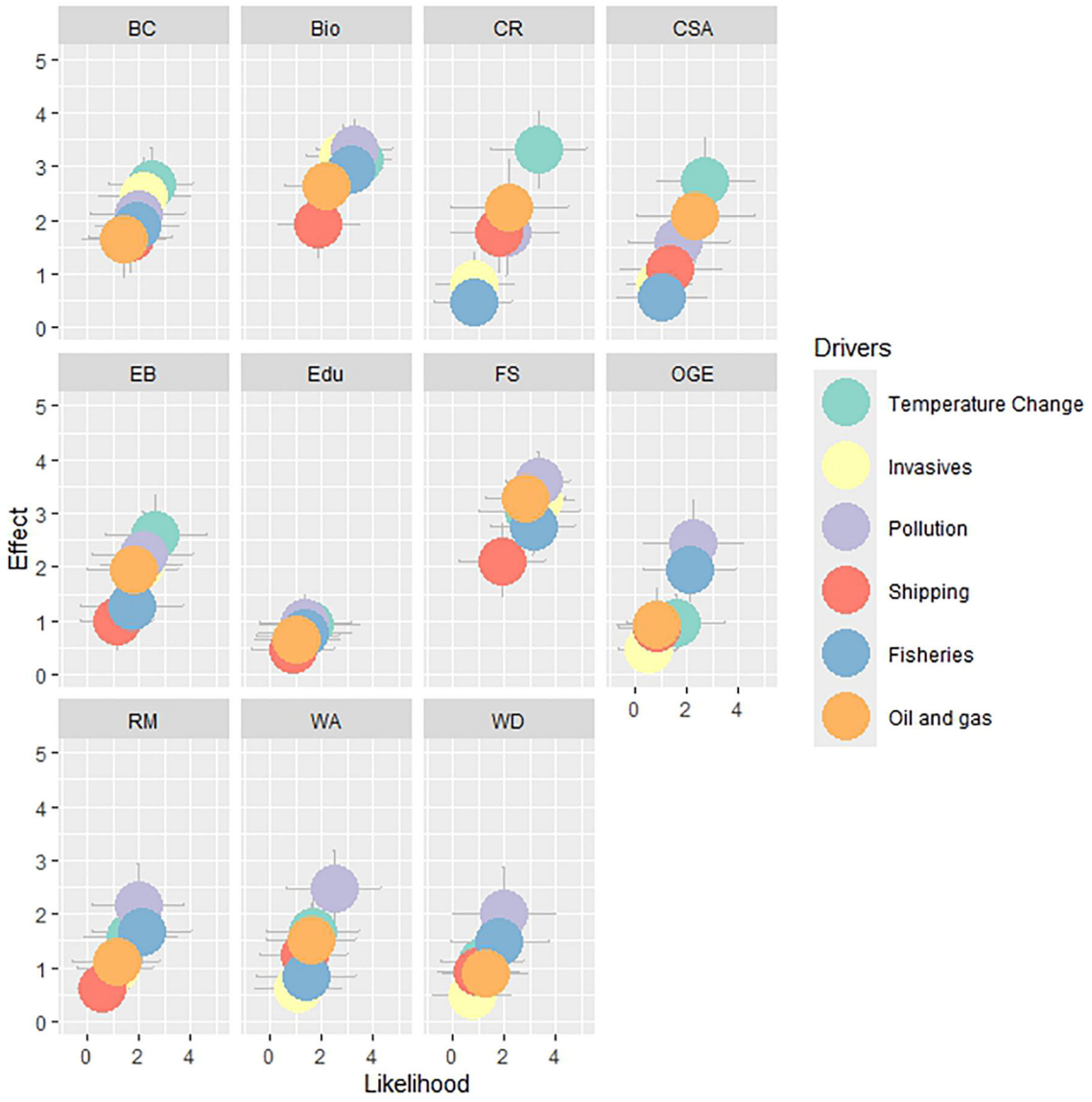

FIGURE 5
Risk levels for ecosystem services caused by various human activities and pressures. The *y*-axis represents the severity of the effect, ranging from 1 (low severity) to 5 (high severity). The *x*-axis represents the likelihood of the effect, ranging from 1 (low likelihood) to 5 (high likelihood). The plots display mean values with standard deviations.

threatened services with the highest certainty. Climate regulation is also perceived to be among the greatest at-risk services, at least in relation to "temperature change". In contrast, education is perceived as the least threatened service, albeit with the lowest certainty. In Figure 8, temperature change and pollution are recognized as the most threatening pressures, with higher certainty levels for the services of Bio, CR, FS, and OGE, and lower certainty levels for BC, CSA, EB, WD, WA, RM, and Edu. Shipping is considered the least threatening activity with the lowest certainty. This result may reflect how well temperature change and pollution have been studied in the literature. A caveat is, of course, that most of the respondents are natural scientists who work on topics related to fisheries, climate regulation, and biodiversity.

4 Discussions and conclusions

The literature on the effects of natural pressures and human activities on ESs in the Barents Sea is limited (Noring et al., 2016; Ottersen et al., 2023). This study aims to address this gap by assessing the potential impacts on ESs in the Barents Sea. We employ the DAPSI(W)R(M) and CICES frameworks to identify human activities, pressures, and ESs, establish their causal links, and use the risk matrix approach for assessment. An expert survey is utilized to evaluate risk perceptions of natural pressures and human effects on ESs. Certainty assessment is also conducted to examine the background knowledge supporting the effect and likelihood of risk.

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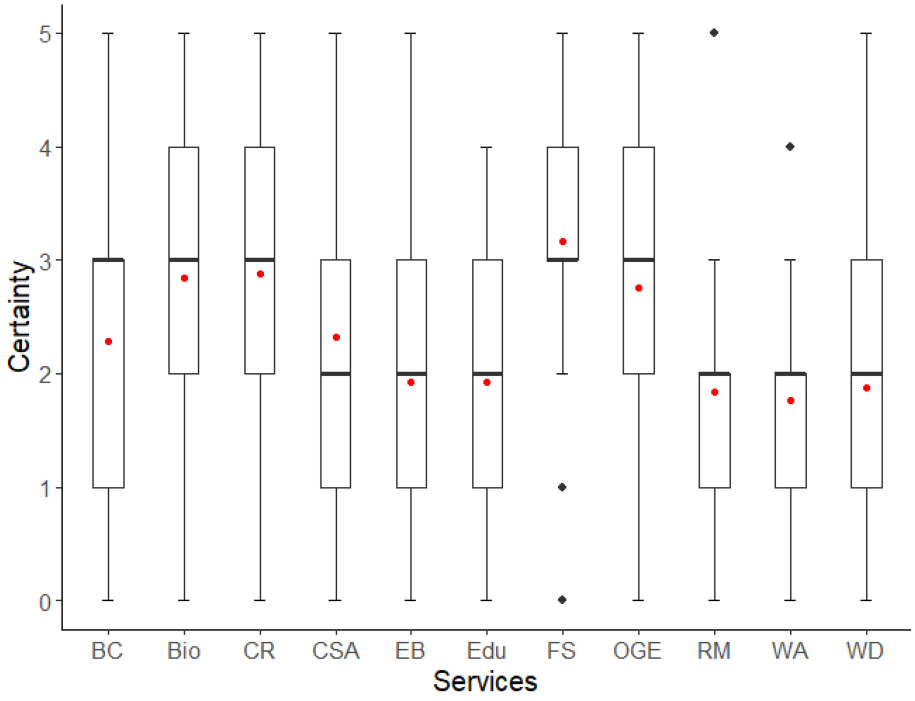
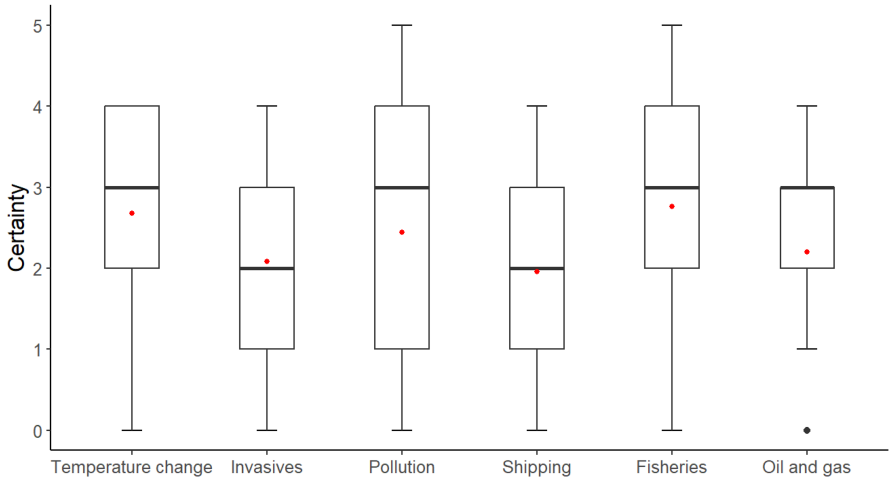


a)



b)

FIGURE 6
Certainty in relation to **(A)** ecosystem services and **(B)** human activities and pressures. The *y*-axis represents certainty, ranging from 5 (very certain) to 1 (very uncertain). The *x*-axis represents the identified pressures and activities/ecosystem services. The boxplots display median values, 25th and 75th percentiles, and max and min values. Black dots and red dots present outliers and mean values, respectively.

The results indicate that perceived risks vary among different services under various human activities and pressures; however, most risks fall within the medium or low-risk range. The most threatened ESs are the production of fish/shellfish and biodiversity, while education is the least threatened. Temperature change and pollution are identified as the pressures posing the greatest risk, though these risks are not classified as high. Shipping is considered the least threatening activity. Overall, certainty levels are generally low, with slightly less certainty regarding ESs compared to activities and pressures. The highest certainty level for ESs is assigned to fish/shellfish, followed by climate regulation and biodiversity services. Among activities, fisheries have the highest certainty level, showing less variation compared to the pressures of temperature change and pollution, This is notable, as the latter two pressures are associated with somewhat higher perceived risks.

TABLE 4 Pairwise comparison of certainty levels between human activities and pressures.

	Fisheries	Invasives	Oil and gas	Pollution	Shipping
Invasives	0.013*	–	–	–	–
Oil and gas	0.018*	0.49	–	–	–
Pollution	0.25	0.069	0.26	–	–
Shipping	0.002*	0.63	0.095	0.019*	–
Temperature change	0.61	0.009*	0.033*	0.36	0.004*

p-values are obtained using the Wilcoxon test statistic.
**p*-values at the 5% significance level, following correction using the Bonferroni and FDR methods.

4.1 Management implications

Addressing all identified risks is challenging due to resource limitations and inherent trade-offs between ESs. This raise the question: where should greater management efforts be focused. Should priority be given to ecosystem services with the highest perceived risks? Or could it be that when we have better knowledge, we feel more confidents about assessing the risks? Our assessment reveals that fisheries is not identified as the highest-risk activity in this study, despite having the greatest certainty among activities. Interestingly, fisheries is often ranked as a top-risk activity in other studies (e.g., Hansen et al., 2022; Pedreschi et al., 2023). This demonstrates strong confidence in the scientific foundation of the fisheries management system in the Barents Sea. Extensive efforts in science and management—more than for any other marine sector (e.g., annual fish stock monitoring surveys, annual stock assessments, and a well-developed system for management advice and harvest control rules)—have contributed to a successful transition to sustainable harvesting of the dominant fish stocks in the Barents Sea over the recent decades (Gullestad et al., 2017).

Meanwhile, fish/shellfish production and biodiversity services face the highest risks from temperature change and pollution pressures, which are associated with high certainty levels. This suggests that management strategies should prioritize these areas to mitigate risks effectively. These strategies could include investing in an advanced monitoring systems to detect early signs of temperature anomalies and pollution levels, enabling timely management; strengthening regulations to control pollutants entering marine ecosystems; and encouraging sustainable fishing practices that minimize bycatch and habitat destruction. Additionally, raising public awareness about the impacts of temperature change and pollution on marine ecosystems can promote community involvement in conservation efforts.

The study found that fisheries-associated risk was scored slightly higher for biodiversity than for fish/shellfish, aligning with Siwertsson et al. (2023). This demonstrates that fisheries affect the broader ecosystem, causing significant bycatch by capturing nontarget species and habitat destruction, rather than just impacting the targeted species. Conservation efforts may need to strengthen the focus on protecting marine biodiversity in addition to managing the target fish and shellfish stocks. This includes implementing additional measures to reduce bycatch, protect critical habitats, and enforce sustainable fishing practices. Management strategies should focus on ecosystem-based approaches rather than single-species management. This could involve setting biodiversity conservation targets and enhancing monitoring and enforcement to ensure compliance with sustainable fishing regulations. Policies and regulations may need to be revised to address the broader ecological impacts of fisheries. This could include stricter controls on

TABLE 5 Pairwise comparison of the certainty levels between the services.

	BC	Bio	CR	CSA	EB	Edu	FS	OGE	RM	WA
Bio	0.12	–	–	–	–	–	–	–	–	–
CR	0.081	1.0	–	–	–	–	–	–	–	–
CSA	0.89	0.062	0.048	–	–	–	–	–	–	–
EB	0.28	0.006*	0.008*	0.085	–	–	–	–	–	–
Edu	0.50	0.001*	0.012*	0.12	1.0	–	–	–	–	–
FS	0.0029*	0.24	0.18	0.017*	0.004*	0.001*	–	–	–	–
OGE	0.18	0.70	0.70	0.14	0.044	0.008*	0.096	–	–	–
RM	0.15	0.002*	0.004*	0.075	0.87	0.82	0.000*	0.007*	–	–
WA	0.065	0.001*	0.002*	0.044	0.93	0.51	0.000*	0.003*	0.80	–
WD	0.20	0.02*	0.016*	0.18	0.92	0.92	0.001*	0.007*	0.80	0.63

p-values are obtained using the Wilcoxon test statistic.
**p*-values at the 5% significance level, following correction using the Bonferroni and FDR methods.

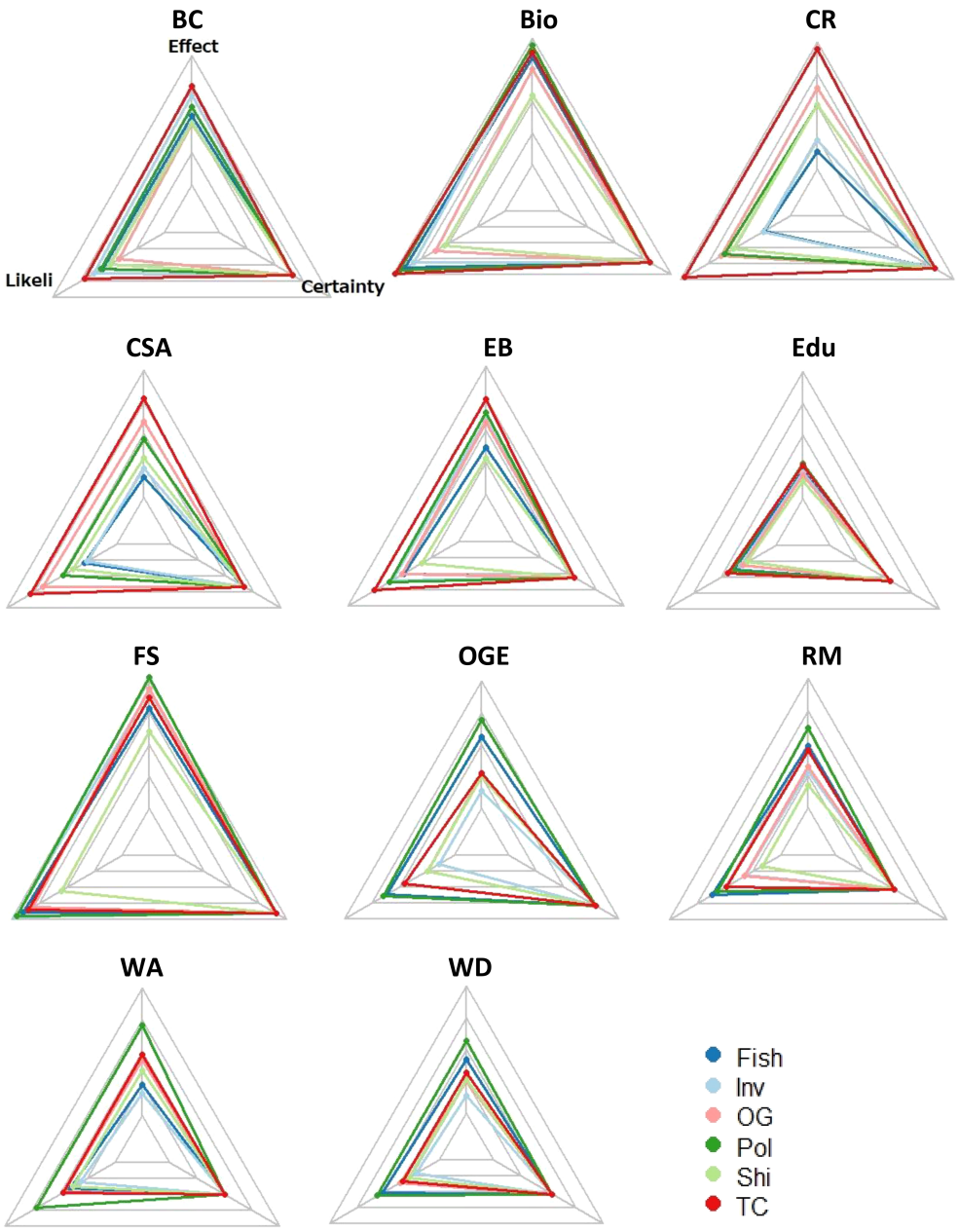


FIGURE 7
Effect, likelihood, and certainty levels of ecosystem services affected by pressures and human activities. Mean values are shown on a scale from 0 to 3.5, with 3.5 representing the maximum observed level.

fishing gear and methods, catch limits that consider ecosystem health, and more robust environmental impact assessments before allowing fishing activities. Recent efforts along these lines include the establishment of areas closed to fisheries in the northern Barents Sea, which are becoming more accessible to fisheries due to climate warming and receding sea ice (Jørgensen et al., 2020).

The results also point to challenges for management. It is, therefore, essential to define the managed system we wish to achieve, balance trade-offs between ESs, determine which services, pressures, and activities should be prioritized, and identify the necessary risk mitigation measures in practice. The prioritizations depend on both the management level and spatial scale. Local managers may focus on high-risk, high-certainty issues, where immediate actions can be implemented effectively. In contrast, regional authorities are tasked with balancing these with longer-term, uncertain risks, requiring resource allocation between direct interventions and research. At the international level, cooperation becomes crucial for addressing high-risk, low-certainty issues that cross boundaries, necessitating collaborative frameworks and shared resources to manage complex, transboundary challenges.

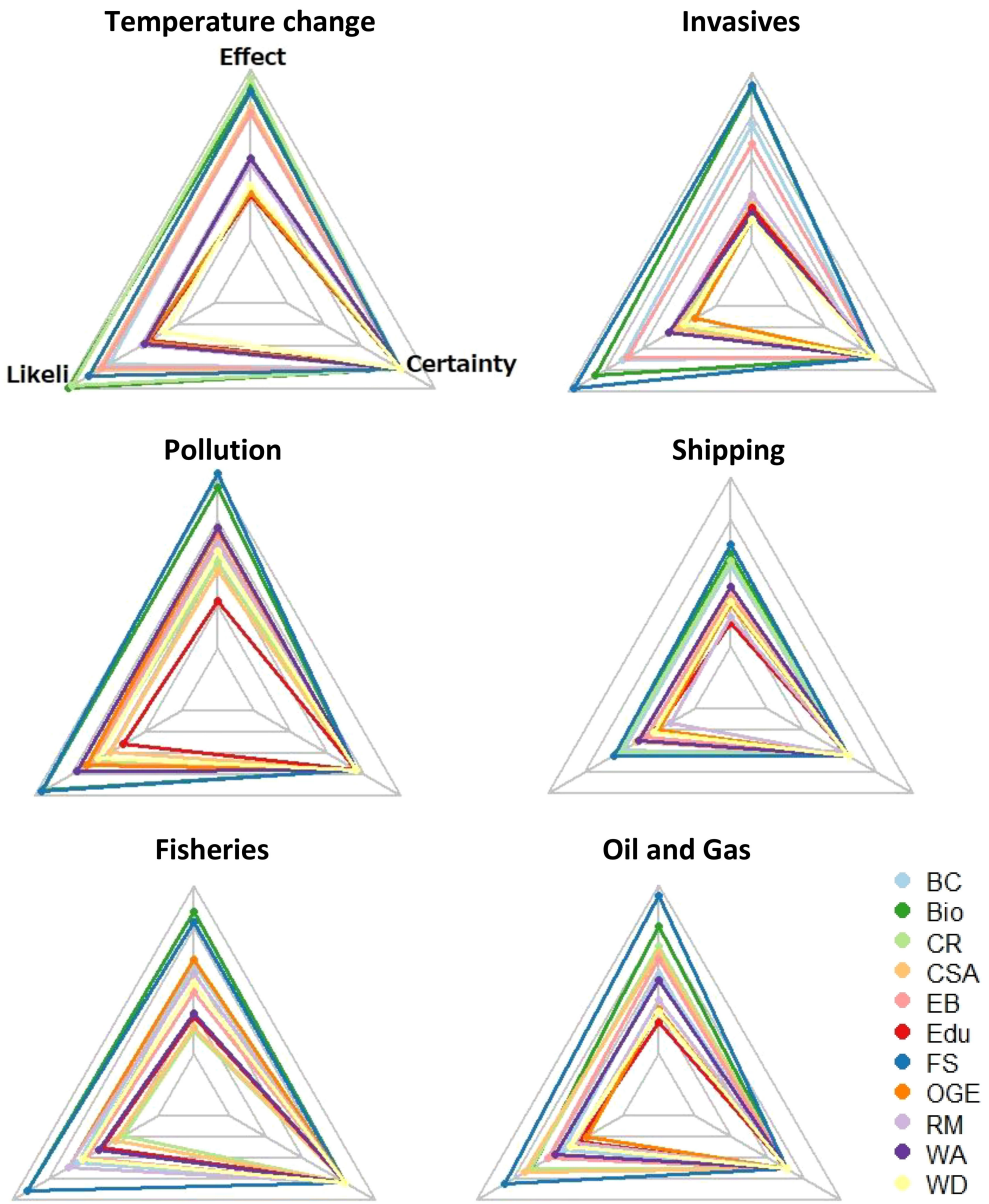


FIGURE 8
Effect, likelihood, and certainty levels of human activities and pressures impacting ecosystem services. Mean values are shown on a scale from 0 to 3.5, with 3.5 representing the maximum observed level.

Such multilevel management systems ensure a comprehensive approach to risk management.

In the context of this study, fisheries represent a significant risk activity with a high degree of certainty. As such, national managers are advised to prioritize this area, as they have the authority to establish regulations, such as closing areas to fisheries in general or restricting the use of specific gears, such as bottom trawling, which impacts benthic habitats within areas of Norwegian jurisdictions (e.g., Jørgensen et al., 2020). Additionally, pollution and temperature change were identified as primary risk pressures for the Barents Sea region. Although these pressures were measured as having lower levels of risk and certainty, their transboundary nature suggests that addressing them requires longer-term efforts, including national or international cooperation for effective risk mitigation.

4.2 Knowledge gaps

The study identifies significant knowledge gaps. The medium and low certainty perceived in all activities, pressures, and ESs indicates limited knowledge of risks in the Barents Sea. This finding is consistent with Siwertsson et al. (2023). Further research is needed to enhance understanding of ESs in relation to activities and pressures, as certainty regarding ESs is generally lower. This involves gathering more comprehensive data and developing advanced models to predict the risks of various pressures and activities on ESs more accurately. Specifically, for carbon sequestration and oil and gas/energy services, which are high risk but low certainty, more in-depth studies are necessary to pave the way for risk mitigation strategies. Since fisheries are seen as impacting biodiversity more than fish/shellfish,

ongoing research and monitoring are needed to better understand the impacts of fisheries on biodiversity. This includes studying the cumulative and indirect effects of fishing on nontarget species and habitats and developing indicators for ecosystem health.

4.3 Limitations of the study

It should be emphasized that the findings are based on the qualified assessments of a limited number of respondents, predominantly from a natural science background. Therefore, the results should be interpreted with caution. Variations in disciplinary backgrounds may lead to different risk perceptions, and imbalanced representation may skew overall results, especially if certain perspectives are under- or over-represented. It would be desirable to analyze the influence of different disciplinary backgrounds on our results, as this would provide valuable insights into how these disciplines influence responses to identification and risk perceptions. Additionally, examining whether project member involvement affects scoring and how interactions during the workshops influence identification and scoring would further enrich the analysis. Unfortunately, the limited number of respondents does not permit such analyses. In this study, a more balanced representation of expertise, particularly from social scientists, is often more desirable, as ecosystem services bridge the natural and social sciences. Ecosystem services are human-centric in focus, with interdisciplinary perspectives. They incorporate knowledge from economics, sociology, anthropology, and political science to address questions about equity, governance, and resource management. Social scientists bring important knowledge relevant to addressing conflicts, trade-offs, and synergies among stakeholders with different interests, as well as insights into the role of governance structures, economic incentives, and policy frameworks in managing ecosystem services. This is especially true for regulating and cultural services, which often have less direct market value but are of significant societal importance.

In this study, the Barents Sea is treated as a homogeneous area, which may not capture localized variations in ecosystem processes or site-specific management decisions. For instance, the risk to marine ecosystems and likely to ecosystem services increases from the open ocean toward the coastal areas due to increasing human activities and impacts (Hansen et al., 2022; Aarflot et al., 2024). While this simplification may affect the accuracy of localized risk estimates, it enables a comprehensive regional overview. Future studies should incorporate spatially explicit data to account for these variations and align the analysis with localized management needs. Additionally, the study focused on individual risks only, but it is important to consider the indirect and cumulative risks of multiple activities and pressures on ESs and their interactions. For instance, the indirect risks associated with temperature change, such as marine heatwaves and policy changes, can substantially impact the ecosystem. These cumulative effects can exacerbate the overall risk to ESs, leading to more complex and potentially severe consequences than those posed by individual activities or pressures alone.

4.4 External validity

4.4.1 Generalizability of methodology

The innovative framework employed in this study offers a significant improvement over traditional risk assessment methodologies and has the potential to be applied in diverse contexts beyond the Barents Sea. Its key innovations—certainty assessment and multivariate risk evaluation—enhance the robustness of risk management decisions and prevent oversimplified approaches that may fail to capture the complexity of marine ecosystems. First, the inclusion of certainty assessment offers a valuable addition to traditional probabilistic risk assessment, which has often been criticized for inadequately addressing uncertainties (Aven and Zio, 2011). By incorporating certainty assessment, this analysis provides an approach that could be adopted in other ecosystem assessments, where understanding the confidence in risk estimates is crucial for a more comprehensive evaluation of potential impacts on ecosystem services. Second, the study emphasizes the importance of viewing risk as a multivariate construct rather than a scalar. Merely multiplying effects by likelihood to determine risk can lead to misguided management decisions (Cox, 2008). For instance, a management strategy for an ES with a high effect but low likelihood of occurrence will differ significantly from that for an ES with a low effect but high likelihood, although both yield the same risk level. This distinction is crucial, as it emphasizes that the nature and context of risks should inform management strategies, rather than relying solely on a numerical risk score.

4.4.2 Generalizability of findings

The findings of this study regarding risks to ecosystem services exhibit varying levels of generalizability to other marine regions. In particular, the high risks associated with temperature change and pollution identified in the study align with globally observed patterns documented in the literature. Numerous studies have demonstrated the detrimental effects of rising sea temperatures on species distribution, reproductive success, and overall ecosystem resilience (e.g., Venegas et al., 2023; Weiskopf et al., 2020). Similarly, pollution, a significant contaminant, has been shown to disrupt ecosystem components, particularly the early life stages of fish (e.g., Aarflot et al., 2024). These pressures represent pervasive effects on marine ecosystems worldwide and are not confined to the Barents Sea.

The recognition of higher fisheries-associated risks to biodiversity in this study, in contrast to the traditional focus on fish and shellfish, and the need for management strategies that prioritize the broader ecosystem rather than specific species, are likely generalizable to other marine regions. The findings align with recent literature emphasizing the importance of considering all service types when assessing risks for marine systems, not only provisioning services but also regulating and cultural services. This shift in focus is particularly significant, as it highlights the interrelationship among various ecosystem components and the importance of protecting overall biodiversity.

4.4.3 Region-specific findings

However, the results also highlight region-specific nuances that may limit their universal applicability. Although temperature change was identified as the greatest risk to most ESs, as indicated in the literature, this study did not find that this risk and certainty were always considered high for all the services. One reason might be that the focus on direct risks over indirect ones (e.g., those mediated through policy changes) mirrors local stakeholder priorities, which may vary across other marine contexts. Similarly, the projected timeline for temperature change in our study is based on a 25-year timeframe. This regional perspective limits the extrapolation of results to areas where alternative timelines might influence risk assessments. For instance, in Collins et al. (2019), the respondents do not seem very concerned about abrupt changes, such as marine heatwaves, within a 100-year projection. In contrast, Kjesbu et al. (2022) found that near-future climate change has a highly mixed impact on fish stocks in the North-East Atlantic.

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 studies involving humans were approved by Norwegian Center for Research Data (NSD). The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

TP: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. CA: Conceptualization, Data curation, Methodology, Writing – review & editing. HS: Formal Analysis, Methodology, Visualization, Writing – review & editing. MS-M: Conceptualization, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1493592/full#supplementary-material

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Shifting sands of marine eutrophication assessments: building a future approach for UK marine waters

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The assessment of water quality, and in particular, of eutrophication, has been a core activity to establish, disseminate, and communicate the impact of anthropogenic influences on coastal and marine waters in the United Kingdom (UK) and globally. To date, the UK assessments of eutrophication have focused heavily on indicators, either singularly or in combination, associated with a numerical threshold, with supporting science concentrating on defining relevant thresholds and relating exceedances to management actions. However, as our understanding of the complexity of estuarine and coastal zone processes in terms of variability, time lags, ecological interactions and climate resilience has evolved, so too must the structure of our water quality assessments. This paper presents a review of existing UK eutrophication assessments, identifying what has worked and where gaps still exist, particularly as our ecosystems face rapid changes. From the gap analysis, we present a series of recommendations for future eutrophication assessments, assessing the feasibility of implementing those recommendations through consideration of effort, complexity and costs. This work presents a set of headline activities offering a renewed and revised approach to the structure of UK eutrophication assessments that will progress complex data flows, achieve enhanced alignment between directives, embed new indicators, greater understanding of ecosystem impacts and consideration of the shifting climate baseline.

KEYWORDS

eutrophication, nutrients, pelagic community, OSPAR, UK Marine Strategy

1 Introduction

Excess nutrients from fertilizer application, pollution discharge, and sewage are transported from lands to oceans, impacting on coastal water quality and ecosystem health (Devlin and Brodie, 2023; Devlin et al., 2023; OSPAR, 2023; Paerl and Piehler, 2008; Painting et al., 2007; Carstensen et al., 2011). Terrestrial runoff of

waters polluted with excess nutrients (primarily nitrogen and phosphorus compounds) from point sources, such as sewage treatment works (STW) discharges and aquaculture, and diffuse sources such as fertilizer losses via river discharges, have had devastating adverse effects in coastal and marine ecosystems globally (Ngatia et al., 2019; Ryther and Dunstan, 1971; Smith, 2003). Biomass production of plant matter in coastal waters is often naturally limited by the availability of nitrogen and/or phosphorus and increased anthropogenic inputs of these substances can lead to increased biomass that disturbs the natural ecological balance in marine ecosystems (de Raús Maúre et al., 2021). This disturbance, the process of eutrophication, is seen globally as one of the biggest threats to marine ecosystem health. Eutrophication, like climate change, is a cross country, cross sectoral issue with coastal regions throughout the world being impacted through the input of national and transboundary elevated nutrients (Laurent et al., 2018; Meier et al., 2019).

Eutrophication has a substantial impact on our coastal and marine systems and can limit access to ecosystem services by acting as a pressure on biodiversity and wider ecosystem approaches and industries such as shellfish harvesting and fisheries (Rhodes et al., 2017; Kermagoret et al., 2019). Even at a low level, increased nutrient loads and changing proportions of nutrients can result in changes in phytoplankton biomass and communities which can affect higher trophic level species (Duarte, 2009; Duarte et al., 2009; Carstensen et al., 2011; Frenken et al., 2023; Ibáñez et al., 2023; Dory et al., 2024). Species shifts are frequently characterized by high biomass bloom events which can have significant economic impacts as they reduce attractiveness and amenity value of coastal waters resulting in societal upset (Willis et al., 2018; Andersen et al., 2019). Increased phytoplankton biomass reduces light penetration which in turn causes habitat loss by limiting areas where seaweeds and seagrasses can grow (Carolina, 2002; Foden et al., 2005). These habitats are important for maintaining fish nursery populations and biodiverse benthic organisms. More serious eutrophication impacts involve hypoxic events which harm many organisms but are particularly damaging to sessile benthic fauna, whose loss again affects the food web and biotic water quality regulation. Extreme hypoxia and anoxia lead to a loss of both biotic and abiotic water quality regulation, as previously sequestered nutrients re-enter the water column and bacterial denitrification processes change (Best et al., 2007; Devlin and Brodie, 2023). Well-documented adverse ecological responses of increased nutrient discharge to coastal and marine waters from across the world include harmful algal bloom events (HABs) (Paerl, 2008; Glibert and Burford, 2017), changed preponderance and dominance of certain types of fast growing plankton over other, more long-lived and structural benthic primary producers (seagrass, coral, macroalgae) (Lapointe et al., 2019, 2020), the creation of hypoxia and subsequent "dead zones" (Diaz and Rosenberg, 2008) habitat degradation, and adverse changes in aquatic food webs (Carpenter et al., 1998; Gross and Hagy, 2017).

Generally, the UK eutrophication assessment approaches focus on single metrics ("indicators") associated with a numerical threshold which are then integrated into one outcome of overall status (Best et al., 2007; Devlin et al., 2007a,b, 2009, 2012a; Greenwood et al., 2019). Historically, work has focused on the development of those thresholds, how they relate to ecosystem function and how to guide mitigative management actions from the outcomes of the assessment (Bricker et al., 2003; Bricker and Devlin, 2011; Ferreira et al., 2011). However, effective mitigation of eutrophication requires consideration of many layers of complexity, needing multiple, often cumulative actions over large spatio-temporal scales (Thornton et al., 2013). These challenges are well known with many studies recognizing the complexity of the problem due to large variations in hydrodynamics, water supply, inputs and susceptibility (Cloern, 2001; Cloern and Jassby, 2009; Duarte, 2009; Duarte et al., 2009).

As our understanding of the complexity of the coastal zone, in terms of variability, time lags, ecological interactions and resilience has evolved, so should the structure of our eutrophication monitoring and assessment. Pauly (2019) identifies the concept of shifting baselines, the phenomenon where each generation accepts the baseline as the earliest condition it experiences, with shift in baselines typically toward degradation. Our ecological systems are much different from decades ago facing multiple pressures whilst our technology to collect vast amounts of data continues to grow. Understanding this changing baseline in a complex pressure-response system requires multiple layers of information to inform and direct our understanding of what constitutes an acceptable and sustainable level of use for the marine environment. In addition, our shifting baseline needs to consider declining climate resilience, through cumulative impacts from multiple pressures, and the interactions of these pressures with increasing global temperatures (Atkins et al., 2011b; Patrício et al., 2016; Elliott et al., 2017; Laurent et al., 2018; Meier et al., 2019). Efforts to tackle eutrophication need to address the entire land-sea continuum from catchment to coast and be supported by monitoring a range of complex interactions and impacts (Thornton et al., 2013). Future approaches to eutrophication need a re-analysis of the issues, updating our frameworks and a rethinking of the complex solutions to achieve sustainable use of the marine environment.

This paper presents the outcomes of an evidence review and prioritization exercise, identifying gaps in current UK eutrophication assessment frameworks which have not fully considered how our system is changing and what is needed in future assessments to account for the complexity of the pressures that drive the impacts and the scale of potential solutions. It presents a review of historical and current eutrophication assessments that are being implemented in UK coastal and marine waters, identifying successes and challenges. The review and national consultations with eutrophication experts provided the baseline to identify five key challenges that need to be resolved for future eutrophication monitoring. We describe those challenges and outline a series of recommendations that can help achieve future success in eutrophication monitoring and assessment.

2 Methods

Part 1 of this work describes historical and current eutrophication assessment policies, identifying the aim of the assessments, the area in which it was applied, who was responsible for implementation, the structure of the assessment, and what

was achieved though the implementation. This review, alongside national consultations with UK eutrophication experts provided the basis for part 2, a quantitative analysis of future eutrophication needs which were characterized into five broad thematic areas exploring future data needs, potential for further alignment, potential for new indicators, embedding greater understanding of ecosystem impacts and consideration of climate change. Part 3 presents a prioritization of the main recommendations under each theme, considering cost, feasibility and outcomes.

2.1 Review existing eutrophication assessment frameworks

We reviewed the existing environmental policies responsible for the assessment of eutrophication in the UK's coastal and marine waters, detailing their basis and implementation, overlapping spatial extents, and their component indicators and thresholds. We explored the evolution of eutrophication policy from coastal and marine areas and identify successes of both monitoring and policy implementation associated with UK eutrophication assessments. Finally, we summarized the indicators and reporting structures that form the assessment frameworks. The focus of this review was coastal to marine and freshwater eutrophication assessments were not included.

2.2. Identify key evidence gaps in current practices

Information from the review alongside national consultation with eutrophication experts across UK agencies were discussed in terms of what has worked and where gaps still exist. Topics considered essential to improve future eutrophication monitoring and assessment were characterized into five thematic areas exploring future data needs, potential for further alignment, potential for new indicators, embedding greater understanding of ecosystem impacts and consideration of climate change within eutrophication assessments. From these consultations, we identified evidence gaps within five broad themes ("data," "alignment," "indicators," "ecosystem," and "climate") to identify knowledge and evidence needed for better informed and effective management of eutrophication (Figure 1).

2.3 Prioritization of activities required to fill evidence gaps

Alongside the recommendations for future eutrophication assessments, an assessment of feasibility was carried out, developed from the review and expert knowledge of what is currently occurring in UK national eutrophication monitoring programs. Feasibility of developing solutions to the key evidence gaps is reported against the effort required to achieve recommended activity, the scale of complexity and potential costs of implementation. We finish with a discussion on those recommendations and how best to achieve successful implementation of a revised, updated eutrophication monitoring and assessment strategy for coastal and marine waters.

3 Results

3.1 Review existing eutrophication assessment frameworks

3.1.1 Developing environmental directives

The design, establishment and management of eutrophication assessments in the UK have been influenced by the experience gained through the implementation of EU directives now transposed into UK law and that of the devolved administrations, and the consecutive development of monitoring to comply with the requirements of the different directives addressing eutrophication. The UK also continues to be a signatory to international conventions, in particular that of OSPAR (the Oslo and Paris Convention for the Protection of the Marine Environment of the North Atlantic). We review the application of national laws and partnerships associated with the assessment in eutrophication in UK coastal and marine waters. Figure 2 gives a timeline of the implementation of key policies and associated assessments.

Eutrophication emerged as a major issue in the 1970s, with concern over the input of sewage outfalls into UK rivers. Rising awareness around sewage outfalls and direct nutrient inputs meant that eutrophication from the 1970s and into the 1990s was driven by the need to mitigate point source pollution with programmes of management measures focused primarily on the reduction of phosphorus and nitrogen from sewage treatment. Much of this initial work was developed from frameworks such as the EU Urban Wastewater Treatment Directive (91/271/EEC) (European Commission, 1991a) and the EU Bathing Water Directive (2006/7/EC) (Figueras et al., 1997; European Commission, 2006). The EU Urban Wastewater Treatment Directive (91/271/ECC; hereafter UWWTD) required Member States to ensure that urban areas collect and treat wastewater which would otherwise pollute rivers, lakes and seas and succeeded at altering compliance choices and improving related national policies (Kemp, 2001). It required compliance by 1998 for wastewater treatment for all settlements of >2,000 population equivalents to have (at least) secondary treatment with more advanced treatment required for towns leading to a step change in sewage treatment from the late 1990s. Whilst the EU Bathing Water Directive was aimed at bacterial reduction, there was a positive effect of catalyzing greater nutrient reductions from STWs.

However, issues around diffuse runoff from farming and agricultural practices through the 1980s and the 1990s that were not mitigated by the UWWTD resulted in the parallel development of polices aimed at the reduction of nutrient runoff from agriculture. The implementation of European directives continued with the onset of the Nitrates Directive (91/676/ECC), which aimed to protect water quality by preventing nitrates from agricultural sources that pollute ground and surface waters and by promoting the use of good farming practices (European Commission, 1991b; Massarelli et al., 2021). The Nitrates Directive was a major step toward acknowledging and protecting water against pollution from agriculture (Tunney, 1994). The implementation of Nitrogen

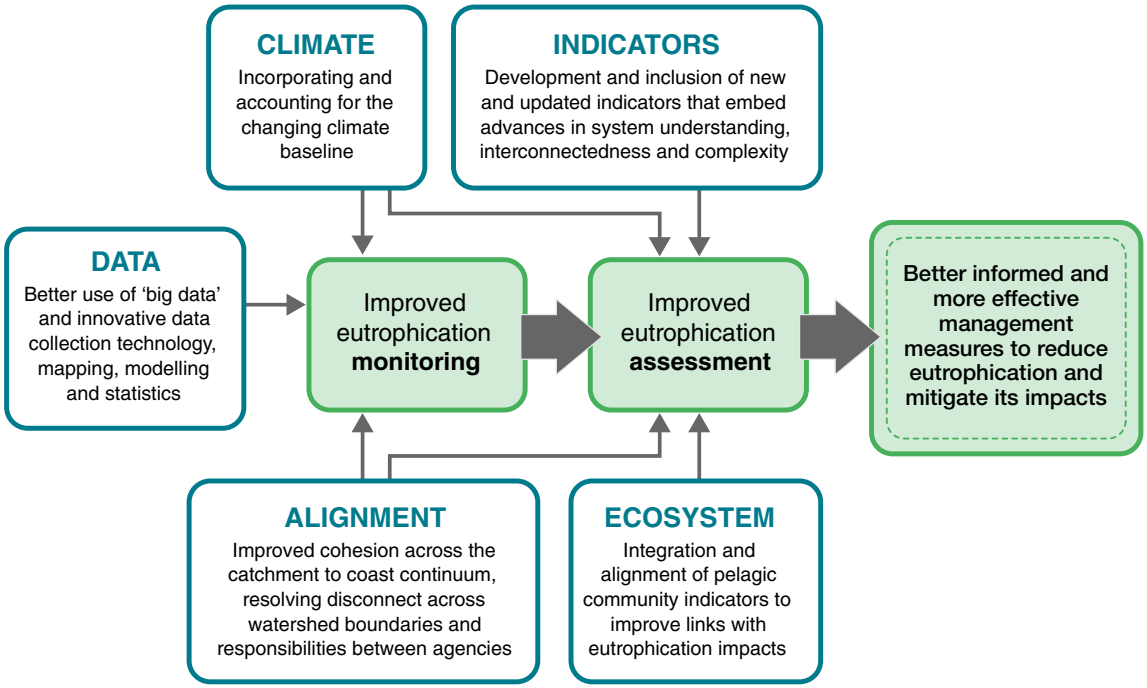

FIGURE 1
Five broad themes considered for the improvements of future marine eutrophication assessments.

Vulnerable Zones (NVZs) provides an example of a catchment-based program to reduce excess groundwater nitrogen (Smith, 2000; Johnson et al., 2007; Worrall et al., 2009) where areas of elevated nitrate sensitivity were identified and, in these areas, limits on nitrate additions were imposed.

The assessment of the impact of eutrophication in the UK for estuaries and coastal waters commenced with the EU Water Framework Directive (2000/60/EC; WFD) from 2001. This covers transitional and coastal water extending for one nautical mile (1 nm) beyond the low water mark for England, Wales and Northern Ireland and 3 nm from the "coastal baseline" in Scotland (European Commission, 2000). Between 2006 and 2008, all agencies collaborated formally to develop the WFD tools and methods for the initial assessments. The EU WFD was developed as a river basin programme, connecting upstream activities with downstream ecological health. Eutrophication assessments in coastal and offshore waters (beyond the WFD waters) were also developed from the requirements of the EU Marine Strategy Framework Directive (2008/56/EC; MSFD) (European Commission, 2008). The overarching aim of the MSFD was to implement measures to achieve Good Environmental Status (GES) by 2020. First, Member States developed marine strategies consisting of an initial assessment of environmental status, along with articulating the defining characteristics, targets and indicators representing Good Environmental Status (GES). Monitoring programmes to measure progress toward GES were then established, and, where necessary, programmes of measures to achieve or maintain GES were implemented. Implementation of the WFD and MSFD resulted in shared knowledge between participating countries, development of national indicators, and a robust monitoring framework that allowed tracking of the reduction of eutrophication pressures and impacts (Borja, 2005; Devlin et al., 2007a).

Additional marine eutrophication assessments are carried out under OSPAR, the mechanism by which 15 Governments and the EU cooperate to protect the marine environment of the North-East Atlantic. OSPAR started in 1972 with the Oslo Convention against dumping and was broadened to cover land-based sources of marine pollution and the offshore industry by the Paris Convention of 1974. These two conventions were unified, updated and extended by the 1992 OSPAR Convention. Eutrophication assessments are carried out under the OSPAR "common procedure" (OSPAR COMP) (Devlin et al., 2023). The OSPAR eutrophication assessment was implemented for OSPAR COMP1 (1996–2000) and OSPAR COMP2 (2006–2014) with OSPAR COMP3 (2013–2018) providing an updated Common Assessment Criteria for the Eutrophication status of the OSPAR Marine Area. The most recent "OSPAR COMP4" has recently been concluded and provides an updated eutrophication thematic assessment (2019–2023) for 15 countries across the North-East Atlantic (Devlin et al., 2023).

Brexit and departure from EU legislation has meant several changes to the UK environmental policies which were responsible for the assessment of eutrophication in coastal and marine waters. The WFD was transposed into separate environmental legislation for England, Wales, Northern Ireland and Scotland so that supporting pieces of water legislation would continue to operate after EU exit (1 January 2021). These are the Water Environment (Water Framework Directive) (England and Wales) Regulations, the Water Environment and Water Services (Scotland) Act 2003 (WEWS Act 2017) and The Water Environment (Water

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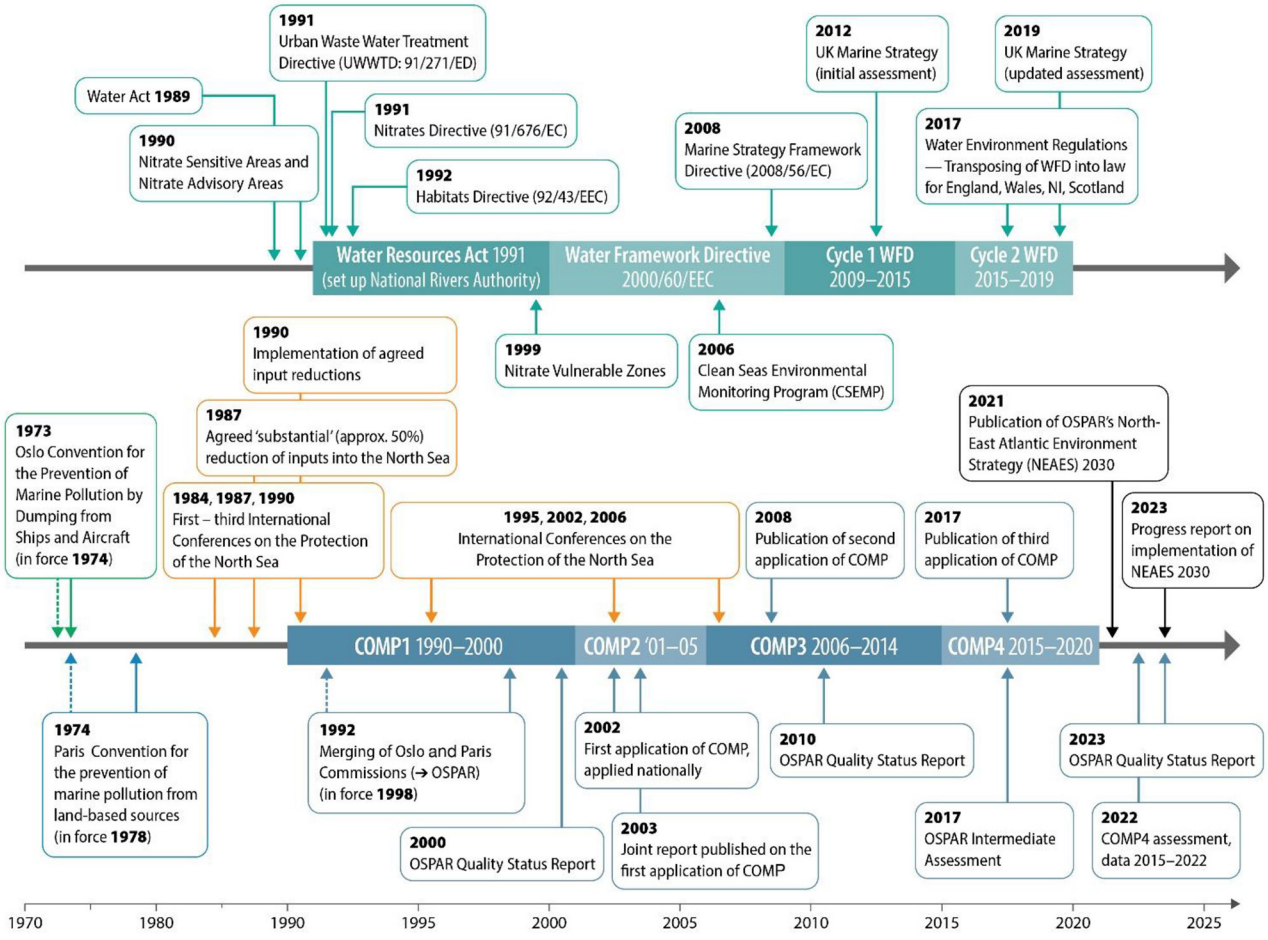

FIGURE 2
The evolution of eutrophication assessments for coastal and marine waters in the UK. The upper timeline focuses on the implementation of EU and national legislation with the bottom timeline showing the development of international agreements and frameworks, specifically the implementation of OSPAR.

Framework Directive) Regulations (Northern Ireland) 2017. For the purposes of this paper, the different regional approaches will be called WFD/WER—representing the three regional approaches for the Water Environment Regulation and Water Framework Directive across the UK, which is still the primary environmental directive that assesses transitional and coastal waters in the UK For coastal and offshore waters, the EU MSFD was transposed into national legislation through the Marine Strategy Regulations 2010 (covering England, Scotland, Wales and Northern Ireland) (DEFRA, 2012, 2019) and now sits within the UK Marine Strategy (UKMS). The DEFRA (2012) required action to achieve or maintain GES in our seas by 2020. The Regulations require the production of a "Marine Strategy" for all UK waters and that the approach is coordinated across all four UK Administrations and cooperate with other countries sharing our seas. This has resulted in the UK Marine Strategy Part One: an assessment of marine waters, objectives for GES and targets and indicators to measure progress toward GES (DEFRA, 2012, 2019) with the third report recently published (DEFRA, 2025). Eutrophication assessments under the recent UK Marine Strategy Part 1 include the coastal assessments carried out under WFD/WER and the coastal and offshore assessments carried out under the OSPAR thematic assessment (COMP4) with the two source assessments merging outcomes together but not fully integrating the source data.

3.1.2 Eutrophication indicators for UK monitoring and assessment

The type of indicators that make up a eutrophication assessment framework vary depending on the specific assessment, though many commonalities exist between eutrophication directives. The assessment of eutrophication usually includes (at least) three indicators: dissolved inorganic nutrients (nitrogen and phosphorus), phytoplankton biomass (typically measured as chlorophyll-a) and dissolved oxygen (Devlin et al., 2011, 2007a; Greenwood et al., 2019; Scavia and Bricker, 2006; Smith and Schindler, 2009; Van Beusekom et al., 2019).

Eutrophication has been defined as "the progressive enrichment of nutrients, leading to excessive plant growth,"

and developed tools to classify nutrient and plant status (COM, 2017). Eutrophication may be present if one of the sensitive biological elements (particularly phytoplankton or opportunistic green algae) are moderate or worse and the supporting element of nutrients (DIN in marine waters) is also moderate or worse. These conditions should be persistent over a period of assessment cycles and investigations suggest that the causes of failure are strongly linked to nutrients. The overall eutrophication assessment is based on this evidence and other supporting parameters.

The assessment of eutrophication in the recent OSPAR eutrophication thematic assessment is based on the degree of nutrient enrichment (Category I), the direct effects of nutrient enrichment (Category II) and the indirect effects of nutrient enrichment (Category III). For Category I, the nutrients common indicator is derived from winter mean concentrations of dissolved inorganic phosphorus (DIP) and dissolved inorganic nitrogen (DIN) (Heyden and Leujak, 2022). For Category II, the Chlorophyll common indicator is derived from growing-season mean concentrations of chlorophyll (Prins and Enserink, 2022) where chlorophyll EO and water sample data are combined, weighted as a function of *in-situ* confidence. For Category III, the Dissolved Oxygen common indicator assesses the concentrations of dissolved oxygen near the seafloor (Devlin et al., 2022). Assessment criteria and their corresponding area-specific assessment levels as set and agreed for COMP4 are applied for each given area. The results obtained are integrated to give the classification for the given area. The overall result of the assessment depends on the outcome of the direct and indirect effects (Categories II, III), following the one-out-all-out principle (OOAO) (Devlin et al., 2011; Ferreira et al., 2011). The UK Marine Strategy is a combination of WFD/WER and OSPAR methodology (Devlin et al., 2023).

We present a comparison of the indicators across the three main UK eutrophication directives within each category in Table 1, summarizing key eutrophication indicators, assessment criteria, and geographical coverage across these frameworks. Indicators are grouped into "Category I" which relate to causative factors including nutrient loads and nutrient enrichment, "Category II" which include the direct effects of nutrient enrichment (impacts on phytoplankton biomass and community), and "Category III" which include the indirect effects of nutrient enrichment (reduction in light penetration and dissolved oxygen concentration). The WFD/WER nutrient assessment is an aggregation of two indicators (Winter DIN and Winter DIP), whilst the OSPAR assessment is based on Winter DIN and Winter DIP measured separately. The WFD/WER uses the outcome of the nutrient indicators to formally identify high risk areas for eutrophication while the nutrient indicators are not considered in the final OSPAR assessment outcome, and assessment areas that have failed nutrient indicators under the UKMS have been designated as only partially meeting GES. There are also differences between the chlorophyll and dissolved oxygen indicators and how they are used in the final assessments within WFD/WER and OSPAR. Again, these are small but significant, and result in multiple differences between the two approaches for the final assessment of eutrophication (Greenwood et al., 2019).

3.1.3 Designating eutrophication status

Indicators are assessed by comparison to their respective thresholds; however, outcomes are classified differently under each separate eutrophication frameworks. The WFD/WER eutrophication assessment includes five assessment outcome categories with "high" the most positive and "poor and bad" indicating the most perturbed, and "moderate" and "good" designating somewhat negative and somewhat positive intermediate states, respectively. Geographically specific "reference conditions" (and class boundary thresholds) for each indicator under WFD/WER were constructed based on a combination of scientific review (Borja et al., 2004), thresholds accepted under previous directives and international agreements (e.g. OSPAR, Foden et al., 2011; Devlin et al., 2007a; Painting et al., 2007), expert knowledge and investigations of outputs between water bodies at low and high risk of eutrophication (Devlin et al., 2007b). Thresholds were also validated and modified by the consensus process of the first phase of the NE Atlantic Intercalibration process (Heiskanen and Carletti, 2009).

OSPAR designates spatial assessment areas as "problem" or "non-problem" areas with respect to eutrophication. In the first three OSPAR COMPs, OSPAR Contracting Parties evaluated the eutrophication status of their national marine waters using national assessment levels (thresholds) to assess nutrients and chlorophyll a (OSPAR, 2017). For OSPAR, assessment levels that were indicative of good ecological status (non-problem area) were based on reference conditions reflecting non-eutrophic conditions with boundary between "good" and "moderate" status derived by adding a 50% deviation to the reference condition. However, OSPAR Contracting Parties used different approaches in establishing reference conditions to derive these values, leading to variable assessment levels and different outcomes of the eutrophication assessment across national borders (Malcolm et al., 2002; OSPAR, 2003, 2008a, 2017; Foden et al., 2011). OSPAR COMP4 improved this through the development of an ensemble model approach used to derive pre-eutrophic conditions (Lenhart et al., 2010; van Leeuwen et al., 2023). Nutrient loads into the NE Atlantic were estimated from rivers under reference conditions, using the European model E-HYPE and observations (Lenhart et al., 2010; Stegert et al., 2021). The chlorophyll concentrations were modeled corresponding to the estimated nutrient concentrations under reference conditions. To allow for natural variability with a "slight disturbance," and in the absence of more specific information, the assessment level was defined as the concentration 50% above the area-specific background concentration derived from the ensemble model approach (Borja, 2005; OSPAR, 2003, 2008b). The UK Marine Strategy uses a combination of WFD/WER and OSPAR indicators and thresholds for coastal and offshore areas and applies the terminology "in/achieving GES" and "not in GES" for each indicator.

While the different directives for the assessment of eutrophication are somewhat compatible regarding the type of indicators and how they are assessed relative to thresholds, the integration frameworks, how individual indicator outcomes are brought together to provide a classification of eutrophication, status depends on what elements/indicators are used for the assessment. WFD/WER implements a "one out all out" (OOAO)

TABLE 1 Summary of current UK eutrophication indicators used to inform each indicator within the three UK frameworks [Water Framework, Water Framework Directive Regulations (WFD/WER for England, Wales), or Water Framework Directive (Northern Ireland, Scotland)], UK Marine Strategy and the OSPAR Common Procedure (COMP).

Category	Indicator	Current UK eutrophication assessment frameworks		
		WFD/WER	UK Marine Strategy—Part 1	OSPAR Common Procedure 4 (COMP4)
Areas assessed		Transitional (estuarine) waters (TW) to coastal areas up to 1 nm of coast	Coastal waters (CW) up to 3 nm, plumes and offshore waters	Plumes and coastal waters (seaward of 1 nm) and all UK marine waters
I. Drivers of eutrophication: physico-chemical	**TN and TP**—total nitrogen and phosphorus loads (inputs from land to sea)	Not used.	Common indicators outcome from OSPAR applied; no UK specific analysis.	Common indicator for trends in loads (diffusive sources, riverine inputs and direct discharges from sewage and industry) as well as atmospheric TN since 1990 at the scale of OSPAR sea areas. Not assessed against thresholds
	Nutrient concentrations—elevated level(s) of winter DIN and/or DIP	Winter mean DIN, DIP over 6-year period compared to "reference" level + 50%	WFD/WER methodology used for coastal waters and OSPAR COMP4 methodology used for plumes and offshore waters	Winter mean DIN over 5-year period compared to "reference" level + 50%
	N/P ratio—elevated winter N/P ratio	Used as part of "weight of evidence" to designate future risk	Common indicators outcome from OSPAR applied; no UK specific analysis	Trends in N:P ratios presented as part of INPUT reporting
II. Direct impacts from Elevated nutrients: Direct biological impacts	**Chlorophyll-*a* concentration**—90th percentile or mean	Mean of annual 90th percentile value of chlorophyll (March to Sept) calculated over 6-year period compared to "reference" level +50%	WFD/WER methodology used for coastal waters and OSPAR COMP4 methodology used for plumes and offshore waters	Mean of annual 90th percentile value of chlorophyll (March to Sept) calculated over 6-year period compared to "reference" level +50%
	Phytoplankton indicator species (area-specific)—Elevated levels of nuisance/toxic indicator species increased duration of blooms	Single species and total taxa count of all phytoplankton species (identified through microscopy) compared against "reference" taxa counts	In coastal waters only: single species and total taxa count of all phytoplankton species (identified through microscopy) compared against "reference" taxa counts	Not implemented for UK waters—though narrative of phytoplankton changes in biodiversity assessments included in OSPAR reporting
	Macrophytes including macroalgae (area-specific) Elevated levels (biomass or area covered) of opportunistic green macroalgae Area and size of saltmarsh and seagrass systems	Opportunistic macroalgae (used only for coastal waters) Extent and density and biomass, of nuisance green macroalgae on sediment, together with overwintering and entrainment. Measure during the period of maximum growth once every 3–6 years	Not included in eutrophication assessment in UKMS	Not implemented in OSPAR assessment
		Saltmarsh—metrics of area extent, dominance of saltmarsh zones, saltmarsh taxa diversity		
		Intertidal seagrass—change in species composition, change in areal extent of beds, change in percentage cover Subtidal Seagrass—bed extent, bed density, maximum bed depth		
III. Secondary impacts from elevated nutrients: indirect biological impacts	**Oxygen deficiency**	Dissolved Oxygen (DO) calculated from surface samples. 5th percentile calculated for each assessment area	Dissolved Oxygen (DO) calculated from surface samples. 5th percentile calculated for each assessment area	Bottom DO (July to October)—calculated from deepest sample within 10 m of seabed. 5th percentile calculated for each assessment area

(Continued)

TABLE 1 (Continued)

Category	Indicator	Current UK eutrophication assessment frameworks		
		WFD/WER	UK Marine Strategy—Part 1	OSPAR Common Procedure 4 (COMP4)
	Photic limit (water transparency of the water column)	Turbidity used in nutrient assessment for transitional waters	Not implemented	Not implemented
	Phaeocystis	Not implemented	Not implemented	Considered by OSPAR but not implemented in UK waters

DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; GS, growing season, typically the period between March to September; Winter, November–February.
UK Marine Strategy Part One refers to a nationally based assessment of UK marine waters that measures progress toward GES.

process which takes the lowest value of biological elements (phytoplankton, macroalgae), while the most recent OSPAR common procedure (COMP4) used the lowest value of the chlorophyll and dissolved oxygen indicators, and the UK Marine Strategy (Part 1) combines outputs from both. Nutrients in all three directives cannot, on their own, designate a "failure" if the biological elements do not also "fail." A failure is when a waterbody is designated as less than moderate status under the WFD/WER or not meeting good environmental status (GES) under UK Marine Strategy (Part 1) and OSPAR. However, failing nutrients can cause potential risk, and is designated as a "potential problem area" under OSPAR or high risk of future failures under the recent UK Marine Strategy (Part 1) and is identified in the WFD/WER as failing physico-chemical standards.

3.1.4 From "increased growth" to "changes to the balance of organisms"

In two cases (ECJ, 2004, 2009) the European Court of Justice ruled that the definition of eutrophication in the UWWTD must take account of "significant harmful effects of the accelerated growth of algae and higher forms of plant life resulting from discharges of urban wastewater," that include "an undesirable disturbance of the balance of organisms present in the water." However, because of lack of agreement amongst OSPAR signatories about adding indicators of phytoplankton community composition, the OSPAR Common Procedure has remained focused on the bulk variables, chlorophyll concentration and oxygen deficiency, as the key common indicators of the direct and indirect biological impacts associated with eutrophication of the water column.

This was also the case for the eutrophication Qualitative Descriptor (QD) of the EU Marine Strategy Framework Directive (EU MSFD), as interpreted by the European Commission (COM, 2017). Instead, what we understand as the health, good functioning, and balance of organisms of the plankton in the pelagic habitats, and which COM (2017) refers to as "the essential features and characteristics and current environmental status of marine waters" in relation to the EU MSFD's aim to achieve Good Environmental Status, was assigned (Borja et al., 2010) to the Biodiversity QD and the Food-Webs QD. In a separate process from OSPAR COMP4, Biodiversity and Food-Web indicators have also been assessed by OSPAR in a recent Quality Status Report (QSR) on the pelagic habitats (PH) of the North-East Atlantic (McQuatters-Gollop et al., 2022; Holland et al., 2023a,b). The relevant "PH" indicators PH1/FW5, based on the abundances of plankton lifeforms and Food-Webs, PH2 (also used for Food-Webs) based on biomass at each trophic level, and PH3, based on numerical biodiversity. There is continuing work to disentangle the effects of nutrient enrichment, fisheries and climate change on the PH1 indicators (McQuatters-Gollop et al., 2019; Holland et al., 2024).

There would, thus, seem to be two options for conceptualizing the changes in pelagic habitats/ecosystem state associated with eutrophication. One option is to understand eutrophication as being the increased production of organic matter and changes in the balance of organisms in pelagic habitats are seen as a consequence rather than a part of eutrophication: the view currently taken by the EU in the MSFD (Borja et al., 2010; COM, 2017) and by OSPAR, the latter having separate strategies for eutrophication and biodiversity. The other option is to see nutrient enrichment as one of several anthropogenic pressures on pelagic habitats, leading to perturbations of their normal functioning which may lead to regime shift (Tett et al., 2007, 2013; Gowen et al., 2012) as the most significant of the "undesirable disturbances" that according to the ECJ make up the final component of the eutrophication process.

3.2 Identify key evidence gaps in current practices

3.2.1 Recognizing what has worked is the first step

There have been many successes associated with the implementation of the UK eutrophication assessments, leading to positive program of measures and the reduction of nutrient inputs from both direct and diffuse sources. Starting as early as 1988, the OSPAR Contracting Parties agreed to reduce nutrient emissions to the Greater North Sea by 50%. Since then, several OSPAR Recommendations, land management initiatives and controls from regulations such as the Urban Wastewater Treatment Directive (UWWTD) (Council Directive 91/271/EEC) and WFD/WER have been taken to combat eutrophication. These include measures targeting diffuse run-off from land, atmospheric nitrogen emissions, wastewater, and other point sources. These responses have led to significant improvements in nutrient loadings to the UK marine waters since the start of monitoring in 1990. On a European scale, many measures to reduce inputs have been

implemented by European Union directives covering wastewater treatment, nitrates in agriculture, industrial emissions and water and marine management with dramatic improvements in the form of atmospheric nitrogen input reductions and a reduction in fertilizer use, since 1990 (OSPAR, 2023). The four applications of the Common Procedure have revealed a steadily improving trend in the eutrophication status of OSPAR Regions II, III, and IV. Success can also be measured by the application of the eutrophication assessments, with detailed assessments completed by regulatory agencies increasing our knowledge of high-risk areas, identifying where and how programmes of measures can be implemented.

However, during the last decade, improvement trends have slowed down, with heightened concerns regarding increasing nutrient inputs from diffuse agricultural loads, combined sewage overflows and the growing marine aquaculture industry.

The application and outcomes of these assessments, whilst identifying areas that are at risk from eutrophication, can and should be improved. The original assessments were set up to define eutrophication through a set of indicators, with thresholds that were developed on historical understanding and expert knowledge. This is an evolving area, and our understanding of what is required into the future to ensure our understanding of eutrophication, to fully utilize the many emerging data sources, to look beyond simple indicators of state, and to account for climate change, requires adaptation and updating of our current methods. We present a series of recommendations around the improvement of data, alignment between different UK assessment frameworks, updating and improving eutrophication indicators, embedding ecosystem indicators within the eutrophication assessment and consideration of the interactions between climate and eutrophication (Figure 1). These recommendations set out priority areas for future assessments which are then assessed considering cost, feasibility and outcomes.

3.2.2 Improving data flows

3.2.2.1 Autonomous and remotely collected data

Our long-term monitoring datasets are the critical baselines from which we have developed and continue to develop our understanding of the changes in our coastal and marine systems. However, it is not feasible or affordable to collect all data all the time. The way we collect eutrophication assessment data is evolving, from traditional vessel-based sampling data (*in-situ* sampling and *ex-situ* analysis) to include autonomous data from *in-situ* sensors, satellites, and biogeochemical models (Bean et al., 2017). Furthermore, machine learning and artificial intelligence are changing the way we collect, analyse and report data within eutrophication assessments (Borja et al., 2024). There will always be a need to continue long-term, traditional *in-situ* sampling alongside the collection of new data types to ensure continuity of data collections for analysis and identification of trends and validation of the high frequency data sets (Addison et al., 2018; Mack et al., 2020; Holland et al., 2025), but as our technology changes, so must our approach to data streams, data repositories and assessments. We must consider data processes that can fully integrate novel and high frequency data into our statutory monitoring programs to improve understanding of complex coastal and marine processes (Dafforn et al., 2016; Addison et al., 2018) whilst ensuring robust validation of these new technologies (García-García et al., 2019; Holland et al., 2025).

High frequency and autonomous data collected and analyzed *in-situ* and instruments deployed from ships, continuously running on ships, and deployed on buoys is still not readily used in current assessments, despite increasing the data frequency substantively for some water quality parameters. Nutrient data rely predominantly on *in-situ* samples, with buoy-deployed sensors providing additional high-temporal resolution data in limited areas (Figure 3). Bottom-water oxygen concentrations also rely predominantly on *in-situ* data but have more recently been supplemented with ship-deployed profiler sensor data significantly increasing the spatial and temporal data coverage (Greenwood et al., 2010; Hull et al., 2020, 2021). Chlorophyll is measured from water samples as well as sensors, with increased spatial and temporal resolution resulting from "FerryBox" data: an automated flow through system which continuously measures surface water concentrations aboard the ship, and from remote sensing data (Petersen et al., 2003, 2008; Harvey et al., 2015; Bean et al., 2017; El Serafy et al., 2023).

Remote sensing data can provide a valuable source of monitoring data, that includes chlorophyll, measures of turbidity and primary productivity and ecological health (Devlin et al., 2013, 2015; Petus et al., 2014, 2016, 2019; Capuzzo et al., 2018; Patricio-Valerio et al., 2022; Mohseni et al., 2022). Satellite earth observation data for chlorophyll were used for the first time in the recent OSPAR eutrophication thematic assessment (Devlin et al., 2023; van Leeuwen et al., 2023) combining data from *in-situ* sampling with higher frequency and higher spatial resolution data from remote sensing chlorophyll data (Lavigne et al., 2021) with outcomes transferred into the upcoming 2025 UK Marine Strategy assessments for marine waters (Figure 3). However, remote sensing (satellite) data has not yet been included in WFD/WER assessments due to higher uncertainties in nearshore waters, which are particularly important for eutrophication, and have observation gaps related to cloud cover (Klemas, 2011; Wei et al., 2020). Biogeochemical modeling data can also provide a potential means of supplementing limited observation data including for nutrients and oxygen, but uncertainties and model biases have prevented modeling data from being included in assessments, though some models have been invaluable for setting historical thresholds (Stegert et al., 2021; van Leeuwen et al., 2023). Full integration of high frequency data within relevant assessment areas will improve detection of when and where changes in eutrophication status are occurring.

Whilst frequency of data collection is increasing in some areas due to improved technology, some aspects of the UK's eutrophication monitoring programme are suffering significant reductions related to decreasing sampling-based monitoring in response to budget reductions. For example, the number of offshore samples taken for nutrient concentrations during the winter months which make up the eutrophication assessment period has been decreasing over the last 10 years, given the costs associated with large field programs and offshore sampling. *In situ* vessel sampling is resource intensive and requires ship-based sampling

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	Type of data	Start date	Data characteristics	Spatio-temporal frequency	Use in eutrophication assessments
	Riverine Load	1975	Water quality (ammonium, nitrate, phosphates, total dissolved nitrogen and phosphorus, suspended particulate matter) sampling of rivers at their tidal limit. 'Direct discharges' from sewage, aquaculture and other industries downstream of riverine monitoring stations monitored separately.	Sampling is ideally monthly, though some rivers are monitored weekly and some only quarterly. Direct monitoring is also ideally monthly but now quarterly in many cases. Concentration data are combined with flow measurements to estimate discharges; flow data is available at higher temporal resolution. Data are reported for 39 segments of coast, with more than 150 rivers monitored.	Provides input into national and OSPAR assessments of nutrient discharges, presented as long-term trends of annual loads.
	Ship-based water quality sampling	1975	In-situ samples taken via Niskin bottles from research vessels, analysis carried out ex-situ (boat or laboratory) for salinity, dissolved inorganic nutrients, chlorophyll, phytoplankton community composition and abundance, dissolved oxygen and suspended particulate matter.	Collected on sporadic research cruises, plus targeted monitoring surveys throughout the year. Potential spatial coverage of UK Exclusive Economic Zone (EEZ) offshore.	Main data source for all UK assessments, both inshore and offshore.
	Ship-based sensor data via single or multiple conductivity-temperature-depth (CTD) profilers	1985	Depth profiling of conductivity, temperature, depth, fluorescence, turbidity, dissolved CO_2 (pCO_2), photosynthetically active radiation (PAR) and dissolved oxygen when taking water samples. Data requires different levels of calibration.	Collected on sporadic research cruises, plus targeted monitoring surveys in winter and summer. Potential spatial coverage of UK EEZ.	CTD data has been submitted to the ICES database and can now potentially be used in future assessments, particularly dissolved oxygen data. Agreement on depth profiling data submission still in progress for UK.
	SmartBuoys	2000	Conductivity, temperature, depth, fluorescence, turbidity, PAR, dissolved oxygen. Autonomous water sample data measured by sensors and dissolved inorganic nutrients, phytoplankton community composition and abundance determined on autonomously collected water samples.	Autonomous, high frequency (30 min) measurements at discrete locations.	Autonomous water sample data including water and plankton samples has been submitted to the UK MERMAN database and is available for OSPAR and UKMS assessments.
	High Resolution models	2007	Salinity, temperature, chlorophyll, dissolved inorganic nutrients, dissolved oxygen, suspended particulate matter, phytoplankton groups.	High temporal frequency (seconds–days). High spatial frequency (metres–kilometres).	Not yet used in assessments. However, models were used to develop current thresholds and assessment areas for UK marine areas.
	FerryBox	2009	Conductivity, temperature, fluorescence, turbidity, dissolved oxygen measured by sensors.	Autonomous, high frequency (1–5 min).	Potential spatial coverage of UK EEZ. Data products have been developed based on daily averages. Not yet used in assessments.
	Satellites	2001	Ocean colour measured by sensors. Data requires different levels of calibration.	High spatial frequency (0.3–4 kilometres).	Chlorophyll products included in last OSPAR eutrophication thematic assessment. Satellite data is also included for variability.

FIGURE 3
Different types of data collected in the UK Eutrophication monitoring programs describing the resolution, data characteristics and if the data has been used in UK Eutrophication assessments.

during logistically challenging bad weather months in winter. Sensor data for nutrients tends to be spatially limited to inshore sites and (for UK) at three autonomous sites (Mills et al., 2003, 2004). However, satellite and modeling data offers a new source of data for offshore waters and are already becoming an invaluable source of data for coastal and marine waters.

3.2.2.2 Monitoring inputs from land to sea

Accurate and timely information on nutrient concentrations and nutrient loads is integral to strategies designed to improve human wellbeing and manage the underlying drivers of water quality impairment and inform program of management measures (Joo et al., 2012; Pellerin et al., 2016). UK input monitoring for nitrogen and phosphorus has decreased in recent years, particularly in England and Scotland. For OSPAR, this monitoring consists of riverine inputs as well as "direct discharges" from sewage, industry and marine aquaculture (Axe et al., 2022) and aims to capture 90 % of inputs (Joo et al., 2012; Pellerin et al., 2016). Reductions in data frequency can impact our collective ability to understand if river systems are changing.

Recent studies have identified a common problem for many coastal waters, where abatement of phosphorus loads has occurred at a much faster rate than nitrogen abatement and mitigation (Lu and Tian, 2017; Ngatia et al., 2019; Devlin and Brodie, 2023). This has led to imbalanced nutrient ratios, where rivers and coastal systems are experiencing reductions associated with phosphorus but stabilization and/or or increases in nitrogen most likely due to increases in diffuse N from agriculture and direct sewage inputs. These nutrient imbalances can impact on plankton communities in coastal waters (Romero et al., 2012) but limited monitoring of nutrient loads and concentrations leads to a lack of understanding of the extent of this issue and coupled with changing climate and shifts in seasonality means that we may not be tracking these changes with sufficient confidence in our data.

The recent OSPAR eutrophication thematic assessment also identified issues around the monitoring of aquaculture loads, as the

extent of the growth in aquaculture within the OSPAR Maritime Areas has been substantial (Axe et al., 2022; OSPAR, 2023). A gap exists concerning the agreement of minimum environmental standards for aquaculture across the OSPAR Maritime Area which is relevant to UK waters given the rise of aquaculture in many coastal areas. A more strategic approach to monitoring nutrient inputs could rationalize the collection of high-density data to focus on a few rivers, sub-catchments, and transitional and coastal waterbodies. This would require detailed analysis of existing monitoring data to identify candidate waterbodies that could best represent the types of coastal systems across the UK as well as incorporating land-use data and modeling which are not currently integrated with marine eutrophication assessment frameworks.

3.2.3 Improving the alignment between directives

3.2.3.1 Connecting the catchment to coast

Whilst the WFD/WER, UK Marine Strategy and OSPAR COMP advocate for a river basin approach, the directives are not always aligned. There is a disconnect between geographical boundaries and indicator thresholds which hinders understanding of eutrophication status across the continuum from transitional and coastal to marine waters (Foden et al., 2011). Alignment between decision making on programmes of measures and downstream impacts is not possible when there is disaggregated policy implementation across agencies, reporting to different government areas and stakeholders (Figure 4). Historically, UK terrestrial and marine environmental policies have been largely delivered in isolation despite the marine system being explicitly connected to the land with most of the marine pollution originating from terrestrial sources (Howarth, 2008). This has resulted in a disconnect between inshore and offshore assessments across the arbitrary policy line at 1 nm (3 nm in Scotland) that separates coastal water bodies under WFD/WER from the full extent of riverine plumes and the OSPAR and UK Marine Strategy assessment areas further offshore. This disjointed approach hinders our understanding of how land-based management measures are impacting our coastal systems. There is also a disconnect between eutrophication indicators and thresholds developed for OSPAR and those developed and applied under the WFD/WER, reflected in the UK Marine Strategy where the outcomes from different assessments were combined without full harmonization of data or assessment structures. More work is required to progress beyond the current method of simply combining the coastal and offshore assessment outcomes derived by different methodologies (Devlin et al., 2007a, 2023; Foden et al., 2011).

Future assessments should consider a fully integrated catchment to coast approach (Waterhouse et al., 2011; Brodie et al., 2012; Creighton et al., 2021) which has greater potential to change the input of terrestrial contaminants into our marine environment with subsequent positive effects on the coastal ecosystem. Managing catchments to control diffuse pollution into downstream coastal systems will also provide benefits for freshwater systems. Future eutrophication assessments should be managed more holistically, bringing diverse stakeholders together to ensure common and opposing interests are included, and to assess impacts over the ecological and hydrological boundaries.

3.2.3.2 The importance of riverine influenced areas

Until recently, eutrophication assessments carried out for the UK Marine Strategy and the OSPAR COMP have used assessment areas defined by geographical or political boundaries rather than those which are ecologically coherent and fully represent the extent of terrestrial influence in marine waters (Foden et al., 2011; van Leeuwen et al., 2015; Devlin et al., 2023). The UK coastal zone covers up to 10% of the Exclusive Economic Zone (EEZ) though that number varies dependent on the definition of coastal zone. The coastal zone is dynamic with high spatial and temporal fluctuations influenced by tides, stratification, wind and river discharges, which all influence variation in the water quality measurements. This was recognized within the initial implementation of the EU WFD (Vincent et al., 2022) which developed an approach to defining transitional and coastal typologies characterized by tidal range, mixing, salinity and depth. However, the seaward edge of the coastal assessment areas was defined by a 1 nm offshore limit for England, Wales and NI and by a 3 nm limit for Scotland, leading to abrupt delineations between the nearshore coastal areas assessed under the WFD/WER and coastal to offshore areas assessed under UK Marine Strategy and OSPAR.

Riverine freshwater plumes are the major transport mechanism for nutrients, sediments and pollutants and connect the land with the receiving coastal and marine waters. Knowledge of the variability in the extent of freshwater influence into UK marine waters is relevant for environment managers to develop strategies for improving ecosystem health and risk assessments (Schroeder et al., 2012; Devlin et al., 2012b, 2015). An approach using satellite derived suspended particulate matter (SPM) and *in situ* salinity provided a first estimate of the physical, chemical and biological processes (Greenwood et al., 2019) with the area of riverine influence mapped using salinity and satellite derived suspended particulate matter (Ivanov et al., 2020; Fettweis et al., 2023; Desmit et al., 2024). Sea surface salinity is the most traditional conservative tracer of freshwater discharge; however, it can be difficult to extract direct satellite-based salinity measurements with sufficient spatial resolution for coastal applications (Schroeder et al., 2012).

Although these mapping methods can improve assessments across ecologically homogeneous areas, defining river plumes seasonally and with a relatively high resolution in coastal areas is still required to assess water quality conditions across estuarine and intertidal habitats (Fronkova et al., 2022; Heal et al., 2023). Plume mapping of UK waters has now progressed to deriving and mapping the Forel Ule color scale, as determined from high resolution Sentinel-3 satellite imagery data at 1 km^2 resolution for England and Wales and using the 4 km^2 resolution for Scottish coastal waters (Fronkova et al., 2022). Using the relationship between ocean color and water quality parameters, recent work has defined geographically resolved assessment areas through the mapping of ocean color (Greenwood et al., 2019; Fronkova et al., 2022; Heal et al., 2023) (Figure 5). The most recent OSPAR QSR implemented a new set of ecologically relevant assessment areas (Figure 6) developed specifically for eutrophication assessment with common indicators

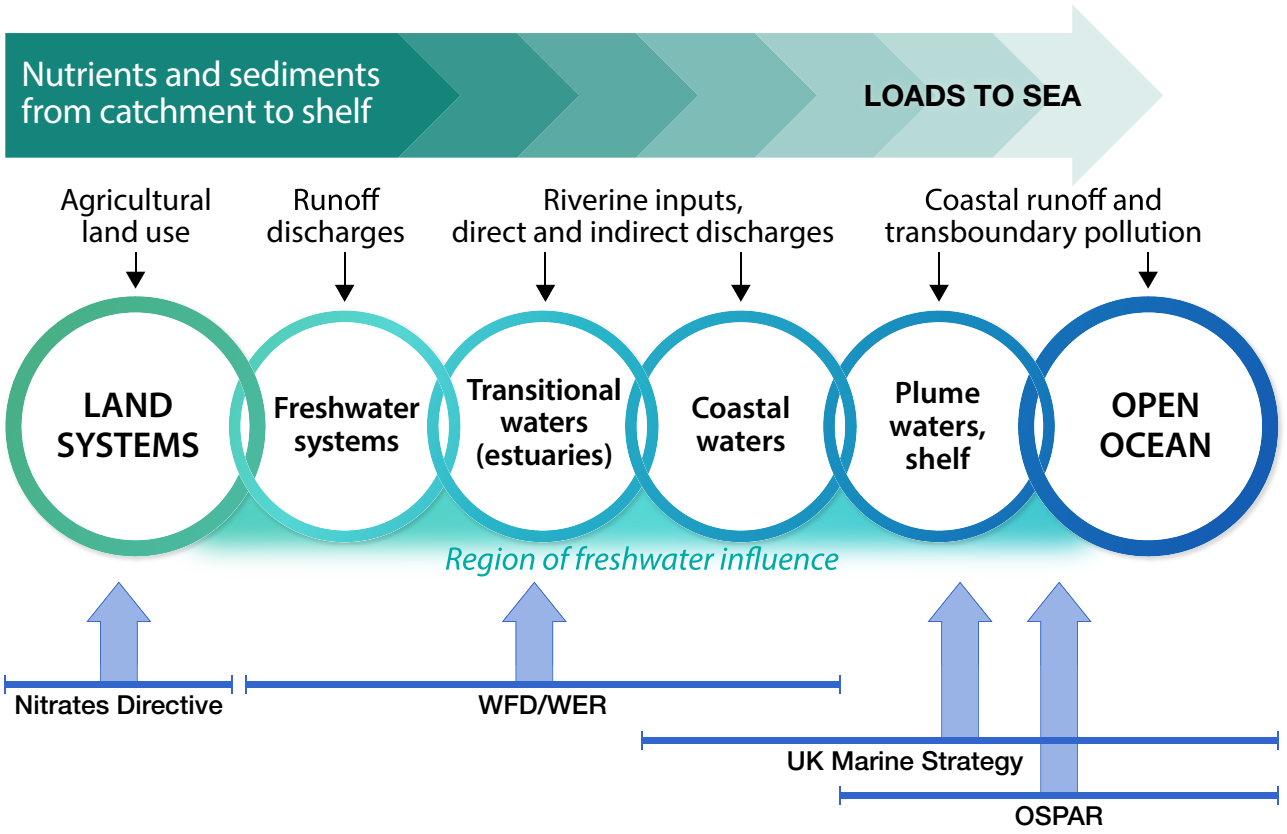

FIGURE 4
Eutrophication assessments span across the land to sea continuum, working across different regulations, upstream to downstream systems and a wide range of stakeholders. Different monitoring programs from across UK environment and regulatory agencies feed into the UK's national eutrophication assessment.

and harmonized thresholds across national boundaries (Devlin et al., 2023; Lenhart et al., 2010; van Leeuwen et al., 2023). The new OSPAR assessment areas and thresholds, carried across for the UK Marine Strategy eutrophication assessment provides a much stronger alignment between nearshore and coastal marine waters than previous assessments, with the inclusion of plume areas and more localized coastal assessment units (Figure 5) which can be expanded into future assessments (Devlin et al., 2023).

3.2.4 Improving our indicators of eutrophication

The eutrophication frameworks, outcomes and subsequent program of measures were based on best available information around key eutrophication indicators including nutrients, phytoplankton biomass (measured as chlorophyll) and dissolved oxygen (OSPAR, 2003, 2008a). WFD/WER assessments also use phytoplankton counts in coastal waters. These indicators are, and continue to be, highly relevant to measuring the extent and impact of eutrophication (Bricker and Devlin, 2011; Devlin et al., 2011). However, using these indicators only can limit our understanding of ecosystem impacts, and there is an urgent need to expand, both in the improvement of our current indicators and through the development of new indicators.

3.2.4.1 Indicators should consider trends and trajectory of change

Measuring nutrient loads and concentrations are important parts of understanding the trajectory of risk and potential impact of eutrophication. Reduction of diffuse nitrogen and other agricultural pollutants after the implementation of EU and UK directives, whilst initially successful, has leveled off over time. The abatement of nitrogen has not kept pace with the scale required across all catchments and diffuse nitrogen losses are now the main source of nitrogen loading into coastal and marine waters (Worrall et al., 2016; Zhang et al., 2022). At the same time, there has been an increase in the farmed fish industry in some coastal regions resulting in increasing point source introduction of nutrients to the environment that are not considered in our current assessments (Olsen et al., 2008; Holmer, 2010; Edwards, 2015). Our current assessments, using a multimetric approach incorporating several indicators, are based on status assessment (a single value aggregated over 6-year cycle), but associated trend assessments are not currently part of the quantitative assessment of eutrophication indicators. The incorporation of trend data into assessments can demonstrate the trajectory of change and help in predictions of future state. However, in the recent UK Marine Strategy and OSPAR COMP, long term changes in nutrient inputs were assessed using Mann-Kendall analysis to detect trends,

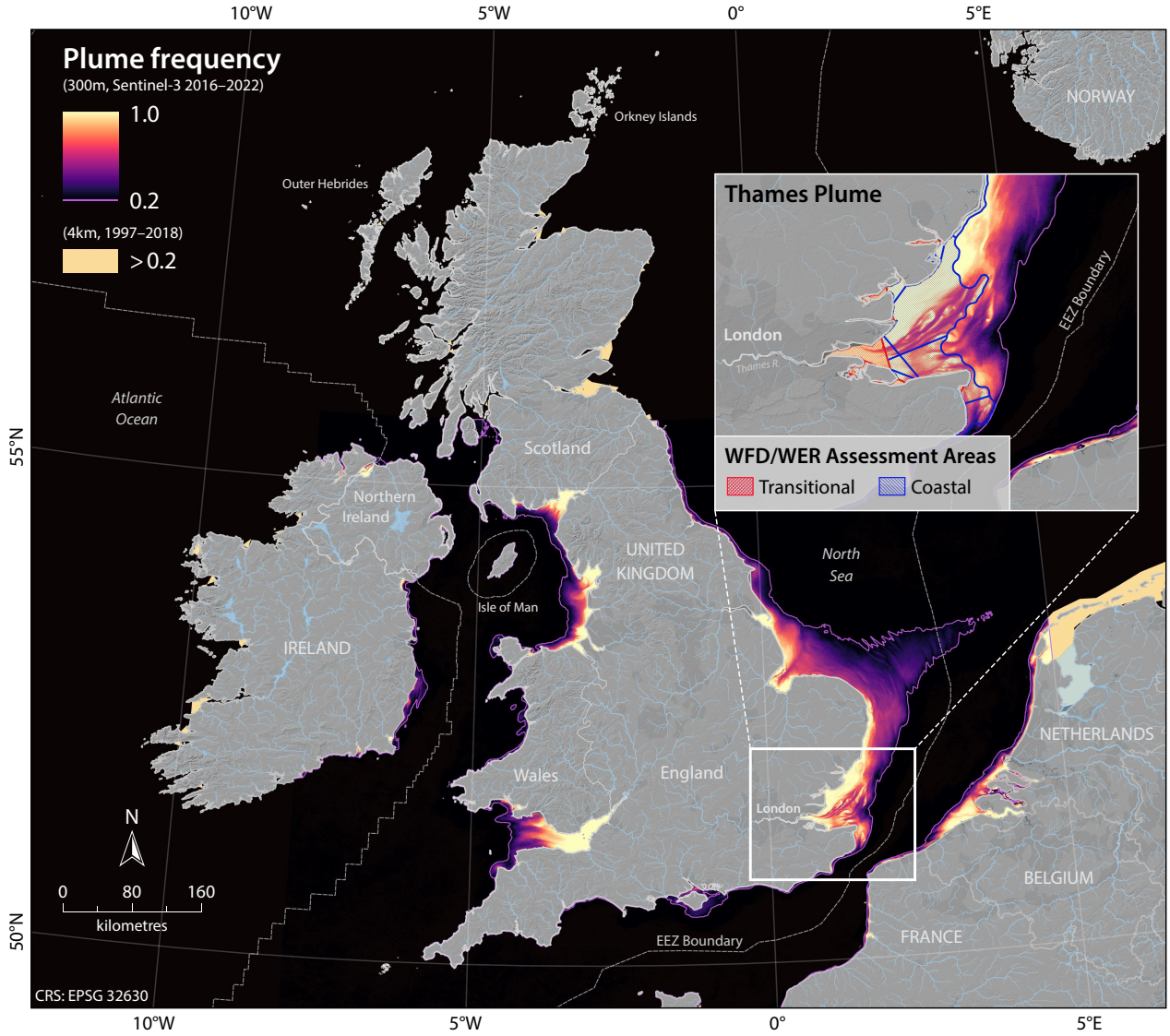

FIGURE 5
Riverine influenced areas for the UK are based on two different types of plume methodologies, with a higher 300 m resolution plume extent derived from the Forel Ule Index (FUI) from Sentinel-3 and lower resolution plume extent derived from Pitarch et al. (2019) 4 km FUI data. The FUI derived from Sentinel-3 has been used to map the extent of flood plumes, with FUI values of 10 or above being representative of riverine-influenced areas. The purple line designates the maximum plume extent, where the area is exposed to riverine plume at least 20% of the time between 2017–2022. Both approaches have been applied in England, Wales and Northern Ireland waters, with only the 4 km resolution imagery applied in Scotland. Development of plume imagery detailed in Fronkova et al. (2022).

quantifying (where present) monotonic trends in timeseries data, based on comparing each year's value to all preceding years (Devlin et al., 2023). This non-parametric method is useful for long term environmental data as it is not affected by any transformation of the annual data values, and it is flexible for time-series with missing data points (Bedford et al., 2020; Desmit et al., 2020). Non-parametric trend tests require only that the data be independent and can tolerate outliers (e.g., resulting from a change in analytical detection limit) and missing values in the data. Expanding the use of trend analysis such as Mann-Kendall will allow greater scrutiny of the direction of travel alongside assessment of state.

3.2.4.2 Indicators that consider susceptibility to eutrophication

Phytoplankton, through their chlorophyll cells, absorb light to provide energy for photosynthesis. Light is rarely limiting in offshore waters, but the more turbid, variable inshore waters can make it difficult for plankton to absorb enough light to grow (Devlin et al., 2008). The clarity and composition of highly dynamic estuarine and coastal waters can help inform susceptibility of the coastal and marine waters to eutrophication (Cloern, 1987, 1999, 2001). Vertical attenuation of light through the water column is attributable to the optically active components of phytoplankton, suspended particulate material (SPM) and chromophoric dissolved

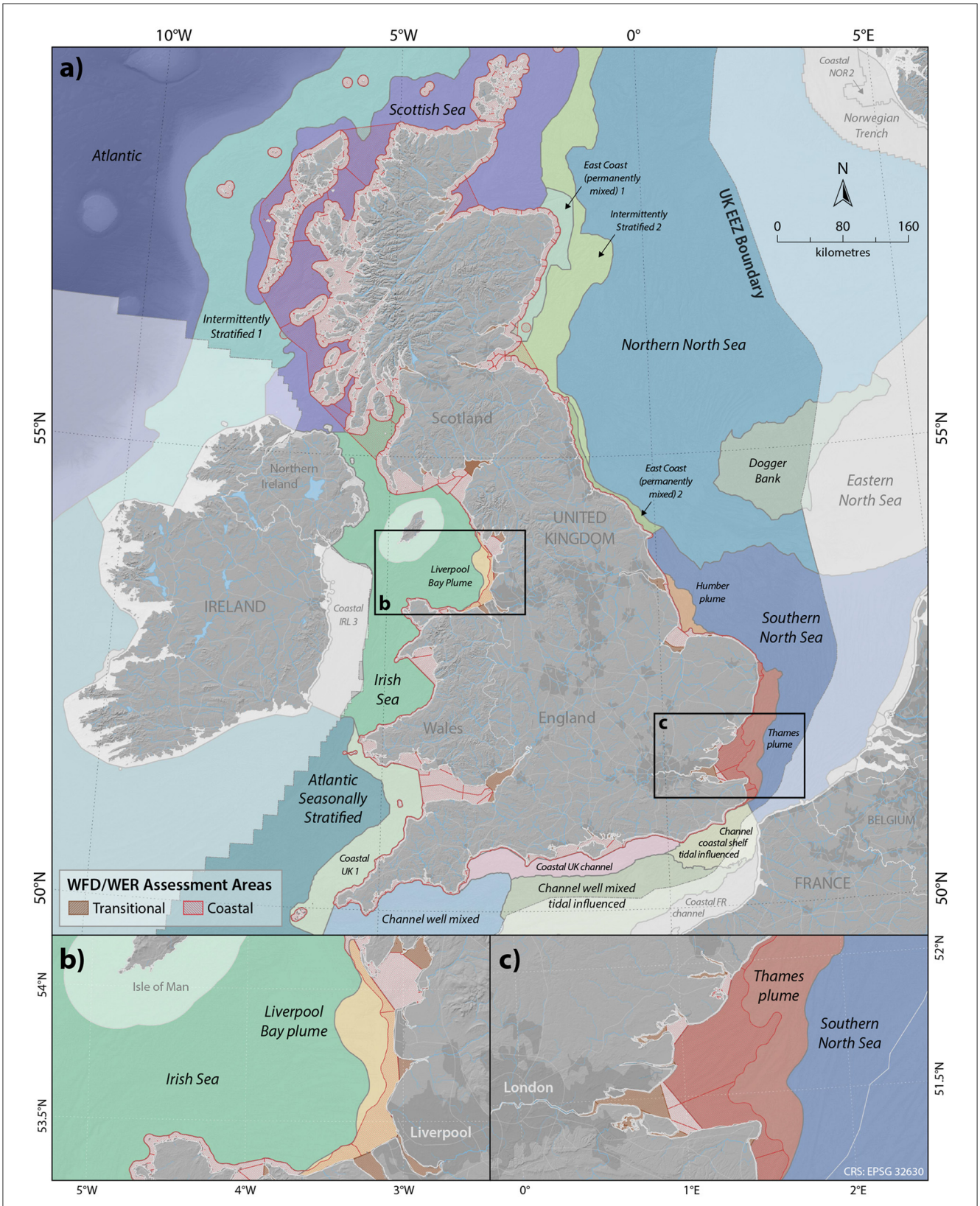

FIGURE 6
UK assessment areas reported under OSPAR Quality Status reporting. Note that several of these areas are shared with other OSPAR member states including Atlantic, Irish Sea, Northern North Sea and Southern North Sea, areas outside of the UK EEZ are lighter in color. WFD/WER coastal assessment units are highlighted in red. **(a)** Full extent of the UK assessment areas for coastal and offshore waters zoomed in to estuarine and coastal areas of **(b)** Liverpool Bay and **(c)** Thames embayment.

organic matter (CDOM). SPM is routinely measured in all UK monitoring programs but is not used as a standalone indicator. However, SPM is used in WFD/WER eutrophication assessments when nutrient concentrations exceed thresholds, and an additional (higher) threshold is applied if SPM is high (Greenwood et al., 2019). In offshore waters, CDOM originates predominantly from bacterial decomposition of phytoplankton cells, whereas in coastal waters, CDOM is dominated by humic and fulvic acids of terrestrial origin and transported to the seas through freshwater runoff from the land as well as autochthonous CDOM from salt marshes, mangroves, inter- and sub- tidal benthic microalgae, seagrasses, macroalgae and corals (Carder et al., 1989). CDOM is not routinely measured for eutrophication monitoring and assessment (Foden et al., 2008) despite being a key measurement for understanding riverine influenced plumes and light dynamics.

CDOM, ocean color, light attenuation, turbidity and SPM are all important elements in understanding the extent of the estuarine and coastal systems and the dynamics of the light conditions. Foden et al. (2008) discuss how applying a simple dose-response model of nutrient enrichment to risk of eutrophication does not consider the important role light plays in marine waters, and limits understanding of the complex interactions at play. Cloern (1999, 2001) recognizes system attributes that "filter" responses to changes in nutrient loading, including the underwater light climate, horizontal exchange, tidal mixing, grazing and biogeochemical processes. This complex response determines susceptibility, which influences the assessment of eutrophication status. The light climate is highly variable in UK waters and therefore of particular significance regarding the risk of eutrophication (Devlin et al., 2008; Foden et al., 2008, 2011).

Over the last century, the world oceans and coastal regions have experienced changes to marine lightscapes in two fundamental ways. Firstly, regions such as the Norwegian Fjords have experienced a long-term reduction in water clarity, referred to as Coastal Darkening (Aksnes et al., 2009) with large-scale drivers that are connected to effects of climate change such as more frequent and intense rainfall, increased temperatures, and other human activities that increase erosion (Dupont and Aksnes, 2013; Organelli et al., 2017; Frigstad et al., 2023). A reduction in the light availability will impact key eutrophication indicators such as phytoplankton (Capuzzo et al., 2018; Opdal et al., 2019; Wollschläger et al., 2021). Secondly, some coastal regions are experiencing a brightening of the night-time light environment linked to urbanization, on- and offshore infrastructures, fisheries, and shipping (Smyth et al., 2022; Davies et al., 2023). Knowledge of changes in natural light conditions needs to be a key part of eutrophication (and climate change) assessments into the future. The latest round of assessments show that the UK has many high nutrient transitional and coastal waters, but most of these were not deemed eutrophic due to not being able to show an "undesirable disturbance." For example, conditions in UK coastal waters with high turbidity and large tidal systems are assumed to not support the proliferation of high biomass (Cloern, 1987; Thornton et al., 2002; Tweedley et al., 2016). However, recent work has shown that high growth can still occur under turbid conditions, with productivity remaining high despite light limitation (Gonçalves Leles et al., 2018). More work on the role of mixoplankton is required as it is now recognized that most phytoplankton and as much as half the protist-zooplankton combine both plant-like photosynthesis and animal-like consumer activity synergistically within the same single-cell (Ward and Follows, 2016; Stoecker et al., 2017; Gonçalves Leles et al., 2018; Mitra et al., 2024).

3.2.4.3 Indicators require improved understanding of natural variability

Our understanding of natural variability needs to evolve alongside our understanding of the complexity of our coastal and marine systems. The recent OSPAR eutrophication thematic assessment used an ensemble model approach to derived pre-eutrophic conditions (Lenhart et al., 2010; Stegert et al., 2021; van Leeuwen et al., 2023). Nutrient loads into the north-east Atlantic were estimated from rivers under historic conditions prior to 1900, using the European model E-HYPE and observations with historic (pre-eutrophic) conditions (Lenhart et al., 2010; Stegert et al., 2021). Reference chlorophyll concentrations were derived corresponding to the estimated nutrient concentrations under reference conditions. To account for natural variability allowing for a "slight disturbance" in the absence of more specific information, the assessment levels (thresholds) were then defined as a concentration of 50% more than the area-specific background concentration derived from the ensemble model approach (Malcolm et al., 2002; Borja, 2005; OSPAR, 2008b, 2022) which set the threshold between Non-Problem and Problem Areas. This is equivalent to the boundary setting good/moderate for the EU Water Framework Directive (WFD) and boundary setting between GES and non-GES for UK Marine Strategy and the EU MSFD (Claussen et al., 2009; Maas-Hebner et al., 2015; Topcu and Brockmann, 2021). However, when using long term monitoring data from the recent OSPAR eutrophication thematic assessment the natural variability for the common indicators (from 2015 to 2020) in UK waters varies between 24% and 56% (OSPAR, 2023). Whilst a deviation from baseline is important for all assessment processes, future assessments need to analyse "true" natural variability and look for commonalities and differences between assessment areas and different indicators.

3.2.4.4 Indicators that consider societal impacts, including environmental, social and economic drivers

Embedding environmental and societal information alongside our more traditional monitoring and assessment processes is required to fully integrate ecosystem state, pressures, stakeholders, and policy (Kristensen, 2004; Borja et al., 2006; Patrício et al., 2016). This could include quantification of economic and environmental connections, greater integration of the reporting of complex interactions between social, economic, and ecological factors, multi-disciplinary frameworks and enhanced community engagements.

One such well known framework that has achieved many positive results is the DPSIR framework, which incorporates Drivers (D), Pressures (P), State (S), Indicators (I), and Response (R). The DPSIR framework is a widely used approach to understand interconnected layers and measure the driving forces of change (Elliott et al., 2017; Kristensen, 2004; Martin et al., 2018; Patrício et al., 2016). Simple messaging and clear linkages between human-induced drivers, pressures, state, impacts, and human welfare are crucial to drive outcomes into policy implementation

(Kristensen, 2004; Borja et al., 2006; Elliott et al., 2017; Martin et al., 2018). Drivers and pressures can be complex and difficult to measure and understanding the interactions between human drivers and ecological pressures is a key component to any monitoring and evaluation program, particularly one that spans from land to sea and multiple stakeholders (Oesterwind et al., 2016). The DPSIR framework has been adopted by the European Environment Agency and others (Borja et al., 2006; Atkins et al., 2011a; Patrício et al., 2016) and describes a framework for assessing the causes, consequences and responses to eutrophication in a holistic way including managing catchment to coast processes (Bowen and Riley, 2003; Langmead et al., 2007; Maccarrone et al., 2014; Le Gentil and Mongruel, 2015). DPSIR frameworks act as decision support systems which can enhance communication, knowledge transfer and interaction among scientists and policymakers, facilitating engagement among stakeholders and enhancing the legitimacy of the decision-making process (Newton and Weichselgartner, 2014).

Additionally, programs that include clear elucidation of cause and consequence, socio-economic pathways, and greater levels of engagement with communities are all attributes of successful monitoring and evaluation programs that could be applicable to UK coastal and marine systems (Figure 7). Embedding a greater understanding of natural capital into monitoring programs has been a successful way to incorporate the system flows between ecology, goods and services, and benefits to human wellbeing (Rhodes et al., 2017). Kermagoret et al. (2019) shows increasing eutrophication leads to a degradation of ecosystem service bundles, particularly for nutrient and pathogen regulation/ sequestration, or for the support of recreational and leisure activities. A cost benefit analysis on freshwater eutrophication in England and Wales, recognizing many data gaps, estimates the damage costs of freshwater eutrophication to be £75.0–114.3 million yr^{-1} (Pretty et al., 2002) highlighting the severe impacts of nutrient enrichment and eutrophication on many sectors of the economy. Estimates of local economic benefits for seaside recreation and waterfront property in Denmark through reduction of agricultural N losses were estimated at €35 million, with co-benefits of up to €57 million (Andersen et al., 2019). Conversely, the value of functioning coastal systems and nature based solutions to remove anthropogenic nitrogen can have wide ranging positive impacts and reduce costs of waste remediation (Watson and Beaumont, 2024). Cost accounting and reporting of natural capital benefits can be a valuable tool for positive policy implementation. Estimates of damage costs against policy response should be a critical part of any future eutrophication assessment.

Integrated approaches like the cross-sectoral and transdisciplinary One Health monitoring and evaluation framework (Stentiford et al., 2020), that emphasizes the interconnections between the health of humans and ecosystems, are highly applicable to an integrated eutrophication approach. These holistic approaches recognize the benefits of programs that are relevant to a range of end-users and contribute to positive changes through management actions that engage and represent the values of a diverse range of stakeholders impacted by the decision making. This is particularly true for local and regional stakeholders but can also extend to international partnerships and frameworks.

Greater engagement of the community, not only through data collection (i.e., "citizen science") but as an important part of the evaluation side, and by becoming embedded in decision making around policy and governance, should be a key requirement of greater success in monitoring and evaluation programs (Bischof, 2010; Cigliano et al., 2015; Darling et al., 2019). Local citizen scientists can cover important spatial gaps and when combined with long-term monitoring data from regulatory agencies, can add benefit to eutrophication monitoring programs (Loiselle et al., 2024).

3.2.4.5 Integration of indicators to multidirectional value of state

Current UK eutrophication indicators are assessed in terms of unidirectional exceedances. This approach does not fully encompass the range of conditions that support positive ecological functioning. For example, a chlorophyll threshold which, when exceeded, indicates only that increasing biomass can potentially result in undesirable disturbance to the ecosystem (Tett et al., 2007). However, recent work has also identified declining primary productivity (Capuzzo et al., 2018) due to warming waters and changing nutrient imbalances (Ryther and Dunstan, 1971; Lu and Tian, 2017; Nohe et al., 2020; Xu et al., 2020). Our eutrophication approach needs to consider the optimal range of values for each indicator, providing benchmarks for upper and lower limits. This approach would recognize that for some indicators, that there is a seasonal and temporal shape to the optimum range that needs to be considered and not just a single upper threshold (Tett et al., 2007, 2008; Bedford et al., 2020). Additionally, many of the indicators are intrinsically linked, and need to be operating in the optimum range across a wide range of interconnected ecological measurements.

Safe Space functioning is an emerging concept that is becoming more visible in our understanding of ecosystem state. Rockström et al. (2009) defined the boundaries for a "safe operating space for humanity, which outlines nine planetary goals that need to be supported together." The underlying concept of ecosystems being dependent on various conditions, all existing in the same conceptual space, should become a tangible part of our future thinking. Eutrophication assessments could develop a range of conditions that need to be met to ensure ecological functioning and resilience (Figure 8). This could be adapted from existing indicators of nutrients, biomass and dissolved oxygen, measures of important physico-chemicals such as turbidity and expand to look at corresponding plankton community metrics focusing on changes in plankton lifeforms impacted by eutrophication and primary productivity.

3.2.5 Improving our understanding of ecosystem impacts

3.2.5.1 Eutrophication as a plankton pressure

Eutrophication is a complex process and often associated with not only changes in overall algal biomass but also with changes in plankton community structure. Common eutrophication indicators (e.g., chlorophyll a, nutrients, dissolved oxygen) are not adequate for understanding biodiversity changes, especially those associated with the proliferations of HABs (Glibert, 2017; Anderson et al., 2002).

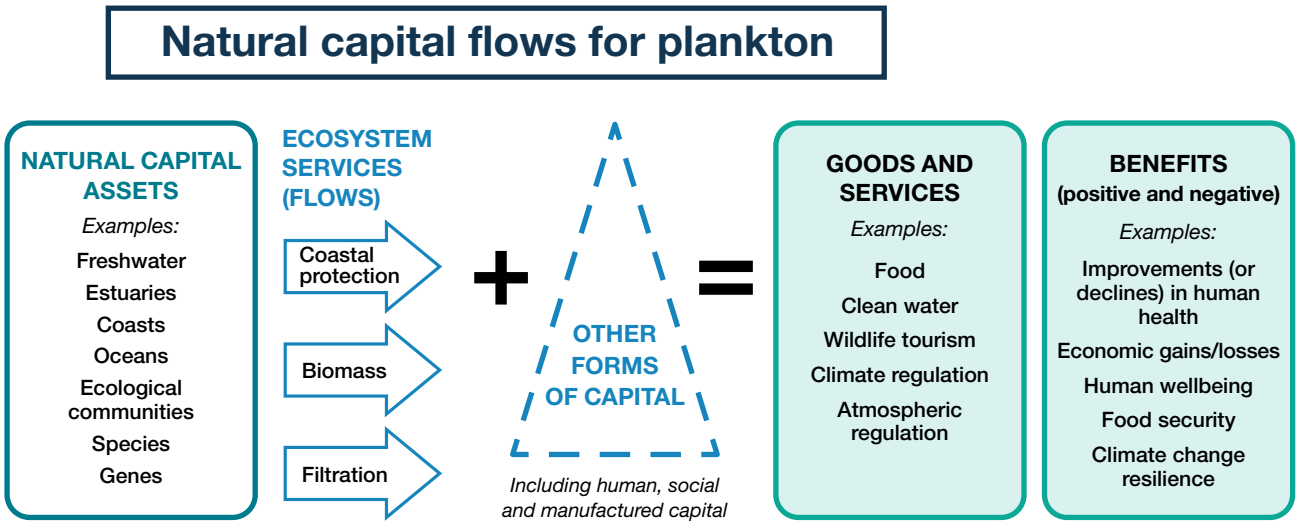

FIGURE 7
Schematic illustration of how natural capital represents the flow between the asset and ecosystem service into goods and services and benefits for humans. Diagram adapted from Devlin and Wenger (2024).

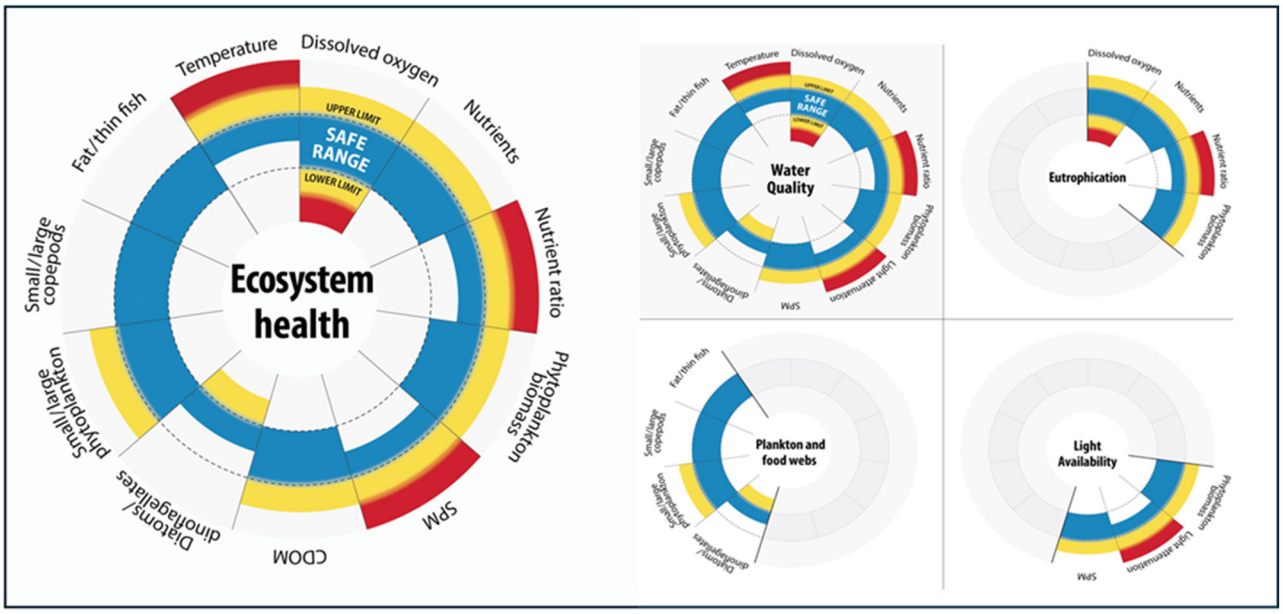

FIGURE 8
Visualization of the concept of "safe space" functioning, which can be adapted to represent a range of conditions that need to be supported together, identifying upper and lower limits around that condition. CDOM, chromophoric dissolved organic matter; SPM, suspended particulate matter.

Many coastal waters are experiencing nutrient imbalances due to the more successful mitigation of phosphorus over nitrogen and the continuing excess of nitrogen over silicon compounds. High N:Si favors non-silicified micro-algae, leading, for example, to blooms of Phaeocystis following silica depletion in the southern North Sea (Davidson et al., 2012). High N:P might favor mixotrophic nanoflagellates, which can obtain P from other micro-organisms, although this seems most relevant under oligotrophic conditions (Duhamel et al., 2019). High N:P ratios also correlate with Phaeocystis colony dominance in the southern North Sea (Lancelot et al., 2009). Many international marine waters have reportedly undergone regime shifts in phytoplankton community composition; the proportion of diatoms has decreased, (predominately in inshore, nutrient enriched coastal waters) whereas that of non-diatoms such as dinoflagellates and cyanobacteria has increased (Xiao et al., 2018; Lu et al., 2023; Chen et al., 2024). A shift in the phytoplankton community composition from diatoms, which have traditionally been dominant, to non-diatoms, can impact on the plankton community and foodwebs (Granéli and Turner, 2002; Verity et al., 2002; Lu and Tian, 2017; Chen et al., 2024). This change has several consequences, including reduced energy transfer to higher trophic levels, higher respiration

rates (higher oxygen consumption and CO_2 production), and accumulation of fewer economically valuable organisms damaging the regulatory, provisioning, cultural, and supporting service functions within the marine ecosystems (Yunev et al., 2017; Chen et al., 2024). The consequences of changes in diatom and dinoflagellate dynamics in the phytoplankton community is a major concern because these taxa play key roles in ecosystem processes and form the basis of many aquatic food webs (Menden-Deuer and Lessard, 2000). Dinoflagellates account for 75% of all harmful phytoplankton species (Smayda and Reynolds, 2003) which can adversely affect human health as well as marine fisheries and aquaculture (Anderson et al., 2002).

Different species of phytoplankton have different traits (Bedford et al., 2018, 2020; Graves et al., 2023; Holland et al., 2023a,b; McQuatters-Gollop et al., 2017), most notably size and shape, growth rate, life history, and behavior such as motility, that together determine their ecological niche and preferred environmental conditions, and phytoplankton are a major driver for global carbon fixation and biogeochemical cycles. Shifts in plankton species composition from diatoms to dinoflagellates may indicate a shift in the balance of organisms due to eutrophication. The composition of the phytoplankton community could be compared with area-specific reference conditions and be expressed by the ratio of diatoms to dinoflagellates. To maximize the utility of the plankton lifeform approach for informing the management of marine ecosystems, changes in the abundance of lifeforms need to be attributed to drivers of change. These drivers can include "directly manageable" anthropogenic pressures such as eutrophication caused by nutrient loading (Bedford et al., 2020; Ostle et al., 2021; Graves et al., 2023; Holland et al., 2023b).

Whilst nutrients and phytoplankton biomass are key indicators for eutrophication assessments, there has been an increasing focus on marine protection and, more generally, biodiversity protection which has led to efforts to connect eutrophication with its impacts on impact on the balance of plankton lifeforms in UK waters (Graves et al., 2023; Holland et al., 2023a; McQuatters-Gollop et al., 2024). Reanalysing historic phytoplankton data collected under the various assessments found an increase in small phytoplankton cells, relative to the decreasing large cells and an increase in the dinoflagellate group, which are generally much less nutritious and more toxic than the decreasing diatoms (Graves et al., 2023). The UK Marine Strategy provided a framework within which to include plankton in the biodiversity assessment and developed plankton tools that applied a lifeforms approach grouping plankton by their common key functional traits (McQuatters-Gollop et al., 2019; Bedford et al., 2020; Graves et al., 2023; Holland et al., 2023a). Improving our ability to track nutrient pressures against biological impact should expand on this by considering pelagic communities explicitly within the eutrophication assessments.

3.2.5.2 Nutrient imbalances and plankton health

Human-induced inputs of phosphorus (P) and particularly nitrogen (N) into the biosphere continue to be problematic for inshore waters. The ratio of N to P, which is sensitive to the relative anthropogenic inputs of the two nutrients, has emerged as a significant driver of environmental change, impacting organisms, ecosystems, and global food security (Penuelas and Sardans, 2023). Historically, P has been the main nutrient controlling upstream freshwater productivity, whereas N limitation is more prevalent in most coastal waters (Brodie et al., 2011; Devlin et al., 2023). However, controls on production and nutrient cycling in estuarine and coastal systems are physically and chemically distinct from those in freshwater counterparts, and upstream nutrient management actions (predominately P controls) have exacerbated N-limited systems further downstream (Paerl, 2008). These changing anthropogenic activities have caused imbalances in N and P loading in UK waters (Figure 9) making it difficult to control eutrophication by reducing only one nutrient. Effective management of inputs of both nutrients are needed for long-term control of eutrophication in our coastal and marine waters. There has been concern about shifting nutrient ratios for some time with increased reporting of the impact of global nutrient loads and concerns on the export of nitrogen increasing faster than phosphorus (Glibert, 2017). Changes in nutrient loading, balances and concentrations can affect plankton, their biodiversity and toxicity with unintended consequences for HABs, mixoplankton, plankton communities and the food web (Gonçalves Leles et al., 2018; Bedford et al., 2020; Graves et al., 2023; Holland et al., 2023a; Mitra et al., 2024).

3.2.6 Consideration of climate resilience and shifting baselines

Climate change is impacting the environmental baseline, with changes in rainfall patterns affecting the delivery of freshwater and associated nutrients and sediment to the coastal marine environment with subsequent effects on ecosystem processes. Climate change has the potential to increase nutrient run off and algal growth and modify the interactions between planktonic and pelagic organisms. Summer rainfall is predicted to decrease alongside increases in the intensity of summer and autumn rainfall events (Cotterill et al., 2023). Shifts in seasonal rainfall patterns can change both the intensity and frequency of nutrient inputs where sudden, large events can cause excessive flooding and pulses of increased inputs and sediments into the marine environment. Predicted changes in the timing and intensity of winter rainfall may lead to increased riverine inputs of nitrogen and phosphorus (Ockenden et al., 2017; Bussi et al., 2016). It is expected that climate change will result in more hydrological extremes and higher river discharges, particularly in the northern parts of the North Sea (Willems and Lloyd-Hughes, 2016). These intense events may lead to large nutrient loads entering the coastal environment, particularly if they coincide with recent agricultural applications of fertilizer or slurry and/or intense rainfall following prolonged spells of very dry weather. Changes in the frequency of such intense events may also lead to changes in discharges from combined sewer overflows (CSOs), with the potential to alter nutrient inputs to the coastal environment. The magnitude of these changes is expected to vary widely between catchments, depending on land use, type of agriculture and agricultural practices and also on future land use and socio-economic developments (Arheimer et al., 2012).

Increased water temperatures have been shown to lead to phenological shifts, biogeographical changes and changes in abundance of plankton (Brander et al., 2016; Eker-Develi et al., 2022). Temperature change and eutrophication are known to affect phytoplankton communities (McQuatters-Gollop et al., 2022),

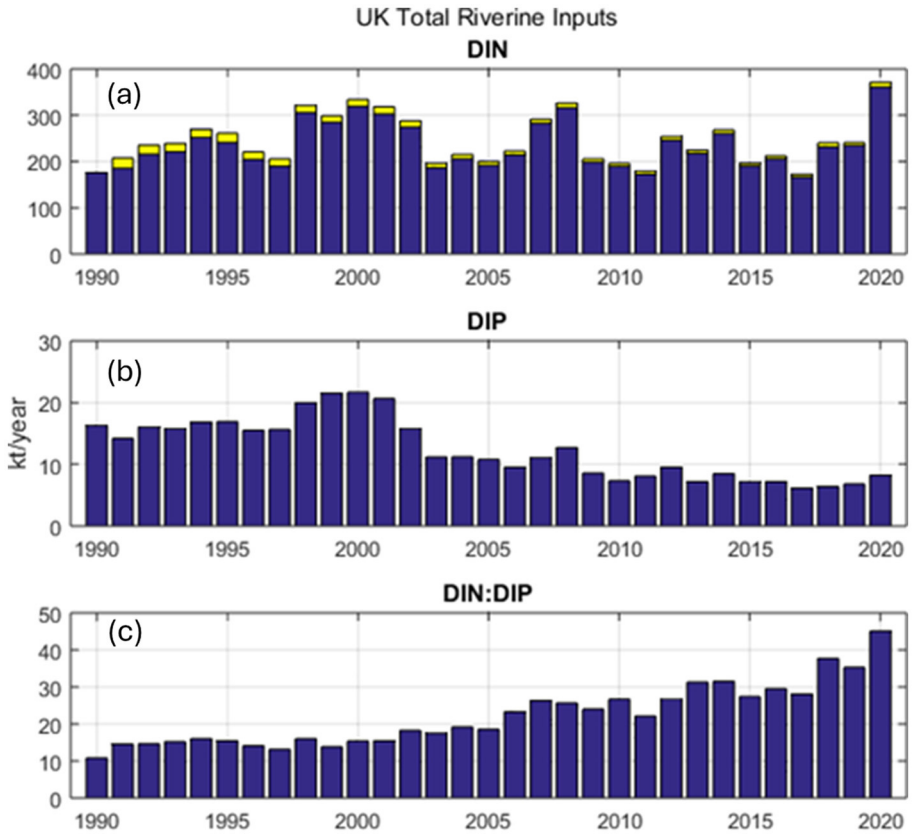

FIGURE 9
Long term changes in nutrient inputs from the UK including **(a)** Dissolved Inorganic Nitrogen (DIN), **(b)** Dissolved Inorganic Phosphorus (DIP) and **(c)** the ratio of DIN:DIP, with the increase or stabilization of DIN compared to decreasing DIP concentration leading to a five-fold increase in DIN:DIP ratio over the past 30 years.

but we have limited information on the effects of interactions between simultaneous changes in temperature and nutrient loading within coastal ecosystems. Ecological time-series are critical for understanding the drivers of change, especially of the interaction between eutrophication and climate factors (Edwards et al., 2010). Such interactions have been key in driving diatom-dinoflagellate dynamics in coastal systems such as the East China Sea where studies have shown that diatoms preferred lower temperature and higher nutrient concentrations, while dinoflagellates were less sensitive to temperature and nutrient concentrations but tended to prevail at low phosphorus and high N:P ratio conditions (Xiao et al., 2018). These different traits of diatoms and dinoflagellates resulted in the observation that increasing stratification and increasing terrestrial nutrient input could promote dinoflagellates over diatoms (Xiao et al., 2018).

Increases in recycling rates of organic matter in the water column with increasing temperature have the potential to increase the availability of inorganic nutrients for phytoplankton growth during the year and therefore increase chlorophyll. Increasing storminess and intensity of rainfall have the potential to increase the turbidity of UK shelf seas. Studies have shown that turbidity in the North Sea has increased over the past 100 years as a result of changes in storminess (Capuzzo et al., 2018; Wilson and Heath, 2019). Changes in the underwater light climate due to increases in turbidity have been linked to decreases in productivity (May et al., 2003). Any increases in storminess during the stratified period could act locally to increase dissolved oxygen concentrations in bottom waters by enhancing mixing from the surface. Increased storminess could also increase resuspension of sediments from the seabed which would increase the oxygen demand for remineralisation of the organic matter, leading to a decrease in oxygen concentration (Mahaffey et al., 2023). Increases in riverine nutrient loads from altered precipitation patterns may enhance algal biomass with the potential to decrease dissolved oxygen in riverine influenced coastal waters through increased oxygen demand when the organic matter is remineralised. Being able to predict the impact of climate change and understand potential mitigation measures is key to successfully managing the marine environment and will require adjustments to our current eutrophication indicators (Table 2).

3.3 Prioritization of solutions required to fill evidence gaps

From our review of eutrophication assessments, we have collated recommendations to improve future eutrophication monitoring programs through addressing the evidence gaps

TABLE 2 Requirements for future eutrophication assessments to fully consider climate interactions for the three common indicators most frequently used across all eutrophication assessments.

Eutrophication indicator	Requirements for and roadmap to achieving eutrophication assessments that account for climate change
Trends in nutrient inputs	• Review/reanalyse historic input data to improve understanding of baseline • Improve link between current monitoring and modeling of inputs in order to integrate available information and inform new monitoring programmes • Improve representation of relevant processes in marine biogeochemical models and related model uncertainty to allow model outputs to be used as a warning system, evaluating the likely marine impacts of potential future input scenarios
Chlorophyll biomass—phytoplankton changes	• Improve incorporation of plankton lifeforms into eutrophication assessment alongside developing links to food web indicators in order to develop a greater understanding of the relationship between eutrophication drivers and plankton community change (i.e., beyond chlorophyll/biomass) and thus consider system-level climate change impacts
Dissolved oxygen	• Determine the mechanisms driving spatial and temporal trends in dissolved oxygen and confidently identify when and where changes in dissolved oxygen are being driven by human-induced activity such as ocean warming or nutrient enrichment from background natural variability • Address the lack of long-term data in regions outside the North Sea and overall poor data resolution which hampers assessment of the occurrence, frequency and spatial extent of oxygen deficiency in UK coastal and shelf waters and the ability to confidently test coastal and shelf-sea models which are required to understand climate change impacts

Development of any new indicators such as pelagic lifeforms would also need to account for changing climate baselines.

within the five themes of data, alignment, indicators, ecosystem and climate.

Following the recommendations to improve future eutrophication assessments, we next provide an assessment of feasibility, developed from the review and expert knowledge of what is currently occurring in UK national eutrophication monitoring programs.

Feasibility of developing and implementing the key evidence gaps into future monitoring and assessment is reported against the effort required to achieve the recommended activity, the scale of complexity and potential costs of implementation (Figure 10). Effort is defined as the level of agency involvement and if the work can be delivered from one or more agencies, the level of stakeholder participation required and if any components of the work has already been agreed. Complexity is a measure of the type of data required to deliver the work, with the more complex systems being more difficult to deliver and includes a consideration of how easily the data changes could be made and if those changes are dependent on cross agency, cross stakeholder agreement. Costs are a simple classification of high costs related to ongoing staff, vessel and field time against lower costs that are not dependent on implementing aspects of a field-based monitoring program.

Key recommendations under each thematic area are described in Figure 11, summarizing the evidence gaps identified through the review and consultation, a list of activities that could address these evidence gaps, and then the outcomes of the feasibility assessment (effort, scale, cost). Additionally, a short narrative on impact of the improvement and progress that has already occurred is presented (Figure 11).

Recommendations for improved data flow require improved accessibility and usability of autonomous data, and clear processes for high level data products from autonomous and high frequency data (Figure 11). There is an urgency to restore nutrient load monitoring to enable clear pathways for a program of measures. Alignment improvements focus on the harmonization of all aspects of the different eutrophication monitoring and assessment frameworks, achieving true integration across the catchment to coast encompassing the full riverine influenced area that links coastal and offshore processes. A range of indicator improvements are presented, including more information on factors that influence susceptibility to eutrophication, refining understanding of natural variability in development of thresholds and consideration of social, economic and environmental benefits. All the indicator improvements could lead to a fully integrated assessment, aligned with the Safe Space theory of a range of conditions that support optimum benefits. Improving our understanding of the ecosystem benefits requires consideration of eutrophication as a plankton pressure, linking nutrient imbalances and impacted water quality with changes in plankton functionality. Finally, climate change and eutrophication are intrinsically linked, with the potential to exacerbate impacts, knowledge of these interactions is critical in a changing climate world.

4 Discussion

4.1 The shifting baseline of eutrophication

Etymologically, eutrophication refers to good nourishment and what was thought to be a natural process in postglacial lake evolution. However, the meaning has changed, as shown by European Court of Justice judgements (ECJ, 2004, 2009), relating to breaches of the UWWTD, that describe it as a process caused by human actions that lead to undesirable disturbance to the balance of organisms and the quality of water. Undesirable disturbance was defined as "a perturbation of a marine ecosystem that appreciably degrades the health" (Tett et al., 2013) or "threatens the sustainable human use of that ecosystem" (Tett et al., 2007, 2013; Ferreira et al., 2011). From the perspective of a natural capital approach, the term "undesirable" is a link (1) to specific concerns about the impact of anthropogenic nutrients on the ecosystem services provided by coastal seas, and (2) to the perturbations of planetary N and P fluxes that are amongst the pressures pushing Earth's biosphere outside a "safe operating space" for humanity (Rockström et al., 2009; Richardson et al., 2023).

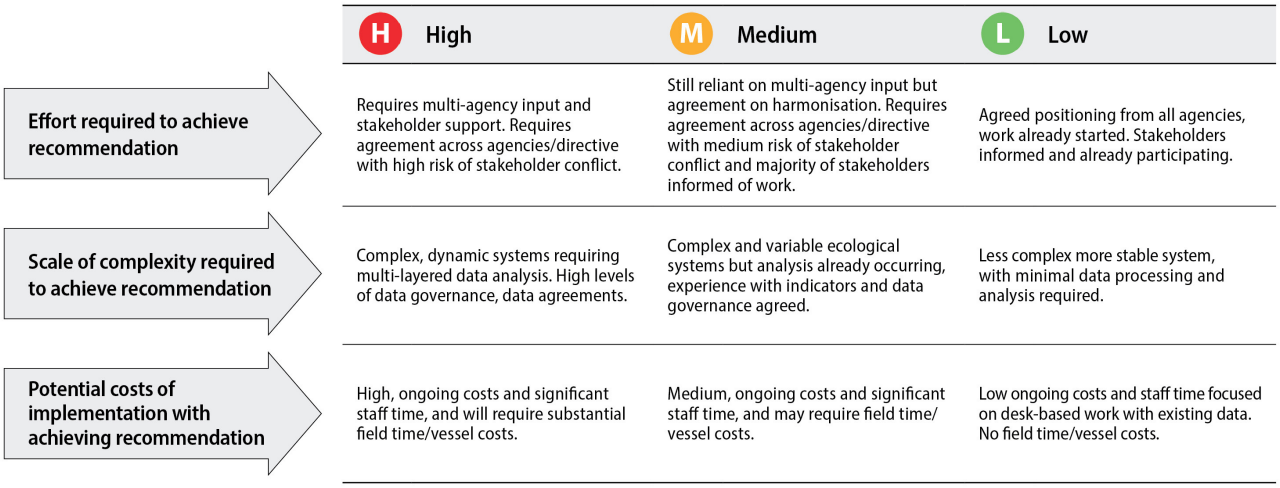

FIGURE 10
Qualitative ranking of different factors for measuring difficulty, complexity and cost of each recommendation for future eutrophication monitoring.

Eutrophication is indeed a wicked problem (Thornton et al., 2013), impacting different ecosystem services and different sectors of society in different ways. For examples, changes in nutrient levels in the southern North Sea have probably contributed to changes in flatfish catches (a provisioning service) and waterbird numbers (a cultural service to birdwatchers) (Engelhard et al., 2011; Philippart et al., 2007; van Roomen et al., 2012). Use of the sea's regulating services for nutrient cycling reduces costs for householders and fish-farmers who might otherwise have to pay for removing nutrients from farm or domestic effluent (Martino et al., 2019). However, overuse of these regulating services runs the risk of harming provisioning and cultural services as a result of e.g. increasing frequency of HABs, shifts in marine food-webs that might be detrimental to commercial fisheries, and more decaying green algae on beaches.

Nutrient pollution is frequently related to diffuse sources, complicating identification and mitigation of the impacts of single sources. Le Moal et al. (2019) acknowledge these difficulties and urge a different approach to diffuse and large ranging nutrient sources where we need to address: (i) the long term cumulative impact of far reaching anthropogenic activities, (ii) the consequences of multiple, and often cumulative, actions which can be very distant both in space and time, (iii) the difficulty in disentangling past and present causes from past anthropogenic legacy (O'Higgins et al., 2014). Our future programs need to consider what Thornton et al. (2013) calls "the wicked problem of eutrophication" where multiple, often cumulative actions, remote both in space and time from the pressure, enact variable responses and trajectories along the land-sea continuum. This is compounded by complex decision-making required from multiple stakeholders with different end-user requirements, limited interactions, and government agencies reporting to different policy levers with increasing costs and reduced funding.

4.2 Contextualizing eutrophication assessments in the UK

Advances in eutrophication monitoring and successful implementation of programmes of measures has been driven by decades of environmental protection offered under policies such as the EU Urban Wastewater Treatment Directive, Nitrates Directive, Water Framework Directive, EU Marine Strategy Framework Directive, the UK Marine Strategy, and the WFD/WER and the requirements to report under the OSPAR COMP and "and for the OSPAR "Inputs of nutrients to the marine environment" indicator. This process recognizes the achievements to date under national and international environmental directives and set out a path toward improving our approach to ensure continued development of our understanding of eutrophication and all its complexities. The shift from assessments under EU environmental directives to a nationally based marine strategy has been challenging but has also acted as a catalyst to rethink how we manage our environment in respect to eutrophication. Ecosystem management requires adaptation and modification, allowing the adaptation of the environmental legislation and management to change as our understanding and the rate and scale of impact changes.

4.3 Refining our future assessments

4.3.1 Improved data flows

We require new and novel ways of collecting data to help us to understand the highly variable processes that influence the scale and extent of eutrophication. Improving our understanding of eutrophication within the national assessments will be achieved through the better use of high frequency and autonomous data and improved technology, ensuring the optimisation of the large datasets. However, the complex process of ensuring sufficient calibration of sensor data and integrating the higher resolution

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Theme	Headline	Evidence Gaps	Activities that could resolve evidence gaps	Feasibility			Impact and Progress
				Effort required	Scale of Complexity	Costs	
DATA	**Autonomous and remotely collected data**	No clear consensus on integrating autonomous and high frequency data alongside traditional monitoring to improve assessments.	Improve accessibility and usability of autonomous data, including the integration of data collected over minutes to days. Agreement on data products extracted from high frequency data. Ensure robust validation to allow inclusion in assessment.	H	H	M	**High impact** through technological advances. **Progress** rapid, driven by a stepwise increase in autonomous and remote data collection. High frequency data improving understanding of variability and biological processes. **Future work** will focus on higher frequency data collection in data-poor areas.
	Monitoring inputs from land to sea	Limited understanding of the impact of reduced monitoring frequency on data confidence and assessments.	Improve confidence in monitoring and assessment of land-to-sea nutrient inputs. Ensure sufficient site location and frequency to track pollution sources from land into coastal and marine waters.	M	M	H	**High impact** when used to prioritise program of measures for reduction of nutrients and improve modeling of land-to-sea inputs. **Progress** underway, particularly if existing monitoring can be built upon and improved.
ALIGNMENT	**Catchment to coast**	Assessment areas, thresholds are not harmonised across different directives.	Harmonise assessment areas, indicators and thresholds from catchment to the coast across different policy frameworks.	M	M	L	**Medium impact** through integrated monitoring and assessment frameworks. **Progress** underway given harmonisation has occurred in coastal to marine waters under OSPAR. Similar techniques could be applied for estuarine to coastal waters under WER/WFD.
	Riverine influenced areas	Limited understanding of the role of the riverine plume, and improving connections between inshore and offshore environments.	Improve monitoring and assessment of riverine influenced areas (plumes) at the boundary between inshore and offshore eutrophication assessments. Improved monitoring at small scale including combined sewage overflows and fish farms.	M	M	L	**Medium impact** through better tracking of pathways from source to sea and improved assessment areas. **Progress** ongoing, with substantive work already made with riverine-plume influence mapped for UK. Differences in resolution need to be corrected, and agreement on the overlap between coastal WER/WRD and plume waters.
INDICATORS	**Trends and trajectory of change**	Trend assessment not included in current eutrophication assessments.	Incorporate analysis of trends and trajectory of changes of status or state into eutrophication assessments.	M	L	L	**Medium to high impact** when used alongside existing assessment frameworks. **Progress** ongoing, through the embedding of trends into assessments, enabling evaluation of change trajectories in final reporting of state.
	Light attenuation	Not enough consideration in eutrophication assessments of susceptibility factors influencing the complex interactions between nutrients and primary/secondary responses.	Incorporate new indicators or update current indicators based on measurements of optical components of the system. Potential indicators include light attenuation (K_d) and Chromophoric Dissolved Organic Matter (CDOM).	M	M	L	**High impact** when used to understand waterbody resilience to eutrophication impacts. **Progress** ongoing through the increased collection of CDOM, and improvements in sensors allowing high resolution data collection of light, SPM, chl-*a* and CDOM. **Future work** will focus on improving data analysis and linking it to biological responses.
	Natural variability and background	Natural variability not incorporated at indicator or area level.	Improve incorporation of natural variability and background conditions in indicator thresholds to ensure that the distinction between natural and anthropogenic is based on real environmental data for each indicator.	M	L	L	**Medium impact** in improving understanding of natural variability (by parameter and waterbody). **Progress** ongoing through calculation of new measures of natural variability for each indicator. **Future work** relies on agreement to change existing approaches in all assessments.
	Holistic approaches	Social and economic frameworks are not an integral part of future eutrophication assessments.	Develop assessment metrics that consider social and economic drivers alongside environmental. Processes such as Natural Capital, DPSIR and OneHealth are all examples of considering eutrophication as part of the ecosystem approach.	H	H	M	**High impact** to consider human and environmental impacts within one assessment. **Progress** ongoing under recent UK marine Natural Capital and Ecosystem Assessment Programmme, alongside well established DPSIR and One Health frameworks. **Future work** needs to consider how to broaden current assessments to measure society and economic gains without increasing costs.
	Integration of indicators	Confusion in the integration of indicators in different assessments can impact on overall messaging.	Implement a Safe Space assessment approach. Improved integration of all indicators to identify a simple and communicable assessment that represents the complexity of the system.	M	H	L	**High impact** in an integrated understanding of cumulative pressures and impacts. **Progress** ongoing with the development of a Safe Space Approach for plankton, building new methodology based on current assessments.
ECOSYSTEM	**Eutrophication as a plankton pressure**	Disconnect between eutrophication and biodiversity impacts.	Improve understanding of links between eutrophication and plankton community health.	M	H	M	**Medium impact** through improved understanding of how nutrients are impacting plankton. **Progress** ongoing, with UKMS and OSPAR linking eutrophication and biodiversity indicators.
	Nutrient imbalances	Current assessments do not consider the role of limiting nutrients impacting plankton community.	Consider linkages between nutrient ratio imbalances and pelagic (plankton) community change indicators within eutrophication assessment. Report N:P ratios in nutrient loads, transitional and coastal waters and offshore alongside pelagic community and food web indicators.	M	H	M	**High impact** as one of key pressures impacting on coastal plankton and foodwebs. **Progress** ongoing across UK government agencies measuring pico-, nano-, phyto- and zooplankton. Link to data recommendations for collection of data in data poor areas (winter periods) to improve N and P data.
CLIMATE	**Climate resilience**	Current eutrophication assessments are limited in responding to changing climate baseline.	Implement recommendations from Greenwood et al., 2024 on the updating of current eutrophication indicators in respect of a changing climate baseline.	L	M	L	**High impact** through improved understanding of climate and eutrophication. **Progress** underway with work by the Clean Safe Sea Evidence Group, which identifies the criteria that will need future proofing for climate impacts.

FIGURE 11
Recommendations for future eutrophication monitoring and assessment in UK marine waters categorized into themes of data, alignment, indicators, ecosystem and climate.

data into data workflows and repositories means that all available data types have not always been available for use in assessment. Ongoing investment into high-quality calibration of autonomous data will be required to allow the transition to a next-generation assessment utilizing available data alongside high-resolution data (Bean et al., 2017; Daniel et al., 2020).

4.3.2 Improved alignment

Disaggregation between the natural gradient of coast to sea does not achieve harmonized assessments. A new integrated approach will help us reveal a fuller picture of the health of our seas and oceans bringing ecosystem, economics and social criteria together to encapsulate the full value of a functioning ecosystem. Future assessments should continue to assess the continuum between estuaries and coastal systems, highlighting the importance of the riverine influenced area that lies between the UK transitional and coastal waters and further offshore assessment areas (Greenwood et al., 2019; Fronkova et al., 2022; Heal et al., 2023). Developing a catchment to coast approach should always encompass clear understanding of anthropogenic change, the technical ability to link that change to an activity or sector, transparent pathways for positive management action, recognition and incorporation of divergent societal concerns and policy tools that support sustainable outcomes for the marine environment (Devlin and Wenger, 2024). Alignment of governance strategies, integrated monitoring programs, more regular cross-agency engagement and harmonized assessments would be a first step in achieving a co-ordinated catchment to coast program.

4.3.3 Improved indicators

4.3.3.1 Trend assessments

Using long term cross-sectoral monitoring data will improve applicability for assessing changes in landscape-level environmental conditions and improve our ability to support short- and long-term management decisions (Maas-Hebner et al., 2015). The presentation of long-term data for nutrient inputs can be valuable in understanding what is changing over time, linking program of measures to reducing nutrient inputs, or conversely, showing the lack of appropriate program of measures resulting in an increase in one or more of the nutrients being measured.

4.3.3.2 Understanding "true" natural variability

Whereas our current suite of environmental indicators (including OSPAR PH1) seems reasonably complete and widely applicable in UK coastal waters, reference conditions and threshold values may need to be set locally and reflect both the local environment and local preferences for desirable conditions.

4.3.3.3 Susceptibility to eutrophication

Understanding of susceptibility and resilience needs further work, and consideration of these complexities should be considered in the development of new indicators or supporting evidence alongside the more traditional indicators.

4.3.3.4 Indicators of social, economic and environmental wellbeing

Assessment of eutrophication needs a social as well as an ecological context. Cost-benefit analysis involving ecosystem services and natural capital could assist in this but will need better models for the response of services to changes in nutrient loading, and for the preferences of different communities (or stakeholder categories) for these services. More integrated assessments such as the One Health approach, the DPSIR approach and natural capital accounting (Ross and Carter, 2013; Cork et al., 2016; Stentiford et al., 2020) explore the multiple interconnections that exist between environmental, animal and human health as a technique to incorporate multiple benefits to multiple end-users. Processes or programmes that could deliver greater social cohesion in our understanding of eutrophication need to measure environmental success through alternative indicators, such as ones that measure the protection of assets within marine natural capital, and holistic approaches that consider health between the environment and humanity as intrinsically linked in terms of water quality improvements. This will enable a safe space approach that is essential to ensuring sustainable and resilient human and environmental health.

4.3.4 Improved understanding of ecosystem impacts

Improvements in our understanding of the complex connections between nutrients and the pelagic community allow us to see how increases and imbalances in nutrients impact trophic interactions and the food web. Incorporating information on pelagic habitats will expand our eutrophication assessments from the more commonly used indicators of nutrients, chlorophyll and dissolved oxygen toward better estimates of plankton community shifts resulting from nutrient imbalances, and related impacts on ecosystem functioning. Further harmonization of data sources and assessment methods between the eutrophication and pelagic and food web assessments is expected to increase comparability and improve understanding of how nutrient loads affect ecosystem functioning and at which nutrient concentrations the ecosystem can be considered healthy (OSPAR, 2023).

4.3.5 Improved understanding of climate change and eutrophication

Climate change and eutrophication are intrinsically linked. While much is known about each individually, it is crucial to understand how they are interconnected and how climate change exacerbates marine pollution. Climate change leads, among other impacts, to floods and droughts which cause stronger variations in nutrient inputs. Future assessments need to consider the ecological effects of this greater variability and how to adequately monitor and assess this shifting baseline for the purposes of future eutrophication assessments (OSPAR, 2023).

5 Conclusion

We can improve our eutrophication assessments, despite the complexity of the drivers and impacts, and the uncertainty related to mitigation and recovery processes. Although this account has focussed on eutrophication in UK estuaries and shelf waters, much of our argument is more widely applicable. Solutions are possible, though almost never simple, and rely

on a combination of long-term strategies, improved sewage and groundwater infrastructure, best management practices around agriculture and aquaculture, detailed monitoring and assessment and close partnerships between all stakeholders, public users, and government. In the UK case, improving stakeholder engagement with river trusts, conservation groups, farmers, water operators and communities needs to continue to be an integral part of the eutrophication assessment.

To enable government to continue to implement these strategies, and successfully measure their progress, UK agencies must continue to work collaboratively to innovate and improve the efficiency of monitoring programmes. This review provides an opportunity to look across national obligations and disparate approaches, identifying key evidence gaps when coastal and marine waters are continually impacted by nutrients alongside other pressures. The historical context of UK approaches to the monitoring and management of eutrophication is important when considering both the science used to inform the design of the current assessments and what science may be needed in the future to ensure robust, evidence-based decision-making. This review provides that historical context, adds the outcomes of expert discussion sessions, and identifies knowledge gaps including those involving human wellbeing and natural capital and, in doing so, sets out a framework to evolve marine eutrophication assessment and management into the future. Bringing together potentially conflicting voices to work collaboratively is the best way to progress and evolve eutrophication assessments. On the larger scale, we need to assess UK marine discharges not only for their contribution to the much-disturbed planetary N and P cycles, but also for their impact on the functioning of marine ecosystems considered as part of the biosphere.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

MD: Writing – original draft, Writing – review & editing. CG: Writing – original draft, Writing – review & editing. NG: Writing – original draft, Writing – review & editing. MA: Writing – original draft, Writing – review & editing. EB: Writing – original draft, Writing – review & editing. MH: Writing – original draft, Writing – review & editing. AM-G: Writing – original draft, Writing – review & editing. PT: Writing – original draft, Writing – review & editing. DT: Writing – original draft, Writing – review & editing. MB: Writing – original draft, Writing – review & editing.

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Conflict of interest

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

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Generative AI statement

The author(s) declare that no Gen AI was used in the creation of this manuscript.

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Does the marine functioning link with the supply of ecosystem services and human benefits? A practical application in the Bay of Biscay

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Marine ecosystem services provide multiple benefits and hold significant economic value; however, the capacity of the marine environment to provide ecosystem services can be compromised by anthropogenic pressures. To ensure proper environmental conditions and human well-being, it is necessary to study the functioning of marine ecosystem services. In this context, the aim of this study is to test whether the Common International Classification of Ecosystem Services (CICES) cascade framework is adequate to explain the flow between the natural and the socio-economic domains and identify its limitations. To this end, the study was divided in two parts: (i) review, compilation and classification of CICES Ecosystem Services Cascade model indicators, for three marine ecosystem service examples (provisioning, regulation and maintenance, and cultural), together with the analysis of the number of indicators and the match of the classification undertaken by the authors in the literature and CICES proposal; and (ii) the application of the CICES Ecosystem Services Cascade model to the practical case study of the anchovy fishery in the Bay of Biscay. The results obtained show that many indicators were incorrectly assigned in the literature to the different components of the CICES Ecosystem Services Cascade model. This study highlights the need to develop a standardized classification and understanding of the marine ecosystem services. Significant correlations between the different five steps of the CICES Ecosystem Services Cascade model were obtained, suggesting that this cascade is effective at explaining the links between a healthy environment and the sustainable supply of ecosystem services and benefits.

KEYWORDS

CICES cascade, indicators, anchovy fishery, ecosystem service value, provisioning ecosystem service

1 Introduction

Coastal and marine environments play a crucial role in maintaining the ecological equilibrium of our planet and supplying human communities with ecosystem services (Peterson and Lubchenco, 1997). These environments are under continuous transformation and protecting service flows require preserving sufficient natural capital stock (both in terms of quality and quantity) (Martínez et al., 2007), as well as the interconnections of the ecosystem components and their relationship with the abiotic environment (Buonocore et al., 2021). The viability of these marine ecosystem services and the benefits they provide to humans are significantly affected by both anthropogenic and natural stressors, and their cumulative effects (Outeiro et al., 2017). Understanding how marine ecosystem services are supplied is essential for the sustainable management of socio-ecological systems (i.e., Ecosystem-Based Management) (Atkins et al., 2011).

From the beginning of the 21st century, several ecosystem services classification frameworks have been developed by different organizations and initiatives. The first one was the Millenium Ecosystem Assessment (MEA, 2005), an international initiative undertaken between 2001 and 2005, conducted by the United Nations and involving over 1,300 experts from 95 countries. The main purpose was the evaluation of the ecosystem's state, the services provided by these ecosystems to humans, and the implications for human well-being. After this, the European Commission, supported by various countries and organizations, created "The Economics of Ecosystems and Biodiversity" (TEEB, 2010). This assessment provided comprehension about the economic value of ecosystem services, emphasizing the undervaluation of these services in the conventional economic and decision-making processes.

Numerous more recent classifications [e.g., The UK National Ecosystem Assessment (NEA) (Watson et al., 2011), Final Ecosystem Goods and Services (FEGS-CS) (Landers and Nahlik, 2013), Nature´s Contribution to People (NCP) (Pascual et al., 2017)], have been developed upon the initial groundbreaking works. Some of the new ecosystem services classifications are specifical for the marine environment (e.g., Atkins et al., 2011; Böhnke-Henrichs et al., 2013; Liquete et al., 2013; Turner et al., 2015). The most accepted classification nowadays in Europe would be the Common International Classification of Ecosystem Services (CICES) (Haines-Young and Potschin, 2012), used by several European Union (EU) agencies and many Member States. The aim of all these different classifications is universal; however, all of them have a particular background, and favor specific contexts and goals (Czúcz et al., 2018).

CICES was developed to have an internationally recognized and standardized approach for ecosystem services assessment and provides a systematic categorization and description of ecosystem services (Haines-Young and Potschin, 2012). This classification was based on the ecosystem services groups defined by the MEA classification, together with a literature review, survey results, workshops, and direct experience from European projects (Culhane et al., 2018; Grima et al., 2023). The result is a classification that is structured into five hierarchical levels (from higher to lower level: Section, Division, Group, Class, Class type), in line with the "best practices" proposed by the UNSD (1999). The utilization of the CICES framework helps scientists, policymakers, and other stakeholders to better understand how ecosystems benefit human well-being, enabling them to make well informed choices regarding ecosystem preservation and management. CICES classification is a dynamic and constantly evolving tool, regularly updated (last version: CICES V5.1) (Haines-Young and Potschin, 2018). There are three different ecosystem services according to CICES, provisioning services, regulation and maintenance services, and cultural services. The three ecosystem service sections are interconnected and collectively contribute to the overall benefits that ecosystems provide to humans (Grima et al., 2023).

In this context, the Ecosystem Services Cascade model, which will be referred in this paper as CICES cascade (Potschin and Haines-Young, 2017) establishes a connection between natural systems and various aspects of human well-being, resembling a production chain, between the natural environment to the socio-economic system (Figure 1 illustrates an example). It starts with the ecological structures and processes created by ecosystems and culminates in the provision of services and benefits that ultimately serve human needs.

Nevertheless, following the CICES cascade model, multiple different frameworks have emerged with the purpose of explaining the environment-human benefit transition. Costanza et al. (2017) argued that a "linear cascade", referring to the CICES cascade, was too simple to explain the connections between ecosystem processes, functions, and benefits to humans, as these links are complex, non-linear, and dynamic. In this study, a diagram with higher complexity was developed, describing those services equal benefits, and the many interactions and feedback that "are required" between the natural capital and other forms of capital to produce the ecosystem services (Costanza et al., 2017). More recent studies have also proposed modifications to the initial model. Elliott (2023) discussed that the cascade diagram produces overlaps between the different concepts involved, adding more confusion to the understanding of the ecosystem service flow. In his model, the ecosystem structure and functioning are considered at the same level within the natural domain (equivalent to environment, in Figure 1). The natural capital flows into the ecosystem services, classified as "provisioning aspects" and "regulating processes" (in this model, cultural services are considered as "provisioning aspects"). Then, there is a transition to the "human domain" (equivalent to social and economic system, in Figure 1), that considers the human capital and assets necessary to provide societal goods and benefits, classified as "extracted provisions", "environmental regulation, hazard and risk reduction including safety", and "cultural, aesthetic and health benefits".

On the other hand, different frameworks have also been developed, without considering the CICES classification or cascade (Barbier, 2017; Culhane et al., 2020). For example, in the scheme presented by Barbier (2017), the ecosystem service is separated from the natural domain and is not distinguished from the benefit concept. This model considers the economic system to

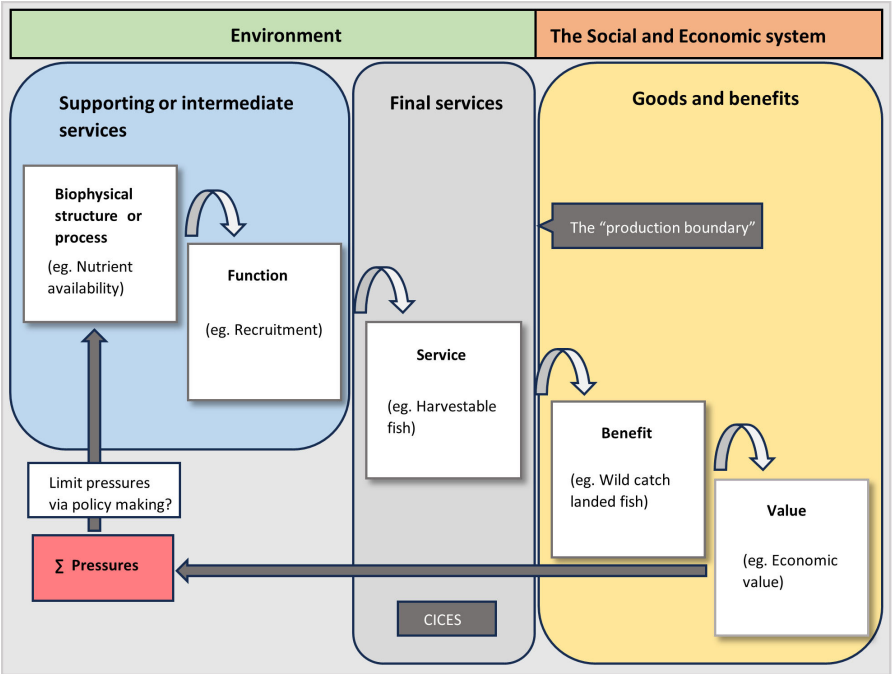

FIGURE 1
Cascade diagram: from structure to functions, to services to benefits to value, showing as example of ecosystem service wild fish for nutrition. Adapted from the Common International Classification of Ecosystem Services (CICES) cascade (Potschin and Haines-Young, 2017).

be the production of the goods and services that lead to human well-being. Although all these different models have varying perspectives, everyone concurs that there exists a - "pathway" through which ecosystem services are delivered, connecting ecological structures and processes at one end to the well-being of people at the other.

Apart from being classified, ecosystem services need to be quantified and monitored to understand their characteristics and trends (Layke et al., 2012). This is usually done using indicators. Indicators are necessary to describe not only the ecosystem services, but the ecological functions responsible for delivering them, the benefits that ecosystem services offer, and the interconnected relationships between all these elements (de Groot et al., 2010). However, direct quantification of ecosystem services is often not possible, and a significant portion of the required data lacks systematic organization and interpretation of the flow between the natural and the socio-economic systems (Balvanera et al., 2022).

Indicators for the environmental domain of the "ecosystem service production chain" are defined as physical elements of the ecosystem measurable with available tools and knowledge (Grima et al., 2023). Indicators for ecosystem benefits and value should demonstrate the realized human use of the service and its economic outcomes of the same (Hattam et al., 2015). These indicators should be understandable for decision-makers and practitioners and serve as a base for establishing an effective monitoring system for the study of ecosystem services (Feld et al., 2009).

Several authors have compiled indicators of ecosystem services, using different terminology and classifications to describe the flow between the environment and the socio-economic system (e.g. Böhnke-Henrichs et al., 2013; Liquete et al., 2013; Atkins et al., 2015; Hattam et al., 2015; Lillebø et al., 2016; Broszeit et al., 2017). Thenen et al. (2020) carried out an exhaustive compilation of marine ecosystem service indicators, following the CICES classification. In this study, the terms that did not follow the CICES criteria were adapted with the objective of having a harmonized set of indicators for each step of the CICES cascade. Also, this review groups all the indicators of the environmental part into one category (ecosystem service capacity), instead of differentiating between biophysical structure or processes and function steps of the cascade.

The difficulty to agree upon appropriate indicators, single classification system and flow models, makes it challenging to compare and provide comprehensive ecosystem service overviews (Busch et al., 2012), compromising the adoption of the whole ecosystem service concept in policies and management of marine systems (Nahlik et al., 2012). Therefore, there is an urgent need to reconcile them to consistently evaluate how the relationships between nature and society evolve, facilitating the efficient integration of these concepts into management and policymaking (McDonough et al., 2017).

In this context, the aim of this study is to test whether the CICES cascade framework is adequate to explain the flow between the natural and the socio-economic domains and identify its limitations. For proving this, firstly, we compiled and classified indicators according to the different components of the CICES cascade, for the three most studied marine ecosystem service types (Thenen et al., 2020). Secondly, to check if the CICES framework allows to explain the ecosystem service flow between the

environment and the socio-economic system, the relationship between the cascade components was tested with available data from a provisioning service: the anchovy (*Engraulis encrasicolus*) fishery in the Bay of Biscay. This example was considered optimal for the exercise because of the large dataset available (data from 1987 to 2022), including data for each cascade step indicator, and because of the management adaptation to sustainable fisheries after a historical collapse of the species population in the Bay of Biscay and the fishery closure (Uriarte et al., 2023).

2 Materials and methods

2.1 CICES cascade indicators

The objective of this part of the study was to review indicators suitability for the CICES cascade and identify inconsistences and incoherences in their classification and implementation for three marine ecosystem services examples, one for each section (provisioning, regulation and maintenance, and cultural).

To identify the indicators, a literature search was carried out within the bibliographic Elsevier's database "Science Direct" and grey literature, focusing on documents published between 2000 and 2024. Articles including marine ecosystem services indicator sets, for "marine ecosystem services" in general and more specifically, for the three examples of ecosystems services selected: fish for nutrition (class: "Wild animals used for the nutritional purposes" – Provisioning), carbon sequestration by marine environments (class: "Regulation of chemical composition of atmosphere and oceans" – Regulation and maintenance) and recreational marine mammal watching (class: "Characteristics of living systems that enable activities promoting health, recuperation or enjoyment through passive or observational interactions" – Cultural). The selection process began with the identification of papers using a specific set of search criteria, with the following search terms: "Marine" or "Ecosystem services" or "Indicators" or "Ecological status" or "Environmental status" or "Provisioning ecosystem service" or "Regulation and maintenance ecosystem service" or "Cultural ecosystem service" or "Fisheries" or "Carbon sequestration" or "Marine mammal recreational watching". All articles selected were read for extraction of indicators that could fit any step of the CICES cascade.

We have followed the most updated CICES classification (Haines-Young and Potschin, 2018) to select the indicators, but also the terminology within the European Marine Strategy Framework Directive (MSFD; European Commission, 2008). Merging both terminologies, allow to link ocean health (= "good environmental status", within the MSFD) to the human activities and pressures that compromise it, and ultimately to the services and benefits available. Hence, the indicators were classified as shown below (Table 1).

Indicators identified in the literature are collated in Appendix Tables A1–A3. First, they were assigned to a step of the CICES cascade, according to the reference from which they had been extracted (Appendix, columns A, "Original classification"). Then, each indicator was cross-checked with the CICES cascade definitions (Table 1) and reclassified, if needed (Appendix, columns B, "Proposed classification in the CICES framework").

TABLE 1 Common International Classification of Ecosystem Services (CICES) cascade step term followed by its definition and one indicator example: MSFD, Marine Strategy Framework Directive.

CICES cascade step	Definition	Indicator example in the Bay of Biscay	Units	Data source and period
Pressure	Relevant anthropogenic pressures (biological pressures, physical pressures, substances, litter, and energy), defined in the MSFD and coming from different human activities at sea or land based.	Harvest-rate		ICES (2022) 1987-2022
Biophysical structure or process	General biotic or abiotic description of the habitat.	Upwelling index	(m^3 s^{-1} km^{-1})	Ibaibarriaga et al. (2023) 1987-2022
Function	Characteristics of the living system that come together (processes) to make an ecosystem service possible.	Anchovy recruitment age 0	(tonnes)	ICES (2022) 1987-2022
Service	Ecological outcomes that ecosystem characteristics or processes generate, that can ultimately benefit people.	Anchovy Spawning stock biomass (SSB)	(tonnes)	ICES (2022) 1987-2022
Benefit	The direct and indirect outputs from ecosystems that have been turned into products or experiences that are no longer functionally connected to the systems from which they were derived.	Total catch of anchovy landed	(tonnes)	ICES (2022) 1987-2022
Value	The importance attributed to the benefits. This can be economic, social, health or intrinsic value.	Economic value of catch	€	(i) ICES (2022) (ii) Ministerio de Agricultura, Alimentación y Medio Ambiente 1990-2021

For indicators accounting for same or similar concepts, harmonization was carried out using common criterion between the different ways of describing what the indicators represent. For example, in the case of the original indicators: "Fish catch" (Appendix Table A1, line 160) and "Amount of fish captured" (Appendix Table A1, line 162), considering that both indicators make reference to the same concept we thought that "Fish catch" was a more accurate and simple description for that example, so we used it to harmonize both indicators. The first classification of indicators was carried out by the main author (AOA) and afterwards reviewed by all co-authors.

Each indicator was assigned to one of these three categories: (i) "correct", when the indicator was originally classified according to CICES criteria, and assigned to the correct step of the cascade (in Appendix Tables A1–A3, cells highlighted in green); (ii) "incorrect", when the indicator was originally classified according to CICES criteria, but assigned to an incorrect step of the cascade (e.g., a function indicator incorrectly classified in the original source as a service indicator) (in Appendix Tables A1–A3, cells highlighted in red); and (iii) "other terms", for indicators extracted from articles that did not follow the CICES classification (e.g., ecosystem service flow, ecosystem service capacity, essential ecosystem service variables) (in Appendix Tables A1–A3, cells highlighted in blue).

The total number and corresponding percentage of indicators classified as "correct", "incorrect" and "other terms" were calculated, considering the ecosystem service section and the step of the cascade that they belong to.

2.2 Practical application to the anchovy fishery

The study area of the anchovy stock, the Bay of Biscay, is an open oceanic bay in the northeastern part of the Atlantic Ocean (Figure 2). Its complex hydrological regime and weather pattern exhibit both temporal and geographical heterogeneities (Borja et al., 2019). An average weak oceanic circulation characterizes this bay, cyclonic and anticyclonic eddies, a poleward flow along the slope driven by wind and density gradients, tidally induced currents over the continental shelf, and freshwater runoff and river plumes, especially from the large French rivers, such as the Garonne (Koutsikopoulos and Le Cann, 1996). Moreover, the seasonality is very evident, and mean sea surface temperature varies between 12°C at the end of winter and over 20°C at the beginning of summer (Koutsikopoulos and Le Cann, 1996), showing an increasing trend of the temperature because of global climate change (Chust et al., 2022).

The European anchovy (*Engraulis encrasicolus*) is a small pelagic fish with a short life cycle and a maximum lifespan of 4 years (Motos, 1996; Petitgas et al., 2013; Uriarte et al., 2016). This species is characterized by rapid growth, high fecundity, and mortality (Motos, 1996). The distribution of this species extends from NW Africa in the south to the North Sea and the Baltic Sea in the north, as well as the Mediterranean Sea, Black Sea, and Azov Sea (Reid, 1966). *E. encrasicolus* has a wide distribution with differentiated populations, and one of these populations is located in the Bay of Biscay (Motos, 1996). The peak of anchovy spawning tends to occur in spring when the environment experiences rapid change. According to Koutsikopoulos and Le Cann (1996) and Sanz and Uriarte (1989), this peak can be brought on by changes in the amount of daylight, the direction of the wind, a decline in freshwater runoff, or a rise in atmospheric and seawater temperatures. The spawning season takes place between March and August (Motos, 1996).

The one-year-old anchovy of the Bay of Biscay recruits support, on average, 60% of the spawning stock biomass (SSB) and most of the annual catch (25-87%) (ICES, 2021). After several years of recruitment failures under a constant capture regime, the fishery collapsed and was closed (2005–2009) (Vermard et al., 2008). Due to the inability to anticipate the size of the population during the first half of the year, when the main fishery occurred, precautionary

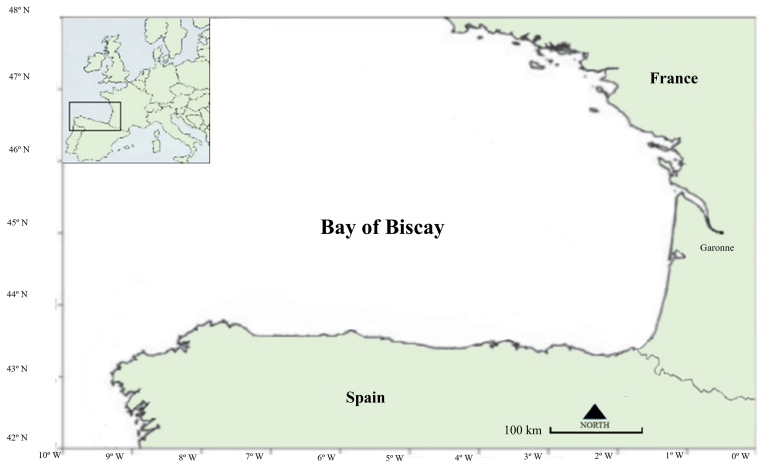

FIGURE 2
Study area within the Bay of Biscay, to demonstrate with a practical case the Common International Classification of Ecosystem Services (CICES cascade).

advice was neglected (Uriarte et al., 2023). In 2008, the EU implemented a long-term management strategy in response to the collapse. The biological risk was reduced in the absence of a recruitment indication by closely coordinating evaluation, guidance, and management, and shifting the management year to begin immediately following the adult spring surveys (Roel, 2009; Uriarte et al., 2023). The addition of an early recruitment indicator from a fall acoustic study on juveniles (Boyra et al., 2013) marked significant progress in 2014 (Uriarte et al., 2023). This permitted further resource utilization at comparable risk levels. As a result, Total Allowable Catches (TACs) are now set on a management calendar basis following the recruit survey. This strategy was unanimously approved and established a successful participatory fishery management approach (Uriarte et al., 2023).

For the anchovy case study, indicators for each different step of the CICES cascade were selected. For the pressure, harvest rate (Table 1) was chosen as the ratio between landings and total stock abundance, which is estimated from the stock assessment with SSB (Ibaibarriaga et al., 2011). The median SSB estimates are considered similar to the true population i.e. the complete stock abundance (Uriarte et al., 2023). Regarding the cascade steps, for the biophysical structure or processes, upwelling index was chosen as the indicator (Table 1). Upwelling is an oceanographic phenomenon that involves wind-driven motion of dense, cooler, and usually nutrient-rich water from deep water towards the ocean surface. Upwelling, and the associated turbulence, have been identified in small pelagic fishes as one of the biophysical processes that can explain the success in recruitment (Bakun and Parrish, 1982), also including the European anchovy (Borja et al., 1998). For the function step, recruitment at age 0 (Table 1), which is the most determinant factor that regulates the anchovy population size, and in general fish population, is their recruitment. Recruitment is the process through which small, juvenile fish advance to an older, larger life stage (Camp et al., 2020). The data available for anchovy recruitment were "Recruitment at age 1", in tonnes, which is the recruitment that can be caught, when the anchovy reaches its legal size for fishing (Uriarte et al., 1996). One-year-old anchovy supports on average 60% of the total SSB. However, for the needs of the CICES cascade, the indicator used was the recruitment at age 0. To estimate it, natural mortality was applied to the data of age 1, and the tonnes available one year earlier were calculated. In the case of service, SSB (Table 1), that can be defined as the combined weight of all individuals in a fish stock that have reached sexual maturity and are capable of reproducing. The estimation of SSB is accomplished by applying the Daily Egg Production Method (DEPM) (Lasker, 1985). For the benefit step the total catch landed of the anchovy was chosen, while for the value, the economic value of the catch, obtained by the fleets of first sale after landings, was selected.

The statistical analysis was carried out using R studio. Linear regression analysis was carried out to check whether these indicators statistically determined the state of the following step of the CICES cascade and how. The linear regressions were performed for three periods: The complete period (1987-2022), before the anchovy fisheries collapse (1987-2004) and after the collapse period (2010-2022). The temporal series was studied separately because the patterns of the links were different, due to the fisheries collapse. The collapse period (2005-2009) was not taken into account as some data were missing due to the fisheries closure. The relationships were analyzed for normality and linearity, respectively. In the case where the regression distribution was not normal (catch vs SSB 1987-2021; Economic value (EV) vs catch 2010-2022), skewness test was carried out to check which variable was asymmetric, and a logarithmic transformation was applied in these cases.

3 Results

3.1 CICES cascade indicators

In total, 84 articles were initially identified, from which only 21 were used finally to extract indicators (Appendix Tables A1–A3). In most cases, the discarded articles either did not include indicators or the indicators included were considered not useful as in relation to the CICES cascade.

The total number of indicators identified in the selected articles was 313. The number of indicators found differed between each ecosystem service type, with provisioning services having the highest number ("wild fish for nutrition"; n: 213), followed by regulation and maintenance services ("carbon sequestration by marine environments"; n: 153), and cultural services ("recreational marine mammal watching"; n: 116) (Figure 3). Despite the differences in number, the proportion of indicators classified across the three different categories (e.g., CICES cascade indicators, "incorrectly" classified and other terms) was similar between the three ecosystem service examples. The indicators correctly classified, according to CICES cascade, represented 39%, 39% and 43%, for provisioning, regulation and maintenance, and cultural, respectively. Similarly, 41%, 32%, and 45% of the provisioning, regulation and maintenance, and cultural indicators were identified by the authors as having been incorrectly classified in the original source. Finally, the indicators classified as other terms were 20% (provisioning), 29% (regulation and maintenance), and 11% (cultural).

The distribution of indicators across different CICES cascade components was not homogeneous within the selected ecosystem services (Figure 4). The total number of indicators regarding the cascade steps was: Biophysical structure and processes (54), Function (76), Service (14) Benefit (72), and Value (69).

Most "biophysical" indicators were adequately classified according to the CICES framework provisioning (65%), regulation and maintenance (62%) and cultural (63%). Comparing the three ecosystem service examples (Figures 4a–c) with the graph showing the total amount of indicators (Figure 4d), it can be observed that the number of indicators for this cascade component did not vary much: provisioning (46), regulation and maintenance (50) and cultural (35).

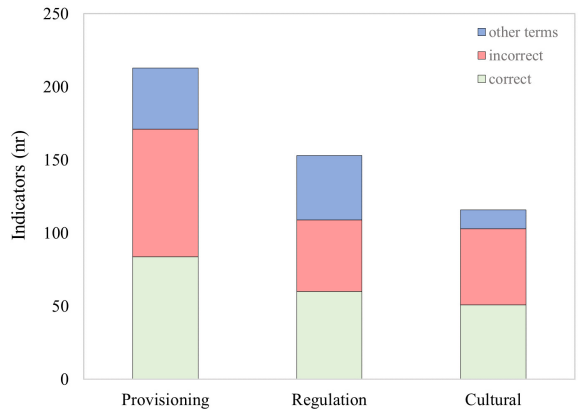

FIGURE 3
Total number of indicators for the three ecosystem services (ES) studied: provisioning (wild fish for nutrition), regulation and maintenance (carbon sequestration by marine environments), and cultural (recreational marine mammal watching). Different colors represent the number of indicators that the authors considered that are correctly classified according to CICES (Common International Classification of Ecosystem Services) in the literature (green), the incorrectly classified ones (red) and other terms (e.g. ecosystem service flow, ecosystem service capacity, essential ecosystem service variables) (blue).

However, in the case of the "functioning" indicators, more than 50% of the indicators found in the literature had not been adequately classified (i.e., observe blue/red ratios, for function bars, in Figure 4d). In this case, provisioning, regulation and maintenance, and cultural indicators (33%, 27% and 59%, respectively) had been classified at the biophysical structure and processes step, instead of at the functioning step Appendix Tables A1–A3.

The lowest number of indicators corresponded to "service" indicators, for which only 14 were found (Figure 4d). In this case only 25% of the indicators were correctly classified, 25% incorrectly classified and the remaining 50% as other terms. Those 43 indicators that had been incorrectly classified in their sources, 25 related to provisioning service, 10 to regulation and maintenance, and 8 to cultural ecosystem services.

In the benefit and value boxes of the CICES cascade, the indicators found for provisioning were much higher than the ones for regulation and maintenance or cultural services (Figures 4a–c). In the case of the provisioning service, 48 benefit and 34 value indicators were found, in the case of regulation and maintenance 12 benefit and 14 value indicators, and for cultural, 12 benefit and 21 value indicators. All the indicators were unique for each ecosystem service. In the case of provisioning, most of the indicators found for value were incorrectly classified as benefit or service or classified as ecosystem service indicators.

In the case of pressure, the provisioning service has the highest number of indicators (30), followed by regulation and maintenance (24), being the cultural service again the one with less indicators (11) (Figures 4a–c). In this case, the majority of the indicators were correctly classified according to MSFD, i.e. provisioning (60%), regulation and maintenance (67%) and cultural (100%) (Figures 4a–c).

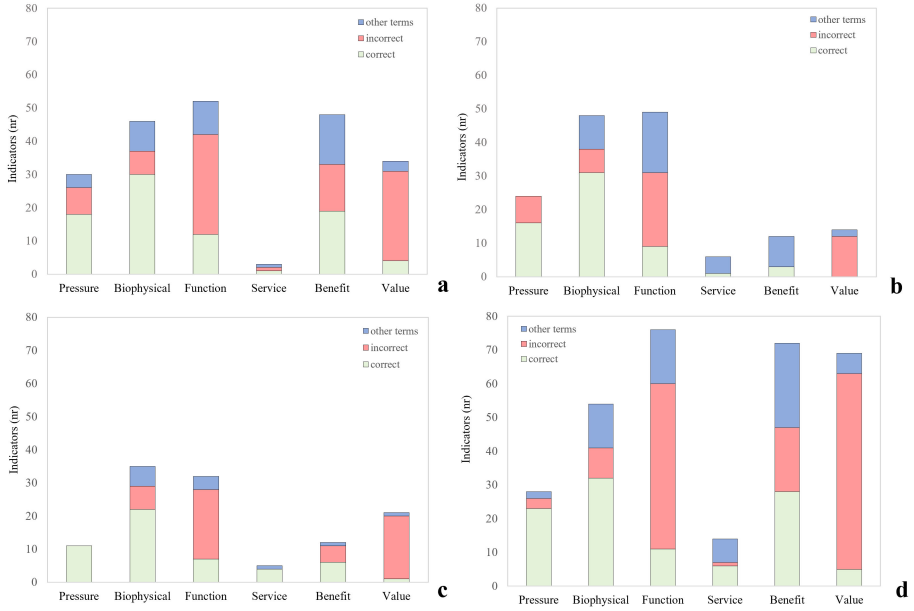

FIGURE 4
Number of indicators found in the literature for three ecosystem services (ES) examples [**(a)** provisioning; **(b)** regulation and maintenance; **(c)** cultural; **(d)** the total indicator number for the three examples], assigned to the different CICES (Common International Classification of Ecosystem Services) cascade components (i.e., pressure, biophysical structure or processes, function, service, benefit, and value) Indicators classified according to CICES in the literature consulted, the ones incorrectly classified, and the ones classified as ecosystem service variables are represented.

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TABLE 2 Pressure effect, as harvest rate of anchovy, on Function (Recruitment at age 0) and Service (Spawning Stock Biomass, SSB), represented by linear regression and p-value.

Period	Complete	Before collapse	After collapse
	1987-2022	1987-2004	2005-2022
Regression	Recruitment= 184746*(Harvest rate)+211737	Recruitment= -61566*(Harvest rate)+136073	Recruitment= 653431*(Harvest rate)+54342
R^2	0.209	0.015	0.188
p-value	0.009	0.629	0.139
Period	1987-2022	1987-2004	2005-2022
Regression	SSB=-162313* (Harvest rate)+139632	SSB=-90360* (Harvest rate)+98502	SSB=-316724* (Harvest rate)+174330
R^2	0.555	0.208	0.175
p-value	< 0.001	0.057	0.155

The regression has been calculated for the complete period and the periods before and after the collapse of the fishery. In red, are significant correlations.

3.2 Practical application to the anchovy fishery

The relationship between pressure on anchovy fishery (measured as harvest rate) and two of the CICES cascade components (Function, as Recruitment at age 0, and Service, as SSB) was determined using linear regression analysis (Table 2). The results showed a negative and statistically significant regression for the complete period (1987-2022) for both relationships (recruitment vs harvest rate, p-value: 0.009; and SSB vs harvest rate, p-value < 0.001). However, when exploring the Pressure effect separately before and after the anchovy fisheries collapse, this relationship was not significant for either the function or the service components (Table 2).

This temporal variation of recruitment and SSB as in relation to harvest rate is graphically represented in Figure 5. Several periods can be identified: (i) between 1987 and 1996, the pressure values were very high, (i.e., harvest rates ranging between 0.5 and 0.74), the recruitment values ranged from 20,080 to 193,041 t and the SSB values from 14,917 to 72,428; (ii) this was followed by a period (1998-2004) with moderate harvest values, that ranged between 0.35 and 0.54, which coincide with a dramatic drop in the recruitment (from 204,823 to 9,394 t) and the SSB (from 89,496 to 29,989 t); (iii) the third period, extends from 2005 to 2009, which coincides with the anchovy fisheries collapse, in which the harvest rate values suffered a dramatic decrease (<0.1) and with very low recruitment and SSB values; and, finally, (iv) the period after the collapse (2010-2022), characterized by low-pressure values (harvest rate between 0.15 and 0.3), and increasing recruitment and SSB values, reaching the maximum of the series.

As a second step, when exploring the links between the different parts of the CICES cascade (i.e., Biophysical components or processes – Function; Function – Service; Service – Benefit; Benefit – Value), the Biophysical components or processes (Upwelling index) did not significantly determine the Function (Recruitment) (Table 3). However, the Function (Recruitment) significantly determined the service (SSB) (p-value < 0.001) (Table 3). The service (SSB, t) showed to affect the anchovy fisheries benefit (Catch, t) significantly and positively for the three periods too (Table 3). The service (SSB) explained for 70% of the catch before-collapse period and after-collapse the relationship seems to be weaker. Finally, the relationship between the benefit (catch, t) and value (€) was only significantly positive for the after-collapse period (p-value: 0.008).

A representation of these links between the different pairs of CICES cascade components can be observed in Figure 6. Although the relationship between the upwelling index and recruitment was not significant, certain similarities in the evolution pattern can be seen (Figure 6a). Periods of higher upwelling values (i.e., 1989-1997 and 2010-2021) corresponded to higher recruitment values, whilst lower upwelling values (1998-2009) matched with lower recruitment (Figure 6a).

As observed before, the recruitment and SSB covaried and were related with a year lap difference (Figure 6b).

Before the fishery collapse, a high proportion of the SSB was caught, being the captures in this period more than 50% of the SSB (Figure 6c). Between 1987 and 1993 the catch followed the SSB evolution, ranging from the minimum catch in 1989 (10,374 t), with also a minimum value for SSB (observed before), and a maximum for both components in 1993 (catch: 40,087 t) (SSB: 72,428 t). After

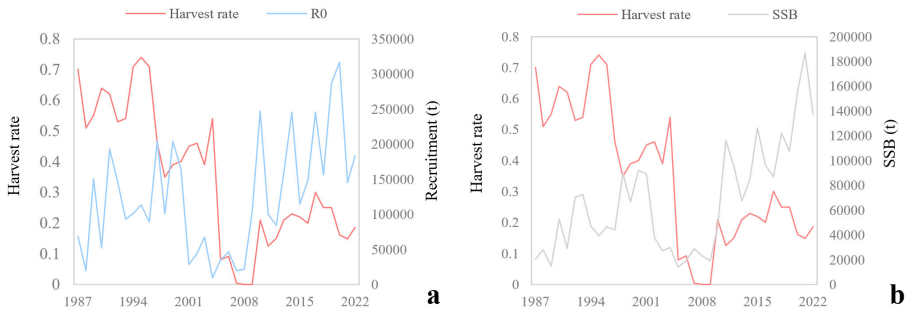

FIGURE 5
Temporal variation of pressure (harvest rate) with **(a)** function (recruitment at age 0) and **(b)** service (spawning stock biomass, SSB).

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TABLE 3 CICES (Common International Classification of Ecosystem Services) cascade component relationships represented by linear regression and p-value.

Period	Complete	Before collapse	After collapse
	1987-2022	1987-2004	2005-2022
Regression	Recruitment= 87.42*(UPW index)+55129	Recruitment= 74.242*(UPW index)+46937	Recruitment= 69.575*(UPW index)+88457
R^2	0.072	0.089	0.033
p-value	0.113	0.228	0.468
Period	1987-2022	1987-2004	2005-2022
Regression	SSB= 0.4856* (Recruitment) +8830.4	SSB= 0.3695* (Recruitment) +11521	SSB= 0.49661* (Recruitment) +16720
R^2	0.817	0.833	0.864
p-value	< 0.001	< 0.001	< 0.001
Period*	1987-2021	1987-2004	2010-2021
Regression	Catch=15302* (logSSB)-48862	Catch=0.3556* (SSB)+8522.4	Catch=0.1219* (SSB)+8545.4
R^2	0.197	0.704	0.444
p-value	0.014	< 0.001	0.018
Period*	1990-2021	1990-2004	2010-2021
Regression	Economic value =4.7018*(Catch) +3E+06	Economic value =-23.793*(Catch) +4E+07	Log Economic value =1E-05* (Catch)+6.2817
R2	0.001	0.025	0.522
p-value	0.8565	0.570	0.008

The regression has been calculated for the complete period and the periods before and after the collapse of the fishery. In red, are significant correlations. *Not considering collapse years (2005-2009). UPW, Upwelling; SSB, spawning stock biomass.

this, SSB had a decreasing pattern for the next five years (1994-1998) (minimum SSB: 39,486 t, 1995). Catches followed the same pattern as the period before, the captures exceeded the half of the SSB all the years, and decreased in values, reaching the minimum in 1997 (22,337 t). As mentioned before, SSB showed an increasing pattern from 1997 to 2000, doubling in some cases the values reached the period before (maximum SSB: 91,838 t); however, the captures maintained the values around 30,000 t during this period. When the SSB started decreasing its values in 2001, catch followed the same evolution reaching a minimum of captures in 2005, with 1,128 t, when the fishery collapsed (Figures 6c, d). In turn, after the collapse, the SSB (service) increased dramatically, but the catches (benefit component) remained at a low level, with a slight increase, and not far from the before-collapse levels, reaching a maximum in 2018, with 30,773 t caught (Figures 6c, d).

Despite these fluctuations in the catches (benefit), the economic value of anchovy landings has been maintained without dramatic changes between 1992 and 1997 (mean value 2.8 million €) (Figure 6d). In 1998, even if catch did not increase its values significantly, the value reached its maximum (6.03 million €), before falling to 3.58 million €, in 1999. The next two years (2000 and 2001), both catches and economic value showed a slightly increasing pattern (Figure 6d). Even if captures decreased sharply, the following years (2002-2004) the economic value maintained its values around 4.5 million €. When the fishery collapsed, the economic value reached its minimum (0.5 million €). After that, the economic value started to increase, following the captures pattern, and maintaining values of around 4 million € (Figure 6d).

4 Discussion

4.1 CICES cascade indicators

Previous studies (e.g. Böhnke-Henrichs et al., 2013; Liquete et al., 2013; Thenen et al., 2020) have listed indicators to determine marine ecosystem services flows, and many others reviewed indicators for investigating ecosystem services in general (de Groot et al., 2010; Egoh et al., 2012; Hernández-Morcillo et al., 2013; Grima et al., 2023). Among all the literature reviewed for this study, Thenen et al. (2020) was the only one that assessed the CICES cascade components for marine ecosystem services. However, they did not follow the CICES cascade terminology strictly, as they grouped the biophysical structure and processes and function steps into "ecosystem service capacity". Other studies focused on marine ecosystem services, but did not follow the CICES cascade classification (Liquete et al., 2013; Atkins et al., 2015).

In our study, the principal problem faced was the terminology used for the assessment of ecosystem services in the literature, which is neither normalized nor standardized across the different frameworks (i.e., MEA, 2005; TEEB, 2010; Atkins et al., 2011; Böhnke-Henrichs et al., 2013; Liquete et al., 2013; Turner et al., 2015; Balvanera et al., 2022; Costanza et al., 2017; Haines-Young and Potschin, 2018; Culhane et al., 2020; Barbier, 2017; Chalkiadakis et al., 2022). This issue has been tackled by assessing the current status of indicators, for the three ecosystem service sections (i.e., provisioning, regulation and maintenance, and cultural) and the steps of the cascade flow (i.e., biophysical structure or process, functioning, service, benefit, and value), where the main confusions for these indicators' classification and the principal gaps have been identified. The different interpretations of this flow and the numerous terminologies led to a general confusion of the terms and the links of the CICES cascade components (Lillebø et al., 2016; Czúcz et al., 2018; Chalkiadakis et al., 2022; Grima et al., 2023; Thenen et al., 2020).

This was observed in our study when looking at the three ecosystem services chosen and the components of the cascade. Considering the different frameworks and proposals around the flows, it was not surprising that more than 30% of indicators were incorrectly classified in their original source according to the CICES cascade. The lack of a unified framework and issue of ecosystem services terminology hindrance the research and interpretation of outcomes in this field (Grima et al., 2023). However, the effects are not the same across ecosystem services (Czúcz et al., 2018)., and each has been explored to a different extent.

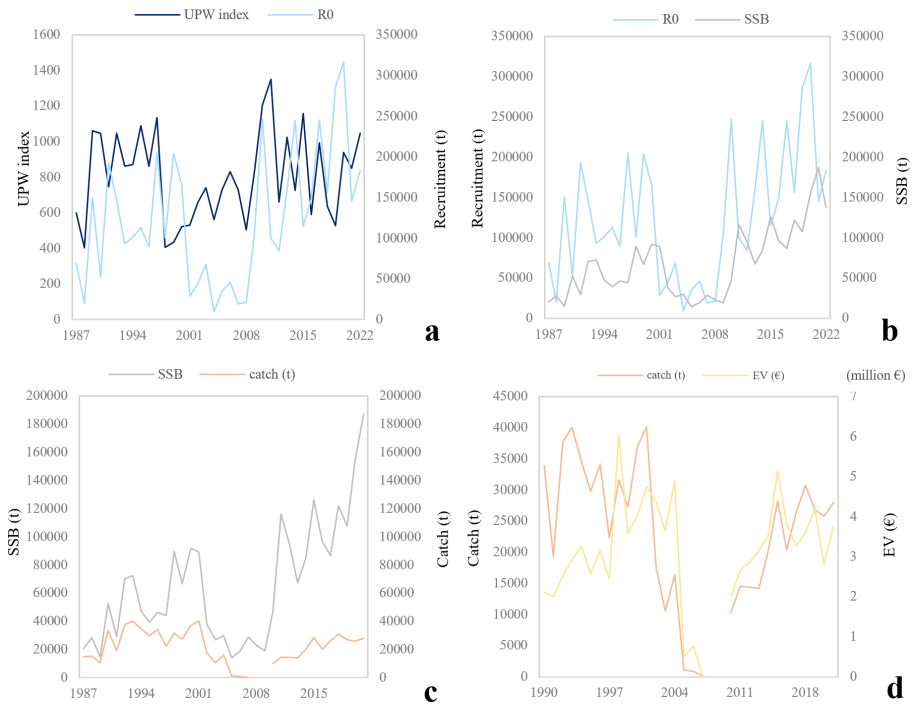

FIGURE 6
Temporal variation of the links between pairs of CICES (Common International Classification of Ecosystem Services) cascade components: **(a)** Biophysical components or processes (UPW, Upwelling index) - Function (Recruitment at age 0 (R0)); **(b)** Function (R0) with Service (SSB, Spawning Stoc Biomass); **(c)** Service (SSB) with Benefit (Catch); and **(d)** Benefit (Catch) with Economic value (EV, in euros).

In line with previous studies (Thenen et al., 2020), we found that out of the three ecosystems services analysed, the provisioning service was the one with the highest number of indicators, specially concerning the benefit and value components of the cascade. This is not surprising since this service primarily relies on fisheries, which is a crucial industry for the global economy, supplying with livelihoods and food to millions of people worldwide (Golden et al., 2021). Moreover, it has been largely studied, and there is a specific science to study the fish populations and dynamics for the fisheries management (Munro and Scott, 1985). Furthermore, food provisioning indicators are relatively easy to measure (Hattam et al., 2015), and broad efforts have been made to assess fish stocks (e.g., ICES stock assessment database) (Froese et al., 2018). Provisioning services are also easier to assign an economic value to, as they are directly linked to market activities and resource extraction (Liu et al., 2010). The massive amount of data related to fisheries can explain the higher number of indicators for each step of the cascade in provisioning, when compared to the other two examples explored. In contrast, much less indicators were found for regulation and maintenance services. This type of services are more challenging to quantify and value, due to their indirect and often non-market nature (Abson and Termansen, 2011). The example chosen for literature indicators assessment, carbon sequestration, has been a hot topic for the last decade and multiple studies had been carried out (Duarte, 2016; Macreadie et al., 2021). Assessing the significance of carbon storage has become increasingly important in recent times, leading to the establishment of the carbon market (Calel, 2013), although these markets have been recently criticised for their impacts on biodiversity (Pascual et al., 2023). Despite the growing interest and the considerable high number of publications on the topic, determining the indicators for the different cascade steps was not easy. The fact that carbon storage is a process complicates the application of the CICES cascade, as it was not clear which indicators should be allocated to each step (more information can be seen in Appendix Tables A1–A3).

The understanding of cultural service nature is even more complicated as they are the least studied ecosystem services (Ghermandi et al., 2012; Martin et al., 2016; Rodrigues et al., 2017; Thenen et al., 2020), and measuring their benefits could be complicated, and so indeed was finding accurate indicators. This may be due to the intangible nature of their resources, which is even more evident for marine environments (Queiroz et al., 2017; Elliott, 2023). The revised literature about marine cultural ecosystem services flows was quite limited, coinciding with other ecosystem service indicators assessments (e.g. Hattam et al., 2015). Moreover, the definitions and measurement procedures for cultural ecosystem service indicators were not clear enough, coinciding with the conclusions also made in other studies (Milcu et al., 2013; Hattam et al., 2015). For example, the boundaries between function and biophysical structure or process are confusing, as both relate to processes that can be important for the ecosystem service delivery (Haines-Young and Potschin, 2018). In our case, we overcame this issue by following the definitions (Table 1) for each cascade step to classify the indicators.

The biophysical structure or process was the first cascade component with the highest number of indicators regarding the cultural service, the second regarding regulation and maintenance and the third regarding the provisioning service. In this case most of the indicators were correctly classified according to CICES. This

may be explained as most (>60%) of these indicators were extracted from the same source (Atkins et al., 2015). Despite this research study did not follow the CICES framework, but UK NEAFO WP3b framework (UK NEAFO, 2014), both (CICES and UK NEAFO) shared the first step of the ecosystem service flow (component and processes), and this specific set of indicators was abundant and appropriate (Atkins et al., 2015). Some of the indicators found for this cascade component were equivalent across the three ecosystem service examples as these indicators described general factors of any marine ecosystem (i.e. nutrient concentration or pH) (Appendix Tables A1–A3).

It was surprising that the cascade category with less (accurate) indicators in the literature was indeed the ecosystem services component. This leads to a question: Is it clear what an ecosystem service is? The definition of ecosystem service, according to CICES, is: *"Ecological outcomes that particular ecosystem characteristics or processes generate, that can ultimately benefit people"* (Haines-Young and Potschin, 2018). It seems that a confusion exists when comes to distinguish what an ecosystem service is, and what flows (determined as other terms in this study) of different components of the cascade for CICES are (Chalkiadakis et al., 2022). This problem has been reported in other ecosystem service indicator assessments (Lillebø et al., 2016; Czúcz et al., 2018; Grima et al., 2023). Lillebø and colleagues (2016) collected indicators from 14 different case studies around Europe and they reported that for the participants the most challenging part was understanding the differences among ecosystem service capacity, flow and benefit. In this study, it was observed that 21% of all the indicators found were originally classified as other terms (i.e., ecosystem service flow, ecosystem service capacity, essential ecosystem service variables), meaning that they follow a logic to classify ecosystem service indicators different to the one used by the CICES cascade. The high number of indicators classified as other terms can be explained because the different frameworks explaining the ecosystem service flows use different terms and concepts (Balvanera et al., 2022; Barbier, 2017; Costanza et al., 2017; Haines-Young and Potschin, 2018; Culhane et al., 2020; Thenen et al., 2020).

One of the steps that creates more confusion is the one from service to benefit. Indeed, some authors do not distinguish between both (Balvanera et al., 2022; Barbier, 2017). In our study, we followed CICES definitions and interpret service and benefit following the definitions in Table 1. In this framework the "production boundary" represents the inputs that a service requires to become a benefit (e.g. harvesting fish for nutrition requires investing energy, time and resources). These inputs have been made explicit in other frameworks, such as Costanza et al. (2017), who highlighted that human and social capital are needed for natural capital to flow (in the form of ecosystem service) and become a human benefit.

The indicator numbers unbalance is especially remarkable concerning the socio-economic side of the cascade (benefit and value). As mentioned before, the provisioning ecosystem service, and in particular, fish stocks have been widely studied for decades in science and managing (Munro and Scott, 1985). The benefit of fisheries can be easily measured, either as wild catch landed fish or employment in fisheries (Appendix Table A1) (Béné et al., 2012; Seitz et al., 2014), while the benefits for regulation and maintenance and cultural services, not only had been less studied, but also are more difficult to measure, as for example healthy climate (regulation and maintenance) or leisure (cultural) (Jarvis et al., 2017; Pouso et al., 2020).

The benefit and the value components of the cascade, which correspond to the socio-economic part of the model, and consequently specific for human, are not really distinguished in the literature (Liquete et al., 2013; Hattam et al., 2015; Atkins et al., 2015; Barbier, 2017). As found in our study, all the value indicators of ecosystem services were originally classified as benefit indicators in the literature; this can be explained because the economic value can be seen as a type of human benefit (Sagoff, 2008).

The differences and mismatches in the classification of indicators into the different steps of the CICES cascade identified in this research calls researchers to once adopted CICES, to be coherent with the meaning of the different terms as used in this classification.

4.2 Practical application to the anchovy fishery

When studying the links within the different steps of the CICES cascade, the relationship between the biophysical structure or process (upwelling index) and the function (recruitment) was not significant. However, previous studies (Borja et al., 1996; Borja et al., 1998; Borja et al., 2008; Planque and Buffaz, 2008; Fernandes et al., 2010; Erauskin-Extramiana et al., 2019) have identified a series of environmental indices affecting the recruitment of anchovy in the Bay of Biscay, including upwelling, turbulence, and stability. It must be noted that the recruitment data used by Borja et al. (2008) were not the same as those used in our study, as the methodology used in the surveys and the estimation of biomass changed (Uriarte et al., 2023). A more recent study (Ibaibarriaga et al., 2023) has concluded that upwelling and turbulence combined are positively related to recruitment, explaining 34.7% of the variability in the recruitment (at age 1).

Due to the biology of the species, the short lifetime and the population concentrations, the factor that mostly determines the recruitment (age 0) biomass is in fact the SSB (ecosystem service), which is used to estimate next year population biomass (Ibaibarriaga et al., 2011). Moreover, data for the recruitment (at age 1) surveys is used to predict the SSB of the next year (Boyra et al., 2013). Thus, these two components are highly correlated, and the results obtained for this link between the two cascade components were expected. Hence, considering that the 1-year-old recruits contribute to about 60% of the total SSB of a year (ICES, 2021), the result of recruitment (at age 0) explaining >80% of the variability of the SSB of the next year can be expected for a short-living species, such as the anchovy of the Bay of Biscay (Motos et al., 1996).

The relationship between SSB and catch was significant and shows that SSB is an appropriated indicator for service, indicating the real capacity of the ecosystem (anchovy population, in this case), to further provide the benefit (anchovy catch). The fact that the relationship between both components was not statistically significant for the complete period, but it was positive and strong when analysing the relationship before and after the collapse individually can be explained

by the different fishery management during each period: before the collapse, management was based on a constant TAC of 30,000 t, regardless ICES advice. However, this TAC did not really condition Spanish and French fishery at that moment, so, in practice, it was an unregulated fishery (del Valle et al., 2001; Lazkano et al., 2013). The catch before the collapse was higher than after the collapse, and positively and linearly related to SSB; just after this period the anchovy fishery collapsed, due to repeated recruitment failures (Uriarte et al., 2023). After the collapse, the catches are more constant, independently of the SSB increase, and this leads to a more "asymptotic relationship" of the component. Even if more data are needed to confirm this in coming years, it seems that the management adopted by the European Commission after the collapse, in which the TAC is thoroughly calculated with more exact estimations of recruitment and SSB (Uriarte et al., 2023), has led to a higher anchovy population (SSB), and as consequence to a sustainable anchovy fishery.

All this comes to a last step in the cascade (value), which in this case is the economic value of the ecosystem service and determines how much money can anchovy fishery provide humans with. In this case, the relationship was not as strong as the function-service or service-benefit relationships. The fact that the value of the anchovy per kilogram varies from year in response to catches and other external factors (García del Hoyo et al., 2023) may explain why the economic value was not related to the benefit (catch) considering the complete period and the before the collapse period. There is a peak in the value (euro kg^{-1}) in the years before the collapse, in which the anchovy become scarce and its value increased dramatically (Roel, 2009; García del Hoyo et al., 2023). After the collapse, the relationship between catch and economic value was significant and positive (Table 2). The economic value after 2010 was maintained in relatively high values and can be maintained in time, contributing to the sustainability of the activity.

Some elements and links of the CICES cascade can be affected by natural and anthropogenic pressures, especially through fisheries (i.e., fishing mortality), but also other (Large et al., 2015). This means that both parts of the cascade, the environmental and the socio-economic parts, can be impacted by different pressures. The biophysical part of the cascade may be the one that is more affected by cumulative effect of human pressures (Stelzenmüller et al., 2009). In this study, harvest rate was not relevant as in relation to the upwelling index. However, other natural or human pressures can affect the biophysical part of the cascade. One of the most obvious is the climate change, which can affect the upwelling index intensity and duration, as it has been observed worldwide (Varela et al., 2015; Wang et al., 2015). Studies by Sousa et al. (2017, 2020) have revealed that this may be especially noticeable in the north of the Iberian Peninsula and may probably affect the anchovy population and fishery in the future.

The pressure indicator used in this study (harvest rate) was explained SSB variability when looking at the whole picture (complete period). The harvest rate before the collapse was really high (between 0.5 and 0.8), and the growth of the SSB was limited by the high fishing pressure, consequence of the unregulated fishery (Uriarte et al., 2023). When the stock started to recover after the

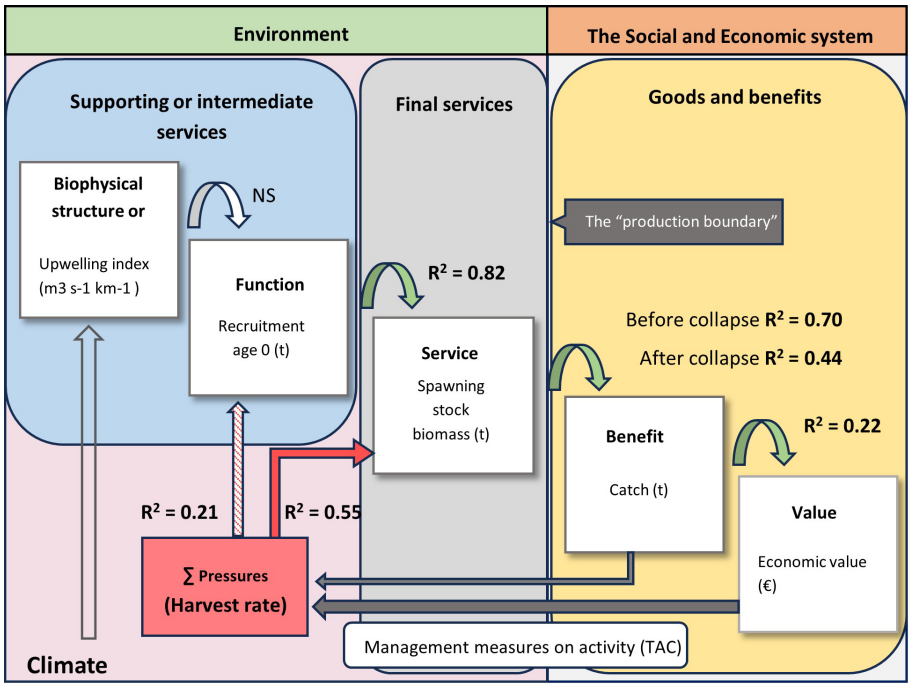

FIGURE 7
Adaptation of the CICES (Common International Classification of Ecosystem Services) cascade 1243 diagram (Potschin and Haines-Young, 2017) after applying it to a real case study: the anchovy of the Bay 1244 of Biscay. The diagram shows the relationships found for the different components of the cascade. In green: 1245 positive and significant ($p<0.05$) relationship between components; in red: negative and significant 1246 ($p<0.05$), in white: not significant (NS; $p>0.05$). TAC, Total Allowable Catch.

collapse, together with the implementation of management measures, the harvest rates were maintained around values of 0.3. These values did not increase even if the SSB reached maximum historical levels, and the recovery of SSB is in part explained by these lower harvest levels (Uriarte et al., 2023). Harvest rate would not directly perturb the recruitment age 0 population, as these fish are not harvested, being affected only indirectly by this pressure by the SSB of the same year.

In Figure 7, the application of the CICES cascade, adapted to our case study (anchovy), is represented considering the findings of this research. The cascade results obtained from the component links are represented with their R^2 values, indicating empirical demonstration of the relationships between the components. There are multiple pressures in the marine environment that can affect differently each of the cascade components, thus we propose to represent this reality in the cascade diagram. Hence, this Figure 7 represents the real application of data to the cascade components links.

In this study only one species (*Engraulis encrasicolus*) and one ecosystem service (provisioning) was considered, and the cascade links were tested with one indicator for each component of the CICES cascade. The large data available for a wide temporal series and having a suitable indicator for each cascade step was crucial to carry out this exercise, which otherwise would not have been possible. However, this is not enough, for a comprehensive understanding of ecosystem services flows and their importance to humans, it is also necessary to better understand the multiple relationships of the marine environment components and the socio-economic part of the cascade (Hattam et al., 2015). Hence, studies including multiple species, ecosystem components, indicators, pressures, different flows and relationships (linear, non-linear), including multivariate analyses, should be undertaken in the future to catch the complexity of the marine environment, as well as the interactions between the different ecosystem service sections.

Human welfare is directly and indirectly dependent of the ecosystem services supply, and the sustainable management of the resources is necessary for the sustainable provision of ecosystem services. We are aware that this study has some limitations, as the analysis of the indicators was focused in three examples, and the application of the cascade was only carried out considering one species. However, despite the limitations of the study, the results highlight the need for scientist and stakeholders to careful use the ecosystem service terminology and proves that the CICES cascade links works when applying it with real data. Therefore, management guided towards maintaining these relationships should allow the sustainable provision of ecosystem services and benefits for humans.

5 Conclusions

The lack of a standard terminology and understanding of ecosystem services components and the relationship and flows between the environment and the socio-economic system, leads to general confusion in the studies about this topic. many indicators are incorrectly assigned in the literature to the different components of the CICES cascade, which makes difficult the comparability across studies. Therefore, a standardization of terminology, classification and understanding is necessary for a holistic and sustainable management of the marine environment and its resources.

Such standardization could benefit the study of ecosystem services flows with real and practical cases, as illustrated with the anchovy of the Bay of Biscay. In this case, adequate indicators and sufficient data for each CICES cascade component, have allowed to demonstrate the links between the environmental and the socio-economic part. Future works should try to consider several species, components, and indicators at the same time, as well as several cumulative human pressures, and even climate change effects, under non-linear relationships.

The approach presented here could be applied to other ecosystem services, as well as explore the complex, multivariate, and non-linear relationships among the cascade components flow. In case of being successful, an operational approach can be proposed for policy-makers to take management decisions on marine ecosystem services mapping, assessment and conservation.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to aolano@azti.es.

Author contributions

AO-A: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. MU: Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Writing – review & editing, Resources. SP: Investigation, Methodology, Supervision, Validation, Visualization, Writing – review & editing. AB: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1497521/full#supplementary-material

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Marine invasive alien species in Europe: 9 years after the IAS Regulation

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Biological invasions, resulting from human activities, exert substantial impacts on ecosystems worldwide. This review focuses on marine invasive alien species (IAS) in Europe, examining the current state, proposing strategies to address the problem, and offering recommendations for enhanced management. Effective management of biological invasions relies on accessible, accurate data to inform decision-making. Information systems such as the European Alien Species Information Network (EASIN), Aquatic Non-Indigenous and Cryptogenic Species (AquaNIS), and World Register of Introduced Marine Species (WriMS) provide comprehensive databases on IAS, but their sustainability requires long-term maintenance, continuous updates, and support. Most countries lack specific monitoring programs for marine IAS, and standardization and improvement of monitoring methods are needed. Port monitoring plays a vital role in the early detection of new arrivals, and recent advancements in molecular techniques show promise for effective IAS monitoring. Risk screening tools are commonly employed to rank taxa based on their invasiveness potential in European regions, but variations in protocols can yield inconsistent results. European impact assessments highlight resource competition, novel habitat creation, and predation as primary mechanisms for negative impacts on biodiversity, while the creation of novel habitats represents a key mechanism for positive impacts. Preventing IAS introductions is critical, and measures such as ballast water treatment systems are implemented to reduce the likelihood of marine introductions. However, understanding introduction pathways remains uncertain for many IAS. Eradication and control efforts for marine IAS have

limited success, emphasizing the need for enhanced biosecurity measures. Climate change, especially ocean warming, can intensify IAS impacts on native species and ecosystems. In climate change hotspots, some tropical aliens may, however, compensate for the loss of thermally sensitive natives with similar traits. Therefore, it is imperative to consider the interactions between climate change and IAS in developing effective management and conservation strategies. Enhancing IAS management in Europe entails i) securing adequate funding, ii) expanding the list of IAS of Union Concern to adequately cover marine invasions, iii) learning from countries with successful biosecurity practices, iv) sustaining information systems, v) improving monitoring and early warning systems with innovative technologies, vi) enhancing prediction models, vii) conducting integrated impact assessments and mapping cumulative IAS impacts, and vii) considering the potential benefits of IAS in ecosystem functioning and services.

KEYWORDS

alien species, biodiversity, biological invasions, ecosystem services, impacts, non-native, pathways, recommendations

1 Introduction

Biological invasions or bioinvasions (Elton, 1958) are among the most influential human-driven processes impacting Earth's terrestrial and aquatic ecosystems (Primack, 1995; Rilov and Crooks, 2009; Ehrenfeld, 2010; Vilà et al., 2011). Both native and non-native species have the potential to undergo exponential population growth and cause outbreaks, i.e., invasions. The dynamics of biological invasions arise from interspecific (direct or indirect) interactions, such as predation, competition, mutualism, or facilitation, often leading to the invader's dominance over functionally similar species in the invaded community (Valéry et al., 2008; Valéry et al., 2009; Valeíry et al., 2013). The success and impact of a biological invasion depend on the interplay of ecological and biological characteristics of both the invader and the species in the invaded community, as well as the environmental conditions. Restricting the definition of biological invasions to a geographical phenomenon specific to non-indigenous species rather than an ecological one is not justified (Valéry et al., 2013). Therefore, invasive alien (=non-native, non-indigenous, exotic) species (IAS) should be regarded as a subset of invasive species, which can also include native or neonative (*sensu* Essl et al., 2019).

Non-indigenous species (NIS) are defined as species that have spread beyond their natural biogeographical range to new regions with the aid of human actions (Essl et al., 2018). IAS are defined by the European Union (EU) IAS Regulation as "alien species whose introduction or spread has been found to threaten or adversely impact upon biodiversity and related ecosystem services" (European Union (EU), 2014), giving the term "invasive" a negative connotation. IAS have rapidly increased worldwide (Seebens et al., 2017), resulting in significant economic costs (Diagne et al., 2021). IAS have the capacity to profoundly alter the structure and functioning of native communities, often leading to the loss of native biodiversity, disruption of ecosystem services, loss of socioeconomic values, and potential impacts on human health (Mazza et al., 2014; Tsirintanis et al., 2022). However, the impacts of IAS can have either (or both) "negative" (reducing the value of a specific property) or "positive" (increasing the value) consequences for specific ecological or socioeconomic attributes, and they can be highly context-dependent (Tsirintanis et al., 2022; Vimercati et al., 2022; Reise et al., 2023).

IAS are recognized in the Convention on Biological Diversity (CBD) as a cross-cutting issue with relevance across all thematic areas. Article 8(h) of the CBD explicitly states that "each contracting Party shall, as far as possible and as appropriate, prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species". Recently, the Kunming-Montreal Global Biodiversity Framework, under decision 15/4, has set the objective to "eliminate, minimize, reduce and or mitigate the impacts of invasive alien species on biodiversity and ecosystem services" through various approaches, with particular emphasis on eradicating or controlling IAS in priority sites, such as islands (Table 1). Multiple global and regional legislative instruments, policies, and guidelines have been established to contribute to the achievement of these global goals (see Table 1). Typically, species introduced before a specific cutoff date are not subject to biosecurity measures and are treated no differently than native species. In some cases, they may even become the focus of conservation efforts (Essl et al., 2018). Biosecurity efforts predominantly target neobiota, i.e., relatively recently introduced alien species or species that have not yet been introduced. However, there is no global consensus on this cutoff date, leading to the use of region-specific temporal thresholds in NIS databases. For example, in Europe and the Americas, the widely accepted cutoff date is 1492, which marks Christopher Columbus's discovery of America and the related initiation of species introductions between the two continents. In the Mediterranean region, some databases have adopted the opening of the Suez Canal in 1869 as their temporal threshold, as it triggered

TABLE 1 International policy context on biological invasions in coastal and marine environments with relevance for European Seas.

Policy	Geography	Environmental objectives
Barcelona Convention (*UNEP-MAP*)	**Mediterranean Sea**	Non-indigenous species (NIS) introduced by human activities are at levels that do not adversely alter the ecosystem.
HELCOM	**Baltic Sea**	To prevent adverse alterations of the ecosystem by minimizing, to the extent possible, new introductions of NIS.
OSPAR	**North-east Atlantic**	Endeavor to limit the introduction of NIS by human activities to levels that do not adversely alter the ecosystems.
Bucharest Convention	**Black Sea**	*Ecological Quality Objective EcoQO 2c:* Reduce and manage human-mediated species introductions.
Marine Strategy (*MSFD Com Dec 2017/848)*	**EU**	*Descriptor 2:* NIS introduced by human activities are at levels that do not adversely alter the ecosystems. *D2C1* Number of NIS newly introduced *via* human activity into the wild […] is minimized and where possible reduced to zero. *D2C2* Abundance and spatial distribution of established NIS, particularly of invasive species, contributing significantly to adverse effects on particular species groups or broad habitat types. *D2C3* Proportion of the species group or spatial extent of the broad habitat type, which is adversely altered due to NIS, particularly invasive NIS.
Invasive Alien Species Regulation 1143/2014	**EU**	Aims to prevent, minimize, and mitigate the adverse impacts posed by these species on native biodiversity and ecosystem services. Rules also aim to limit social and economic damage. For example, *Art. 5* "[…] a risk assessment shall be carried out in relation to the current and potential range of IAS, having regard […] (e) a description of adverse impact of the species on biodiversity…" *Art. 13* Action plans on the pathways of invasive alien species.
Alien Species in Aquaculture EC Council Regulation 708/2007	**EU**	Concerning the use of non-indigenous and locally absent species in aquaculture in order to assess and minimize the possible impact of non-target species on aquatic habitats, based on the "ICES Code of Practice on the Introductions and Transfers of Marine Organisms".
EU Biodiversity Strategy for 2030	**EU**	*Commitment:* Manage established invasive alien species and decrease the number of Red List species they threaten by 50% by 2030.
Convention on Biological Diversity (CBD)	**Global**	*Kunming-Montreal Global Biodiversity Framework, decision 15/4 (Target 6)*: "Eliminate, minimize, reduce and or mitigate the impacts of invasive alien species on biodiversity and ecosystem services by identifying and managing pathways of the introduction of alien species, preventing the introduction and establishment of priority invasive alien species, reducing the rates of introduction and establishment of other known or potential invasive alien species by at least 50 per cent by 2030, and eradicating or controlling invasive alien species, especially in priority sites, such as islands."
United Nations Convention on the Law of the Sea (UNCLOS 1982)	**Global**	"to prevent, reduce and control pollution of the marine environment resulting from […] the intentional or accidental introduction of species alien or new, to a particular part of the marine environment, which may cause significant and harmful changes thereto."
Ballast Water Convention IMO	**Global**	*Article 2:* Prevent, minimize, and ultimately eliminate the transfer of harmful aquatic organisms and pathogens through the control and management of ships' ballast water and sediments, […].
Biofouling Guidelines IMO	**Global**	*Objective:* Minimize the risk of transferring invasive aquatic species from ships' biofouling.

UNEP, United Nations Environment Programme; MAP, Mediterranean Action Plan; IMO, International Maritime Organization.

a surge of Red Sea species into the Mediterranean Sea (Gatto et al., 2013; Essl et al., 2018).

In the EU, the Biodiversity Strategy for 2030 has set the objective of effectively managing established IAS and reducing by 50% the number of Red List species they threaten by 2030. The Marine Strategy Framework Directive (MSFD) recognizes IAS as a significant pressure on marine ecosystems, negatively affecting environmental status. The MSFD indicates that achieving Good Environmental Status requires maintaining alien species at levels that do not cause adverse alterations to the marine ecosystems (Table 1).

In 2014, the EU implemented a comprehensive Regulation encompassing several key elements aimed at effectively managing invasive species (European Union (EU), 2014), hereafter called "the IAS Regulation". The IAS Regulation is a vital biosecurity program that operates at a pan-European level. It mandates thorough risk assessments to assess the potential impact of invasive species and inform appropriate management strategies. It introduced the concept of an EU Black List, which comprises invasive species of Union Concern. The Black List serves as a basis for implementing specific rules and measures for the prevention of new introductions

and further spread, early detection, rapid eradication, and management of IAS, thereby safeguarding the EU's ecosystems. The Black List is dominated by terrestrial and freshwater species, with only two marine species currently included. The first marine species, namely, *Plotosus lineatus*, was introduced to the list in 2019 (European Union (EU), 2019), followed by *Rugulopteryx okamurae* in 2022 (European Union (EU), 2022).

This review aims to evaluate the current state of marine IAS in Europe and explore implemented or proposed strategies developed to date to mitigate IAS impacts. The review is structured to cover the existing knowledge base, information systems, methodologies for monitoring and predicting IAS distribution, pathway management, impact assessments, management options, and the combined effects of IAS and climate change. Drawing from this information, we offer recommendations on how to consider improving current practices for IAS management in Europe. Some of these lessons and approaches are centered in Europe but could be considered and adapted elsewhere.

2 IAS information systems

Biological invasion management policies should rely on timely, accurate, publicly available data that are easily understood and usable for decision-making. For example, the effectiveness of IMO Ballast Water Management Convention (BWMC) measures for preventing the introduction of harmful aquatic organisms and pathogens can be assessed by estimating the reduction in the number of new arrivals through ballast water (Olenin et al., 2014). Similarly, the effectiveness of other conventions, directives, and agreements depends on reliable NIS monitoring data and targeted scientific research. Therefore, monitoring and research data should be collected, quality checked, harmonized, and presented through user-friendly and reliable information systems to be useful for management (Olenin et al., 2011; Lehtiniemi et al., 2015).

The utilization of NIS information systems for research is growing. These systems have been instrumental in compiling national and regional NIS inventories (e.g., Chainho et al., 2015; Ulman et al., 2017; Tsiamis et al., 2019), prioritizing the most impactful IAS, quantifying and summarizing ecological impacts of specific taxa (Katsanevakis et al., 2016), identifying major pathways and vectors of NIS introductions (Katsanevakis et al., 2013; Ojaveer et al., 2017; Pergl et al., 2020), and analyzing species traits and ecological preferences (Paavola et al., 2005; Cardeccia et al., 2018) (Table 2). The use of NIS information systems enhances the analytical and predictive nature of bioinvasion research, shifting from scientific curiosity ("nice to know") to the "need to know" principle driven by management requirements (Olenin et al., 2011).

The European Commission launched the European Alien Species Information Network (EASIN) in 2012 to support European NIS management policies (Katsanevakis et al., 2012; Katsanevakis et al., 2015). EASIN provides easy and open access to harmonized data and information on alien and cryptogenic species, sourced from global, regional, and national databases and scientific literature (Trombetti et al., 2013), through online tools and web services (Figure 1). EASIN's core component is the EASIN Catalogue, the most comprehensive European inventory of terrestrial, freshwater, and marine NIS. The Catalogue's updating and quality assurance is managed by an international Editorial Board of taxonomic experts (Tsiamis et al., 2016). As of July 2023, EASIN included ~13,300 alien and cryptogenic (i.e., of unknown biogeographic status) species, of which ~1,700 were marine or oligohaline. Moreover, EASIN serves as the official information system for the European Commission to support the EU Regulation on IAS (European Union (EU), 2014). Specifically, EASIN features a Notification System that enables member states to promptly notify the Commission of new detections of IAS of EU concern and associated eradication measures.

Aquatic Non-Indigenous and Cryptogenic Species (AquaNIS), founded in 1997 as the "Baltic Sea Alien Species Database", is likely the oldest international online database on aquatic NIS. Over time, it has expanded to cover all European regional seas and later incorporated datasets from other world regions. As of March 2023, AquaNIS contained data on nearly 5,500 NIS introduction events in 25 Large Marine Ecosystems (LMEs). The system features a flexible search engine with several criteria (taxonomy, geography, pathways, biological characteristics, etc.) and an analysis tool for comparing species lists in different LMEs, countries, regions, and time periods (Figure 2). AquaNIS data are regularly updated by the International Council for Exploration of the Seas Working Group on Introductions and Transfer of Marine Organisms (WGITMO). AquaNIS is increasingly used for assessing marine environmental status under the MSFD and supporting decision-making for the IMO Ballast Water Management Convention. Recently, it was equipped with an Early Warning System aimed at preventing the spread of harmful aquatic organisms and pathogens through ballast water.

The World Register of Introduced Marine Species (WRiMS) is a global database connected to the well-established World Register of Marine Species (WoRMS). WRiMS provides taxonomic information for marine species, utilizing the taxonomically authoritative classification and accepted names from WoRMS. It specifically focuses on introduced marine species, distinguishing their native and introduced geographic ranges (Costello et al., 2021). As of 2021, WRiMS included over 2,300 introduced species. The amount and quality of the information entered depend on the availability of experts to update its contents and are affected by regional biases in sampling and taxonomic effort. Despite some errors and outdated information, WRiMS is currently the most comprehensive standardized marine NIS database.

With the advent of Internet technologies and increasing demand from management and researchers, several NIS databases have emerged through short-term national or international projects. However, many of these databases prioritize their design using web technologies rather than focusing on data collection and creating ecologically meaningful output functionalities. At best, these databases prove useful toward the end of a project for generating reports and, occasionally, scholarly papers. However,

TABLE 2 Examples of currently active online information systems on marine, brackish, and coastal freshwater alien species relevant to Europe.

Database (listed by name in alphabetic order)	Launch date	Coverage and scope	Tools and services	Main references
AquaNIS Information system on Aquatic Non-Indigenous and Cryptogenic Species (www.corpi.ku.lt/databases/aquanis/)	1997* (2013)	Global with European focus. Marine, brackish water, and coastal freshwater biota from viruses to mammals	Multi-criteria search engine (by taxonomy, geography, pathways, biological traits, status in recipient region, etc.). Built-in tool for comparison of search results. Early warning system on harmful aquatic organisms and pathogens	Olenin et al. (2014); AquaNIS (2023)
SLU Artdatabanken	2002	National (Sweden) terrestrial, marine, freshwater	Identification, data, and observations	https://www.artdatabanken.se/
Artsdatabanken	2005	National (Norway) terrestrial, marine, freshwater	Knowledge transfer, outreach, scientific support, identification, and maintenance of systematic information. NIS list available at: https://www.artsdatabanken.no/fremmedartslista2018	
arter.dk	2021	National (Denmark) terrestrial, marine, freshwater	Gathering and sharing species observations	Arter (https://arter.dk)
EASIN (https://alien.jrc.ec.europa.eu/easin)	2012	European terrestrial, freshwater, marine	Query and retrieve species information (e.g., records by species scientific name, their environment, impact, taxonomy, and species of Union Concern). Distribution maps of single or multiple species	Katsanevakis et al. (2012); Katsanevakis et al. (2015); Trombetti et al. (2013)
ELNAIS (https://elnais.hcmr.gr/)	2007	National (Greece) freshwater, marine	Database of distribution records, biological invasion experts, related projects, and publications. Inventory of Greek NIS; distribution maps	Zenetos et al. (2015)
Great Britain NonNative Species Information Portal (GBNNSIP)	2011	GB terrestrial, freshwater, marine	Provides access to distribution maps and other information for all non-native species in Britain. Linked to the GBNNSIP is an online "alert system" that has enabled surveillance of many invasive non-native species	Sewell et al. (2010); Roy et al. (2014)
Vieraslajit.fi	2011	National (Finland) terrestrial, marine, freshwater	Identification, legislation, early warning, data, observations	Lehtiniemi et al. (2020)
WRiMS (https://www.marinespecies.org/introduced/)	2015	Global marine	Query and retrieve species information (e.g., taxonomical, distribution, impacts, pathways and vectors, invasiveness status, records, and sources)	Costello et al. (2021)

General biodiversity information systems (e.g., GBIF) and citizen science initiatives are not included.
*In 1997, the "Baltic Sea Alien Species Database" was published online; in 2013, it became AquaNIS.

the long-term utility of a database depends not only on the employed technologies and project deliverables but also on sustained user demand and post-project maintenance (Olenin et al., 2014). Unfortunately, securing funding for database collaboration, adaptation, improvement, and maintenance is often more challenging than developing new databases (Simpson et al., 2006). There are several examples of NIS databases that remained idle, with data not being updated for extended periods, or ceased to exist altogether, becoming inaccessible to users.

One notable example is the DAISIE information system, a product of the project DAISIE (Delivering Alien Invasive Species Inventories for Europe). The project, with a European Commission contribution of €2.4 million, spanned 3 years starting in February 2005 (DAISIE, 2009). Its goal was to create a comprehensive resource on biological invasions in Europe, through an international team of leading experts in biological invasions, cutting-edge database design and display technologies, and an extensive network of European collaborators and stakeholders (DAISIE, 2009). The system compiled and verified over 248 datasets from 98 European countries/regions, making it the world's largest invasive species database.

However, "the DAISIE dataset is no longer maintained but can be used as a historical archive for researching and managing alien plants or compiling regional and national registries of alien species" (GBIF, 2023). While part of the data has been preserved and integrated into other databases, the European Alien Species Expertise Registry, the European Alien Species Database, and the European Invasive Alien Species Information System no longer exist. This is primarily because the project failed to establish mechanisms for long-term maintenance, continuous updates, and the transfer of technology to relevant European entities (e.g., EASIN) for storage, use, and future development.

Several key factors have been highlighted for sustainable database management and advancement (Olenin et al., 2002; Katsanevakis et al., 2012; Olenin et al., 2014; Katsanevakis et al., 2015; Costello et al., 2021):

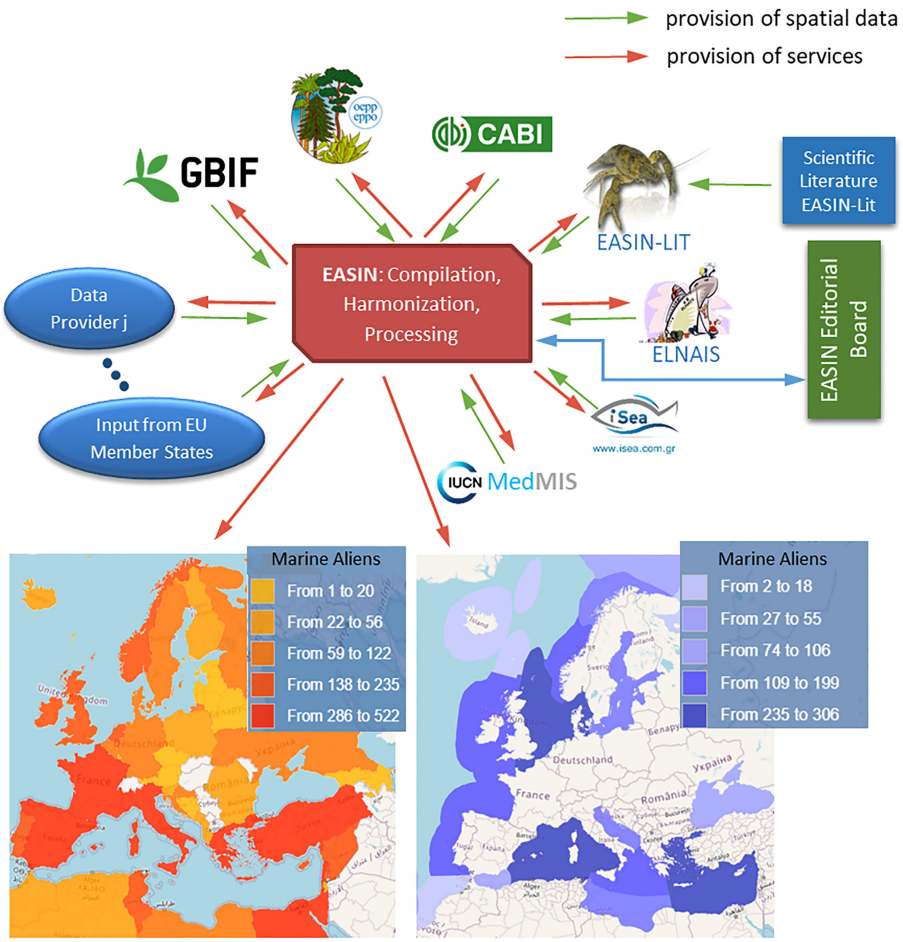


FIGURE 1
European Alien Species Information Network (EASIN): schematic of its concept, main elements, and outputs (bottom left: marine alien species by country; bottom right: marine alien species by ecoregion).

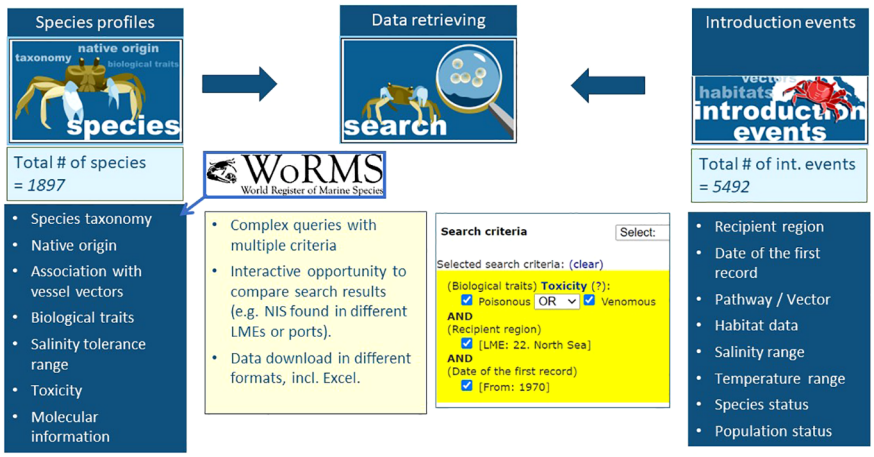


FIGURE 2
Information system on Aquatic Non-Indigenous and Cryptogenic Species (AquaNIS) has a flexible search engine and a built-in comparative analysis tool, which makes it practical for management and useful for research.

- Determine the database's intended purposes (e.g., research, management, environmental status assessment, and early warning). Ideally, a database should be multipurpose.
- Design a user-friendly technical system enabling easy searching, extraction, and basic data analysis.
- Ensure a constant flow of reliable data and engage a highly qualified editorial board.
- Obtain ongoing support from international, regional, or national environmental authorities.
- Due to the rapidly increasing volume of bioinvasion data, innovative approaches, e.g., utilizing artificial intelligence, are necessary for improved data collection, standardization, and analysis.

3 Monitoring strategies

Monitoring recommendations, including sampling adequacy, coordination and coherence among programs, integration of existing monitoring, interoperability, adaptive monitoring, linkages to assessment needs, risk-based approaches, and the precautionary principle, are highlighted within the scope of implementing the MSFD (Zampoukas et al., 2014). Despite the high cost of inaction (Ahmed et al., 2022), challenges are evident in global efforts against biological invasions, with monitoring for timely detection of new NIS, their introduction pathways, spread, and impacts remaining costly and challenging. However, new technologies have the potential to revolutionize invasion monitoring by addressing some of the current difficulties. Here, we present an overview of the current monitoring focus and examples showcasing the potential of novel techniques to enhance the monitoring of marine biological invasions.

3.1 Monitoring the European seas

Regional Sea Conventions (RSCs) have set environmental objectives (Table 1) to tackle biological invasions. They have also implemented monitoring guidelines to aid NIS management across European Regional Seas Basins (Table 3). Collaborative efforts have been undertaken, such as initial port sampling guidelines developed jointly by OSPAR and HELCOM, and the continued activity of the joint task group on BWMC and Biofouling (JTG Ballast and Biofouling). Furthermore, OSPAR and HELCOM have formed an expert group on species invasions (JEG-NIS) to foster discussions on monitoring programs and facilitate the development of joint or coordinated monitoring initiatives wherever feasible.

The MSFD's requirements for assessing the impacts of marine NIS have had an important role in promoting common strategies to address NIS across RSCs. Many of the indicators and guidelines adopted by RSCs (Table 3) aim to align with EU requirements, facilitating reporting by contracting parties, which are also obliged to report under MSFD. The RSCs' guidelines reflect synergistic top-down and bottom-up approaches to influence and align monitoring efforts at regional and national levels.

3.2 National monitoring

Most countries lack dedicated marine NIS monitoring programs (Lehtiniemi et al., 2015), relying instead on existing broad monitoring initiatives. However, NIS often receive limited attention in national monitoring programs (Ljungberg et al., 2011). This is noteworthy since monitoring of the arrival and spread of IAS are required by several international regulations (e.g., European Union (EU), 2008; European Union (EU), 2014), and information on the abundance/biomass of IAS and their impact is required by the MSFD for assessing good environmental status (GES) (Stæhr and Jakobsen, 2023). National inventories of marine NIS have been compiled and published for several EU countries, e.g., Greece (Zenetos et al., 2018; Zenetos et al., 2020), Italy (Occhipinti-Ambrogi et al., 2011; Servello et al., 2019), Portugal (Chainho et al., 2015), Malta (Evans et al., 2015), Norway (Sandvik et al., 2019), Denmark (Stæhr et al., 2020), and Belgium (Verleye et al., 2020), often prompted by international working groups on NIS such as those of ICES (ICES, 2022) in the Atlantic and CIESM in the Mediterranean.

In line with the MSFD, each EU Member State has established improved records of marine NIS in their seas. These baseline inventories were developed through the initial MSFD evaluation in 2012, updated information from EASIN, and an expert elicitation process (Tsiamis et al., 2019). The assessment revealed that Italy, France, Spain, and Greece have the highest NIS richness among member states, while Slovenia, Lithuania, Latvia, and Finland have the lowest. Among the EU ecoregions, the Levantine Sea has the highest NIS richness, followed by the western Mediterranean, North Sea, and Aegean Sea (Table 4).

3.3 Port monitoring

Ports are considered a key hub in the introduction of IAS (Miralles et al., 2021 and references therein) and are valuable sites for monitoring new NIS arrivals. One of the earliest port survey approaches is the CRIMP protocol, initially developed in 1995 to assess marine invasions and survey effectiveness in Australian ports (Hewitt and Martin, 1996). An updated version of the protocol was published in 2001 following 5 years of implementation in practice (Hewitt and Martin, 2001). The protocol was adopted by the IMO GloBallast program for port surveys. However, the CRIMP protocol relies heavily on scuba diving surveys, which are not feasible in all locations. In such cases, qualitative surveys, such as Rapid Assessment Surveys, can provide insights into the presence of alien species and changes in their spatial distribution (e.g., Cohen et al., 2005; Pederson et al., 2005; Ashton, 2006).

Baltic Sea Port Monitoring, based on established protocols (Hewitt and Martin, 2001; Power et al., 2006; Buschbaum et al., 2010; Andersen et al., 2023), was originally designed for granting

TABLE 3 Brief overview of current efforts by Regional Sea Conventions (RSCs) toward improved monitoring and management of NIS in European Regional Seas Basins.

RSCs	Main elements
Baltic Marine Environment Protection Commission (HELCOM)	There is currently no coordinated monitoring specifically targeting NIS in the Baltic Sea, but it is under development. HELCOM has, however, identified a variety of monitoring approaches and methods, which may be used for NIS monitoring, addressing all biotic components, as NIS may belong to any trophic level and be found in various man-made as well as natural habitats. For specific aspects, a series of monitoring guidelines were developed that aim to provide standardized protocols to be used as part of routine bioinvasion monitoring or early detection of new incursions within a pathway hub to support reporting core indicators (e.g., "Trends in arrival of non-indigenous species") and meet environmental (e.g., "Prevention of unwanted human-mediated introductions") and management objectives (e.g., "No introductions of alien species from ships"). These HELCOM guidelines have a particular focus on the use of molecular methods for target NIS, including those adequate for NIS in biofouling and NIS in ballast water of ships and also for the monitoring of NIS in marinas and of mobile and sessile epifauna as well as on the collection of citizen observations on NIS. To support the monitoring plans, countries have agreed on keeping a continuously revised and updated list of target species for the Baltic Sea within HELCOM (2023).
Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR)	There is currently no coordinated monitoring specifically targeting NIS in the OSPAR region. Current reporting guidelines within OSPAR are described in the OSPAR CEMP Guidelines (2022). The need for harmonized NIS monitoring was highlighted in the OSPAR QSR2023 report on NIS (Stæhr et al., 2022). The plan is to collaborate with HELCOM and EU to coordinate and develop a common NIS monitoring guideline, which will make it possible to provide better and more comparable data for all of the NIS (D2) indicators. Assessing new introductions through analysis of trends in new arrivals is currently the main parameter being monitored, for which efforts to develop a baseline distribution list of NIS are being directed. Aligned with MSFD objectives, other parameters to be monitored in the future by OSPAR will be total number of NIS, dispersal range, and rate. For all parameters, standardized ways of monitoring and reporting among contracting parties are being agreed upon, for example, guidelines for most adequate monitoring for early detection.
Convention for the Protection of the Mediterranean Sea Against Pollution (Barcelona Convention)	The 19th Meeting of the Contracting Parties to the Barcelona Convention adopted an action plan concerning species introductions and invasive species in the Mediterranean Sea [UNEP/MPA (2017)] aiming to "promote coordinated efforts and management measures throughout the Mediterranean region in order to prevent as appropriate, minimize and limit, monitor, and control marine biological invasions and their impacts on biodiversity, human health, and ecosystem services". The Action plan requires member states to inventory the alien species reported in the national territory; assess trends in abundance, temporal occurrence, and spatial distribution; estimate the ratio between alien and native species; assess their impacts; and implement monitoring programs to support data collection and assessments. They were also asked to support the database MAMIAS with related data. Regional training sessions have been organized to train scientists from member states on monitoring methods and protocols, including both traditional and novel (eDNA) methods. The Barcelona Convention has adopted the Ecosystem Approach with very similar monitoring requirements as the MSFD.
Convention on the Protection of the Black Sea Against Pollution (Bucharest Convention)	The issue of NIS in the Black Sea is reflected in the Black Sea Integrated Monitoring and Assessment Program for years 2017–2022 (BSIMAP 2017-2022). This program was partially harmonized with the EU MSFD approach and contains measures to address both MSFD and the Black Sea Strategic Action Plan (BS SAP 2009) as regards reduction and management of human-mediated species introductions (EcoQO 2b). Among preparatory actions are the following: finalize the List of Black Sea non-indigenous species (which is periodically updated on the regional level), develop and/or apply indicators (e.g., bio-pollution index), and map areas of non-indigenous species proliferation. In line with BSIMAP, the dedicated indicator "Number of new introduced non-indigenous species (for each 6 years)" has to be mandatorily reported every 6 years to the Black Sea Commission.

NIS, non-indigenous species; MSFD, Marine Strategy Framework Directive; eDNA, environmental DNA.

exemptions from the BWMC. HELCOM's port sampling protocol has been implemented in the Baltic Sea since 2012 (HELCOM, 2013; Outinen et al., 2021), though regular monitoring is lacking in most countries. Finland initiated a port monitoring program in 2022, and Denmark published a port monitoring report in 2022 that was expanded to compare environmental DNA from IAS across seasons (Knudsen et al., 2022). In the Mediterranean, a study compared environmental DNA (eDNA) levels inferred from metabarcoding with fishing fleet activity to detect IAS in harbors around Sicily and the northwestern Mediterranean (Aglieri et al., 2023). In the Bay of Biscay, eDNA metabarcoding was utilized on water samples from major ports for IAS monitoring (Borrell et al., 2017).

3.4 Molecular approaches

Recent years have witnessed an explosion in the application of molecular methods based on organismal or eDNA or RNA due to their rapid technological advancements (Fonseca et al., 2023). In the context of biodiversity monitoring, the most applied methods can be categorized into 1) methods targeted to specific species based on quantitative real-time PCR (qPCR) or digital PCR (dPCR; including digital droplet PCR) and 2) untargeted methods based on metabarcoding of amplified taxonomic marker sequences using "universal" primers with broad coverage. Both types of methods offer advantages over traditional monitoring, including enhanced sensitivity and the ability to identify sparse NIS populations, even when visually challenging to identify life stages or when local taxonomic expertise is lacking (Bowers et al., 2021). Sample collection and preservation are relatively straightforward, requiring smaller sediment volumes, while eDNA can be directly extracted from water filters. In recent years, numerous evaluation and proof-of-concept studies have demonstrated the utility of both approaches for NIS monitoring in the environment and transportation vectors such as ballast water (e.g., Zaiko et al., 2015; Borrell et al., 2017; Rey et al., 2018; Holman et al., 2019; Rey et al., 2020; Bowers et al., 2021; Duarte et al., 2021; Knudsen et al., 2022).

The obvious disadvantage of targeted methods is the requirement of species-specific assays for each NIS of interest, whereas metabarcoding can theoretically detect any species eDNA present in collected samples (Hablützel et al., 2023). When many species are of interest, metabarcoding therefore becomes more cost-efficient. Conversely, targeted approaches generally exhibit higher sensitivity and specificity, allowing for more accurate estimates of

TABLE 4 Numbers of alien and cryptogenic marine and oligohaline species reported in EASIN by ecoregion (*sensu* Spalding et al., 2007), ordered by species richness.

European ecoregions	No. of NIS and cryptogenic species
Levantine Sea	306
Western Mediterranean	277
North Sea	272
Aegean Sea	236
Celtic Seas	199
Ionian Sea	164
South European Atlantic Shelf	136
Southern Norway	110
Adriatic Sea	106
Tunisian plateau/Gulf of Sidra	86
Northern Norway and Finnmark	75
Azores, Canaries, and Madeira	55
Alboran Sea	54
Black Sea	36
North and East Barents Sea	27
White Sea	18
South and West Island	17

In total, 1,671 alien and cryptogenic marine and oligohaline species are reported in the European Seas by EASIN (as of July 2023).
EASIN, European Alien Species Information Network.
NIS, non-indigenous species.

absolute abundance (McColl-Gausden et al., 2023; Sapkota et al., 2023). For successful NIS identification, both approaches rely on the availability of reference sequence data. The specificity of metabarcoding also depends on the phylogenetic resolution of the amplified taxonomic marker, which can be severely limited, e.g., when using partial sequences of the small subunit (18S) rRNA gene that may show little or no variation across metazoans, for which 12S or COI is commonly used. Insufficient database coverage can severely limit the utility of metabarcoding, especially in regions where baseline biodiversity is poorly characterized. For example, Pearman et al. (2021) found that only 31% of 18S and 4% of the unique COI metabarcoding sequence variants obtained from a diversity survey of marinas in Tahiti could be assigned to species. Metabarcoding of eDNA is also dependent on the genetic reference sequences deposited on genetic databases that originate from vouchered museum specimens, as this makes species identification from sequence reads more reliable (Pleijel et al., 2008; Buckner et al., 2021). It is important that the bioinformatic handling of eDNA metabarcode sequence data includes a validation step that allows for identification being based on vouchered sequence data, rather than the most prevalent sequences. It also underlines the continuous importance of having taxonomic expertise in museum collections and the value of natural history collections at museums (Rocha et al., 2014).

To estimate the database coverage of NIS in European waters, we cross-referenced species listed in the AquaNIS and EASIN databases with species in the sequence databases Midori v253 (Leray et al., 2022), PR2 v5.0.0 (Guillou et al., 2013), SILVA 138 SSURef and LSURef NR (Quast et al., 2013), MitoFish v2023-03-23 (Iwasaki et al., 2013), MetaZooGene (downloaded April 4, 2023; Bucklin et al., 2021), and a list of all rbcL gene entries from global data repositories (Omonhinmin and Onuselogu, 2022). Out of 2,197 NIS in European waters, sequence data for at least one taxonomic marker were available for 1,318 species (60%; see Table 5). For 854 species (39%), multiple marker sequences were available.

Sampling design is critical for comprehensive biodiversity coverage, especially in heterogeneous habitats such as ports (Knudsen et al., 2022; Aglieri et al., 2023). Rey et al. (2020) demonstrated this in the Port of Bilbao and its upstream estuary, where 192 samples were taken from various locations using zooplankton nets, filtered water, sediment grabs, and settlement plates. Less than 1% of the species identified through COI and 7% through 18S rRNA metabarcoding were shared among all four sampling methods. Koziol et al. (2019) reported similar findings. This highlights the need for standardized eDNA monitoring protocols and further studies that compare eDNA and traditional monitoring methods.

TABLE 5 Identified reference sequences per taxonomic marker for NIS encountered in European waters extracted from the EASIN and AquaNIS databases (in total 2,209 unique species) per marker and database ("*" denotes a marker from a mitochondria or chloroplast encoded gene).

Taxonomic marker	IAS with ref. sequence	Midori	Meta-ZooGene	PR2	SILVA	Mito-Fish	Omonhinmin and Onuselogu, 2022
COI*	1,096 (50%)	1,069	807	–	–	–	–
18S rRNA	664 (30%)	–	443	484	117	–	–
16S rRNA*	572 (26%)	–	544	54	20	–	–
12S rRNA*	375 (17%)	–	338	–	–	126	–
28S rRNA	83 (4%)	–	–	–	83	–	–
rbcL*	49 (2%)	–	–	–	–	–	49
Any marker	*1,318 (60%)*	*1,078*	*926*	*493*	*191*	*126*	*49*

NIS, non-indigenous species; EASIN, European Alien Species Information Network; AquaNIS, Aquatic Non-Indigenous and Cryptogenic Species; IAS, invasive alien species.

Sampling design for eDNA monitoring must also consider variation in distribution across time and depth. Different depths harbor different NIS, and the eDNA they release to the water will vary (DiBattista et al., 2019; Canals et al., 2021; Merten et al., 2023). Organism distribution fluctuates throughout the year, resulting in seasonally dependent eDNA release (Sigsgaard et al., 2017; Agersnap et al., 2022; Knudsen et al., 2022; Baudry et al., 2023). Diurnal activity patterns impact eDNA levels (Jensen et al., 2022), necessitating nighttime sampling for monitoring nocturnal NIS.

Environmental RNA (eRNA), similar to eDNA, is shed by metazoans or exists in the form of whole live or dead individuals of smaller organisms, making it a potential monitoring target (Lejzerowicz et al., 2015; Keeley et al., 2018). eRNA has the disadvantage of lower stability in the environment (Kagzi et al., 2023) and requires stricter sample contamination and preservation protocols but is likely a better reflection of the presence of live organisms (Pochon et al., 2017).

3.5 Other technological tools

Artificial intelligence (AI) applications for species recognition (Wäldchen and Mäder, 2018) can greatly facilitate marine NIS monitoring. AI has made significant advancements in various areas, including species identification. AI technology, powered by machine learning and neural networks, has revolutionized biodiversity monitoring and species identification, fostering NIS monitoring (Carvalho et al., 2023). Platforms like iNaturalist utilize AI to assign taxonomic names based on uploaded images, with expert verification and training for improved accuracy. Several organizations have developed AI systems for marine species detection, fish and plankton identification, benthic image annotation, and even stock assessment (e.g., Connolly et al., 2021). Tools like Linne Lens enable real-time identification of multiple species from photos and videos, providing instant species recognition using smartphones and internet connectivity. Automated species identification from images and videos has become widespread, offering a cost-efficient approach that archives valuable data for NIS monitoring.

Remote sensing using color infrared (IR) photos has been employed for NIS detection in shallow waters since the 1970s (e.g., water hyacinth, Rouse et al., 1975). Advances in imaging technologies and image processing algorithms have significantly enhanced the effectiveness of remote sensing. Remote sensing techniques are particularly valuable when target species form large homogenous patches, exhibit distinctive features (e.g., flowers), or possess unique chemical properties (He et al., 2015; Bolch et al., 2020). Roca et al. (2022) demonstrated the effective use of multispectral remote sensing data from drones and satellites to monitor the IAS of EU concern *R. okamurae*, providing crucial information for decision-making and species management. However, remote sensing in aquatic ecosystems has limitations due to various confounding factors. To overcome these limitations, high radiometric quality in images, thorough calibration processes, hyperspectral information, customized image timing, and radiative transfer modeling are often required for adequate detection and differentiation of submerged and water column IAS (Bolch et al., 2020).

Furthermore, data mining from social media, although with severe limitations, has been proposed as a promising source of NIS data (Caley and Cassey, 2023).

3.6 Citizen science

An increasingly relevant amount of data to support decision-making and reporting against international targets comes nowadays from citizen science (Pocock et al., 2019). Citizen science observations, especially for charismatic and visible IAS, complement regular monitoring (Giovos et al., 2019; Lehtiniemi et al., 2020). Although citizen-based observations of birds have been utilized for over a century, citizen science has gained wider popularity since the late 20th century (Tulloch et al., 2013). Online applications and global platforms have garnered immense participation and contribute daily to global biodiversity data (Seltzer, 2019). For example, iNaturalist has contributed over 58 million research-grade observations to the Global Biodiversity Information Facility (GBIF) as of March 2023, and these data have been integrated successfully with scientific research for various purposes, evident in over 3,403 publications citing the dataset (Nugent, 2018). Citizen science in environmental monitoring not only compensates for resource limitations in generating comprehensive and up-to-date species presence databases but also holds value beyond data provision, gradually being incorporated into solutions and mitigation actions (Pocock et al., 2019; Ferreira-Rodríguez et al., 2021).

A recent survey identified 103 citizen science initiatives related to biological invasions across 41 countries that contribute to research, policy, and management (Price-Jones et al., 2022). Among the 31 initiatives specifically focused on marine environments, nearly half (47%) aimed to collect species presence or abundance data to map their distribution and spread. NIS detection for early warning programs (16%) and compiling species lists (14%) were also common objectives. Interestingly, citizens are increasingly involved in gathering more complex information, such as evidence of NIS impacts on biodiversity (11%) and generating experimental data for scientific hypothesis testing (5%).

The potential for citizen science to contribute to biodiversity monitoring, including biological invasions, is indisputable (Pocock et al., 2018). However, uncertainties arise during sampling design, data collection, and statistical analyses of citizen science data, as well as linguistic uncertainties that affect information interpretation (Probert et al., 2022). Limitations of citizen science data include accuracy and uneven spatial distribution of observers (Wiggins and Crowston, 2011). Data quality decreases when species are difficult to identify or quantify (Lewandowski and Specht, 2015), especially in cases of low density (false negatives) or co-existence with morphologically similar species (false positives) (Fitzpatrick et al., 2009). Furthermore, citizen science often provides presence-only records, limiting data usefulness for range expansion calculations or species distribution models (Peron et al., 2016). Recognizing these

challenges, efforts have been made to address uncertainties and enhance data reliability in citizen science (Probert et al., 2022).

The most successful instances of marine citizen science focused on the Mediterranean Sea are exemplified by the CIESM Jelly Watch Program initiatives related to jellyfish blooms. These stand out as the most impactful marine citizen science endeavors in the Mediterranean, achieving extensive time coverage, broad geographic reach, and significant citizen participation, resulting in a substantial number of reports (>24,000 jellyfish presence records, and a total of 115,367 presence+absence records) (Marambio et al., 2021). In Italy alone, data collected from 2009 to 2014 comprised >15,000 presence records contributed to the discovery of new NIS for Italy and the western Mediterranean (e.g., *Phyllorhiza punctata* and *Mnemiopsis leiydi*, in Boero et al., 2009) and even the finding of a jellyfish species new to science—undisputedly classified as cryptogenic in the northern Adriatic Sea (Piraino et al., 2014).

Coupling citizen science with eDNA monitoring is a promising approach in both marine (e.g., Tøttrup et al., 2021; Agersnap et al., 2022; Suzuki-Ohno et al., 2023) and freshwater habitats (Biggs et al., 2015). Citizen science involvement in eDNA monitoring allows for broader geographical sampling and public engagement in biodiversity research (Agersnap et al., 2022), including educational benefits (Tøttrup et al., 2021; Knudsen et al., 2023). However, careful consideration is needed to mitigate the increased risk of sample contamination from unwanted DNA due to the inexperience of participants in eDNA protocols. Incorporating negative and positive controls in sample analysis can improve the validity of citizen science-based eDNA monitoring (Tøttrup et al., 2021). Another advantage of citizen science is the potential cost reduction associated with eDNA monitoring, as demonstrated by studies in Denmark where volunteers collected and filtered water, eliminating the need for a field biologist. Leveraging citizen science and traditional approaches for eDNA monitoring can enhance understanding of biodiversity loss and the impacts of climate change, similar to approaches used for terrestrial organisms (Hudson et al., 2014; Newbold et al., 2015; Outhwaite et al., 2022). Furthermore, eDNA monitoring has shown superior performance compared to traditional surveys, leading to its implementation in national surveys (De Brauwer et al., 2023; Kelly et al., 2023).

4 Predicting biological invasions

As the costs of invasions are high, there is a global need to predict invasions before they occur and to adjust monitoring or management policies (Wylie and Janssen-May, 2017). Several attempts have been made, mainly using species distribution models (SDMs) to predict favorable areas for species (e.g., Kotta et al., 2016; Liversage et al., 2019; Poursanidis et al., 2022) and assess the vulnerability of marine protected areas (MPAs) to IAS (e.g., D'Amen and Azzurro, 2020a; Stæhr et al., 2023). Additionally, studies have explored factors contributing to successful invasions, such as life-history traits or global invasion history (Vilizzi et al., 2019; Vilizzi et al., 2021; D'Amen et al., 2022; D'Amen et al., 2023).

When modeling and projecting species invasions, several challenges arise, such as the need to extrapolate to novel conditions due to the lack of analogous conditions in the invaded region (Mesgaran et al., 2014), niche pioneering (part of a species' fundamental ecological niche observed only in its invaded range) or niche expansion (Atwater et al., 2018), and niche unfilling (niche space that is occupied in the native but unoccupied in the invaded domain) (Strubbe et al., 2013). Biased predictions can result from excluding limiting variables from models, e.g., ignoring the minimum winter temperature for thermophilic Lessepsian species (Dimitriadis et al., 2020). Ignoring these challenges led to biased predictions of the lionfish distribution in the Mediterranean Sea (Poursanidis, 2015; D'Amen and Azzurro, 2020a). For example, predictions by Johnston and Purkis (2014), based on a biophysical model, incorrectly suggested that the lionfish would not successfully invade the Mediterranean, but the subsequent rapid expansion of the species proved these predictions false (Dimitriadis et al., 2020; Poursanidis et al., 2020; Poursanidis et al., 2022).

Over the past two decades, modeling the fundamental ecological niche (i.e., ecological niche models) and correlating the presence or absence of species with environmental factors (i.e., SDMs) have gained popularity for projecting the expansion of marine IAS (for thorough reviews, see Marcelino and Verbruggen, 2015; Robinson et al., 2017; Melo-Merino et al., 2020). To enhance predictive accuracy and overcome inherent limitations associated with correlative modeling tools, several advancements have been proposed. Hybrid distribution models, incorporating physiological performance estimates (called physiology SDMs), outperformed regular SDMs and provided more realistic range shift forecasts for marine invaders (Gamliel et al., 2020). Similarly, applying temperature constraints on the reproductive phenology of invaders improved the predictions by niche models (Chefaoui et al., 2019). To account for niche variations between native and invaded ranges, models coupled with univariate niche dynamics projected shifts under novel conditions (D'Amen and Azzurro, 2020b). The hypothesis of phylogenetic conservatism of ecological niches, which posits that closely related species share similar or identical niches, has been applied through supraspecific modeling units, i.e., combining occurrences of focal IAS and sister species in their native ranges. This approach has enhanced projections of invasion potential (Castaño-Quintero et al., 2020).

Monitoring marine NIS, whether using traditional or molecular methods, often suffers from imperfect detectability, which can lead to false predictions of occupancy (Issaris et al., 2012; Darling et al., 2017). Several methods have been developed to estimate occupancy based on presence–absence data, considering the imperfect detection of the target species (MacKenzie et al., 2006). These methods involve multiple visits to each site and have been widely applied in all environments. Cost-efficient protocols for data collection through scuba diving or snorkeling and modeling occupancy in the marine environment have been developed, involving multiple observers (Issaris et al., 2012). Such approaches have been used to document cascading effects due to native-invasive species interactions (Dimitriadis et al., 2021) for large-scale multi-species monitoring efforts (Gerovasileiou et al.,

2017; Crocetta et al., 2021) or for explaining IAS spatial patterns (Salomidi et al., 2013). In monitoring programs coupling molecular and traditional methods, site occupancy–detection (SOD) modeling holds great promise for converting eDNA-positive detections into robust estimates of species distribution (Darling et al., 2017). Positive correlations have been observed, for example, between eDNA levels and tidewater in SOD for a marine endangered goby on the Californian coast (Schmelzle and Kinziger, 2016) and between oxygen levels and eDNA from an endangered crayfish threatened by the expansion of introduced crayfish (Baudry et al., 2023).

It is crucial to anticipate future invasions and their risks for effective strategy and policy development, risk management, and research prioritization (Ricciardi et al., 2017; Vaz et al., 2021). In the framework of the IAS Regulation, an important horizon scanning study was conducted at the European scale, bringing together international experts to identify potential IAS in terrestrial, freshwater, and marine environments (Roy et al., 2019). From an initial list of 329 species, 66 were identified as very high, high, or medium risk for the EU, including 16 marine species (*P. lineatus*, *Codium parvulum*, *Crepidula onyx*, *Mytilopsis sallei*, *Acanthophora spicifera*, *Perna viridis*, *Potamocorbula amurensis*, *Symplegma reptans*, *Ascidia sydneiensis*, *Balanus glandula*, *Ciona savignyi*, *Dictyospaeria cavernosa*, *Didemnum perlucidum*, *Dorvillea similis*, *Rhodosoma turcicum*, and *Zostera japonica*). Tsiamis et al. (2020) developed a scoring tool that aims at identifying the most likely invasive species in European waters. In the Baltic Sea, Jensen et al. (2023) conducted a horizon scanning study that identified 38 potential IAS, with 31 species meeting the invasiveness scoring criteria by Tsiamis et al. (2020). That horizon scan was combined with hydrodynamic models to predict the potential spread of these species after arrival in commercial harbors and marinas. Dobrzycka-Krahel and Medina-Villar (2023) developed a stepwise tool to identify potential IAS in the less saline parts of the Baltic. In Cyprus, horizon scanning using expert elicitation identified 45 marine species with potentially adverse impacts on biodiversity, economy, or human health, such as the venomous fish *P. lineatus*, a species of EU concern (Peyton et al., 2019; Peyton et al., 2020).

5 Pathways of marine IAS in Europe

The first large-scale assessment of marine NIS pathways of introduction was conducted a decade ago (Katsanevakis et al., 2013), based on the Hulme et al. (2008) pathway classification. With the use of the EASIN Catalogue (version 2.3), the assessment identified 1,369 marine NIS in European seas, with 1,257 associated with likely pathways of introduction. The study revealed a rising trend in new introductions, with shipping as the primary pathway for over half of the species. The second-most common pathway was marine and inland corridors, mainly the Suez Canal, with aquaculture and aquarium trade following in terms of the numbers of introduced species. Interestingly, aquaculture showed a notable decrease in new introductions from 2001 to 2010, attributed to regulatory measures at national and European levels (e.g., ICES, 2005; European Union (EU), 2007). In contrast, introductions through other pathways, particularly aquarium trade, showed a consistent increase. The assessment underscored the ongoing expansion of the Suez Canal and the reduced barriers to the entry of Red Sea species as factors that are likely to facilitate the invasion of the Mediterranean Sea by additional Lessepsian species. These Lessepsian species have been greatly facilitated by climate change, and the increased temperatures of the eastern Mediterranean and currently dominate demersal communities (Box 1).

The CBD Pathway Classification Framework has become a global standard in recent years (Convention on Biological Diversity [CBD], 2014; Harrower et al., 2018). It consists of six broad categories: Release, Escape, Transport-contaminant, Transport-stowaway, Corridors, and Unaided. These are subdivided into several subcategories. EASIN has incorporated the CBD classification of pathways based on expert assessments that addressed implementation challenges (Pergl et al., 2020). According to the latest data in EASIN (March 2023), the main pathways of NIS introductions in Europe are "Transport-stowaway" and "Corridors", followed by "Transport-contaminant", "Escape from confinement", and "Release in nature" (Figure 3A). However, when considering only high-impact NIS (as defined in EASIN), species introduced through "Transport-stowaway" and "Transport-contaminant" appear to have a greater impact compared to those introduced through "Corridors" (Figure 3B).

Quantifying changes in pathways over time and space is crucial for understanding the dynamics of species introductions (Essl et al., 2015). These changes are influenced by complex interactions between environmental and socioeconomic factors, species traits, and the regions involved. Nunes et al. (2014) investigated the spatial distribution of initial introductions of marine NIS in European Seas, including all Mediterranean countries. They identified key entry points for invasions based on distinct geographic patterns related to different pathways (Figure 4). Aquaculture introductions were prominent in France and Italy, Lessepsian species were primarily found in Levantine Sea countries, shipping introductions were widespread near major ports, and species introduced through inland canals were primarily observed in the southern Baltic countries (Katsanevakis et al., 2014a; Nunes et al., 2014). In the Mediterranean, the Suez Canal was the most important pathway, responsible for over half of marine NIS introductions (Zenetos et al., 2012), whereas in all other European Seas, shipping was the dominant pathway (Nunes et al., 2014).

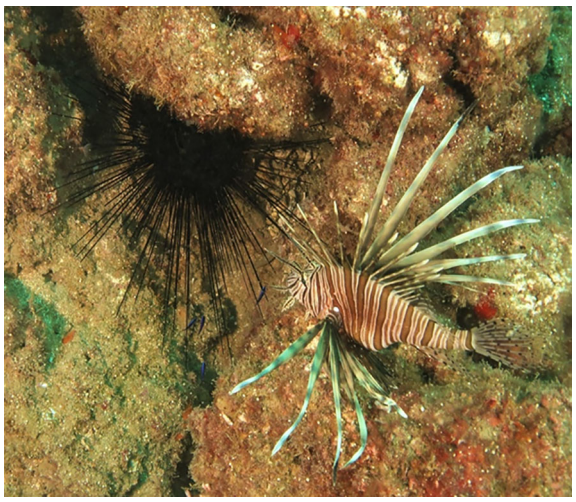
Pathway assessments for NIS entry and spread involve uncertainties, particularly when introductions are unintentional and poorly documented (Essl et al., 2015; Katsanevakis and Moustakas, 2018). Examples include species traveling as ship stowaways or using canals as corridors. Assigning specific pathways for these species often relies on assumptions or ecological inferences rather than concrete evidence. Overlooked or insufficiently studied pathways, such as aquarium trade (e.g., Padilla and Williams, 2004; Vranken et al., 2018) and marine litter (e.g., Barnes, 2002; Carlton and Fowler, 2018; Barry et al., 2023), may have greater significance than currently recognized. Transparently addressing these uncertainties and providing

BOX 1 The Levant bioinvasion and climate change hotspot: a look into the future of Mediterranean biodiversity

The southeastern Mediterranean, known as the Levantine basin or the Levant, is probably the most invaded region of the global ocean (Edelist et al., 2013; Costello et al., 2021). It is also one of the fastest-warming regions (Ozer et al., 2016; Rilov, 2016; Pastor et al., 2020) and a major global change hotspot, driven by fast tropicalization (Rilov et al., 2019b). Mollusca, for instance, is dominated by alien species due to the collapse of native populations (Rilov, 2016; Albano et al., 2021). The co-occurrence of intense warming and thermophilic bioinvasions makes it challenging to ascertain the primary cause of the native species decline (especially non-harvested ones). Experiments and correlative studies have indicated that warming is likely the main driver for species decline, such as in the case of the purple sea urchin *Paracentrotus lividus* (Yeruham et al., 2015; Yeruham et al., 2019), fish (Givan et al., 2018), and possibly mollusks (Albano et al., 2021). Recent experimental work further supported this, showing that tropical alien species are more resilient to warming than native species (Rilov et al., 2022).

Considering the formation of a new Levant ecosystem dominated by alien species, an important question arises: how does this process impact ecosystem functioning and services? To address this, indirect methods such as biological trait analysis can be used, using traits as proxies for functions. Recent research revealed distinct traits between native and alien assemblages, indicating that aliens cannot fully compensate for the loss of native species (Steger et al., 2022). Additionally, direct measurements of ecosystem functions through experiments have shown that alien macrophytes can restore lost biomass due to invasive rabbitfish grazing, unlike vulnerable native macroalgae (Peleg et al., 2020; Mulas et al., 2022), and therefore compensate for the reduction of blue carbon.

With ongoing warming and the influx of invaders to the Levant, the collapse of native species and the spread of alien domination are expected to rapidly extend westward and northward in the Mediterranean Sea. Thus, the current situation in the southeast corner of the Mediterranean Sea likely foreshadows the future of other parts of the basin, serving as a warning sign for the entire region (a "canary-in-the-coal-mine"). MPAs alone may not effectively combat NIS in such climate change and bioinvasion hotspots (Rilov et al., 2018; Frid et al., 2021). Given the native species collapse and proliferation of tropical aliens, regardless of protection from local human pressures, it is necessary to adapt and reconsider conservation objectives and indicators of success, adjusting criteria for good environmental status accordingly (Rilov et al., 2020).



The Red Sea alien lionfish *Pterois miles* and the alien urchin *Diadema setosum* meet again on the reefs of the Israeli coast (photo: G. Ra'anan).

estimates of pathway assignment uncertainty would be valuable (Zenetos et al., 2012; Katsanevakis et al., 2013). Clear and consistent pathway definitions and guidelines are essential to ensure consistent application by different assessors, which can be facilitated through a pathway manual.

Secondary pathways of spread within Europe are important but poorly studied. Unaided dispersal by ocean currents is the most important secondary pathway, often surpassing primary pathways in importance. In the Aegean Sea, unaided dispersal from neighboring countries accounted for 56% of NIS introductions,

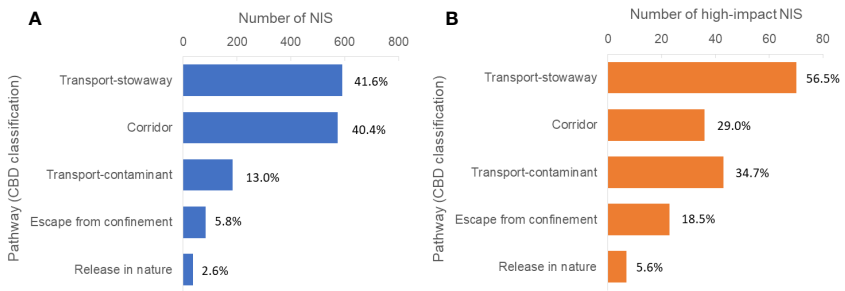


FIGURE 3
Number of marine NIS **(A)** and high-impact NIS **(B)** in European Seas known or likely to be introduced by each of the main pathways, according to the CBD classification. Percentages add to more than 100%, as some species are linked to more than one pathway. High-impact NIS are according to the EASIN classification. Data retrieved from EASIN (March 22, 2023). NIS, non-indigenous species; CBD, Convention on Biological Diversity; EASIN, European Alien Species Information Network.

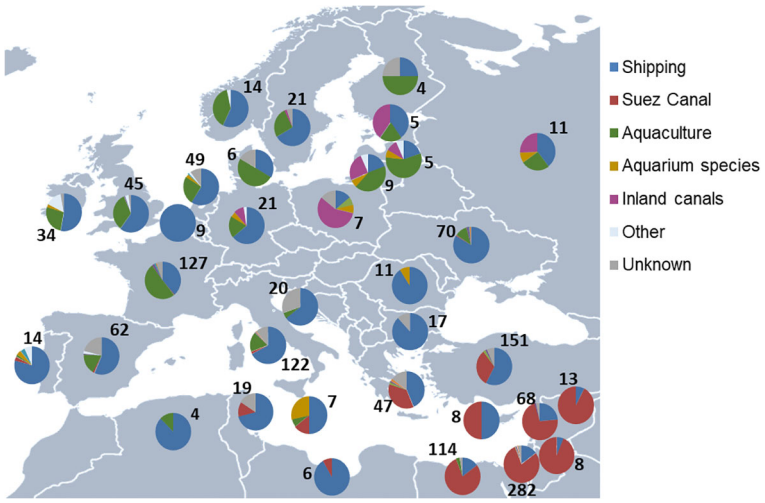


FIGURE 4
Pathways of introduction for first European records of marine NIS per recipient country (i.e., countries of initial introduction in Europe). For clarity, data are shown for countries with more than two recorded first introduction events (numbers shown next to the charts). Adapted from Nunes et al. (2014). NIS, non-indigenous species.

followed by "Transport-stowaway" (35%) (Katsanevakis et al., 2020). In the Baltic Sea, shipping and natural NIS spread from the North Sea dominate among the pathways for established NIS (Ojaveer et al., 2017).

6 Impacts on biodiversity, ecosystem services, and human health: assessing and mapping impacts

IAS impact and risk assessments are increasingly demanded by managers for informed decision-making. Risk screening can help identify species with invasive potential in the area of interest, requiring further analysis of their potential impacts (Ricciardi and Rasmussen, 1998; Copp et al., 2005). IAS often share life-history traits, such as frequent reproduction, large body size, long life span, high degree of omnivory, and a climate match with the area of interest (Statzner et al., 2008; Chan et al., 2021). Moreover, invasive species tend to have broad tolerance to abiotic conditions (Leuven et al., 2009) and a history of being invasive in other regions.

Several protocols exist for IAS impact and risk assessment, such as BPL/BINPAS (Olenin et al., 2007; Narščius et al., 2012), EICAT (Hawkins et al., 2015), SEICAT (Bacher et al., 2018), FISK and related tools (Copp et al., 2005; Copp, 2013), GABLIS (Essl et al., 2011), GB-NNRA (Baker et al., 2008), GISS (Nentwig et al., 2016), Harmonia+ (D'hondt et al., 2015), ISEIA (Branquart, 2009), and NGEIAAS (Sandvik et al., 2013). These tools rank taxa based on their threat level in the risk assessment area at a specified spatial scale. Until recently, there was no standardized and evidence-based system to classify the positive impacts of alien species; EICAT+ covered this gap by offering a protocol to categorize the magnitude of positive NIS impacts (Vimercati et al., 2022). The screening tools vary in objectives, taxonomic resolution, and target (e.g., specific habitats or pathways), as well as complexity, approaches to assess uncertainty, and scoring systems used. These variations may result in significant differences and inconsistencies in the assessment outcomes; selection of assessors, clear assessment guidelines, and adequate training are important in addition to arriving at final decisions collaboratively by consensus (González-Moreno et al., 2019).

A pan-European systematic review of NIS impacts (Katsanevakis et al., 2014b) identified 87 marine species in Europe with documented high impacts on biodiversity or ecosystem services. The study revealed that food provision was the most affected ecosystem service both positively and negatively. Other services negatively affected included ocean nourishment, recreation and tourism, and life cycle maintenance, while cognitive benefits, water purification, and climate regulation were among the services often positively impacted. Additionally, 49 assessed species were considered ecosystem engineers, altering habitats through physical or chemical modifications. The study acknowledged a potential bias against NIS, suggesting that positive impacts might be underestimated.

Tsirintanis et al. (2022) studied the impacts of biological invasions on biodiversity, ecosystem services, and human health in the Mediterranean Sea. They identified various biological mechanisms through which NIS affect Mediterranean ecosystems, resulting in both negative and positive impacts (Figures 5, S1; Table S1). Negative impacts on biodiversity were primarily due to competition for resources, followed by the creation of novel habitats and predation (Figure 5; Table S1). NIS structural ecosystem engineers can completely transform seascapes and substantially change community composition, leading to the loss of native species (García-Gómez et al., 2021; Mancuso et al., 2022). Alien predators and grazers cause significant negative impacts on Mediterranean ecosystems by consuming native biota (Sala et al., 2011; Kampouris et al., 2019).

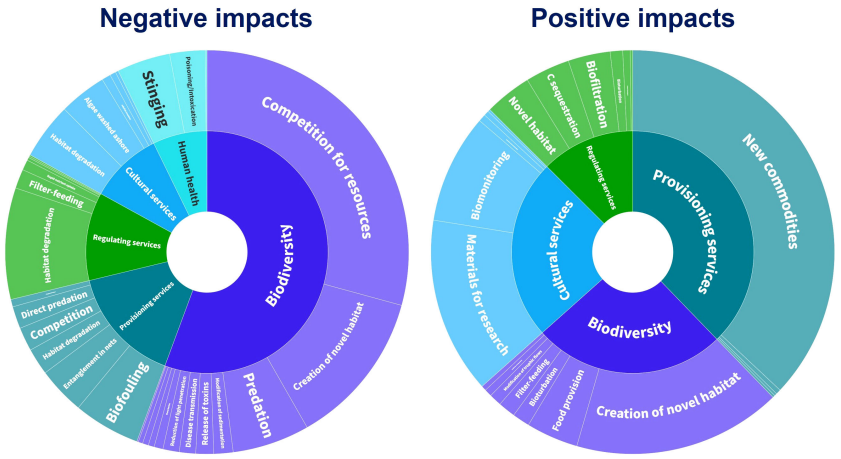


FIGURE 5
Mechanisms (outer circle) of IAS impacts on biodiversity, ecosystem services, and human health (inner circle) in the Mediterranean Sea (circle compartment size corresponds to sample size). Based on Tsirintanis et al. (2022). IAS, invasive alien species.

Predator–prey interactions in the marine environment are dynamic ecosystem processes influenced by local environmental factors and species' ecological features, capable of affecting multiple food-web levels (Rilov, 2009).

Biofouling is the primary mechanism of negative impacts on provisioning services, with many IAS densely colonizing aquaculture facilities and reared species, leading to significant economic losses (Tsotsios et al., 2023). IAS also greatly impact cultural services through the degradation of highly valued habitats, algae massively washed ashore, and jellyfish blooms reaching coastal waters, negatively affecting tourism (e.g., Ghermandi et al., 2015; Ruitton et al., 2021). Habitat degradation is the primary mechanism through which IAS negatively impact regulating services. Regarding human health, IAS primarily cause negative impacts through stinging or poisonings/intoxications (Galil, 2018; Bédry et al., 2021) (Figure 5; Table S1).

Many positive NIS impacts have been reported in the European Seas (Katsanevakis et al., 2014b; Tsirintanis et al., 2022). In the Mediterranean, provisioning services benefit the most from NIS introductions through the provision of new commodities. Various fish, mollusks, and crustaceans have proven a boon for the fisheries and aquaculture sector, especially in the Levantine Sea (e.g., Katsanevakis et al., 2018). The creation of novel habitats is the most important mechanism of positive effects on biodiversity, as alien structural ecosystem engineers provide new habitats and shelter for various species through the formations they create (Katsanevakis et al., 2014b; Guy-Haim et al., 2018; Figure 5). Cultural services are positively affected by research conducted on NIS specimens for future potential exploitation of molecules for pharmaceutical or industrial applications (e.g., Genovese et al., 2012; Nekvapil et al., 2019). Regarding regulating services, the creation of novel habitats, carbon sequestration, and biofiltration are the most important mechanisms contributing to positive impacts (Figure 5; Table S1).

Evidence of reported impacts is mostly of medium strength (Figure 6; Table S1), predominantly from direct observations (e.g., novel habitat creation, competitive overgrowth of sessile organisms, or predation effects derived through stomach content analysis), followed by non-experimental-based correlations between a species presence/abundance and an impact, and modeling to project impact consequences (Figure 6; Table S1). Many reported impacts are only based on expert judgment. Only a small percentage of NIS impacts are supported by robust evidence from manipulative or natural experiments (Katsanevakis et al., 2014b; Tsirintanis et al., 2022; Figure 6).

Several indices have been developed to assess NIS ecological impacts and ecological status considering NIS presence. ALEX (ALien biotic indEX; Çinar and Bakir, 2014) evaluates NIS impacts on benthic communities, aligning with the EU Water Framework Directive classification system; Piazzi et al. (2015) also recommended its application. ECOfast, an ecological evaluation index for shallow rocky reefs, was recently developed (Kytinou et al., 2023). ECOfast-NIS, a variant of this index, penalizes the presence of certain NIS that have negative impacts on local food webs. CIMPAL (Cumulative IMPacts of invasive ALien species) is a conservative additive model based on IAS and habitat distributions, reported magnitude of ecological impacts, and the strength of such evidence (Katsanevakis et al., 2016). CIMPAL has been implemented for the Mediterranean Sea (Katsanevakis et al., 2016), the European scale (Teixeira et al., 2019), and other marine regions like Maltese waters (Bartolo et al., 2021) and the Aegean Sea (Tsirintanis et al., 2023).

Despite extensive negative impacts, global documentation of marine IAS-related extinctions remains scarce. A recent global review on drivers of marine extinctions reported IAS as responsible for 27 out of 786 extinction cases (seven global and 20 local extinctions) (Nikolaou and Katsanevakis, 2023). Among the seven globally extinct species due to IAS, six were seabirds and one was a diadromous fish, while the invasive species causing the

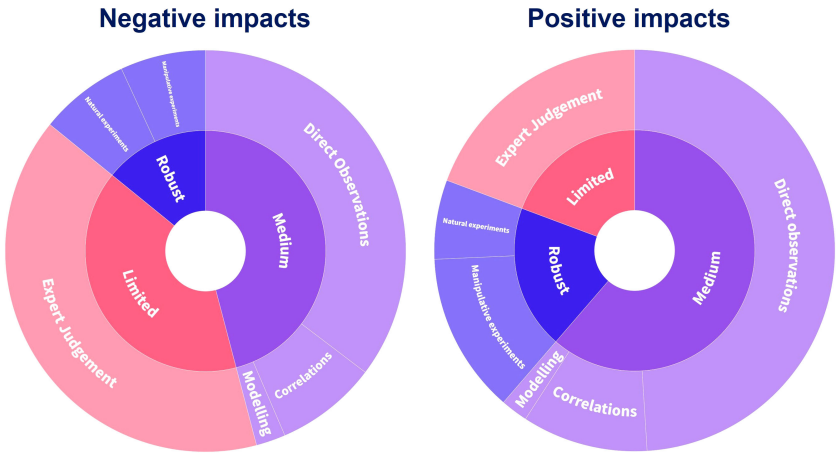


FIGURE 6
Type of evidence of IAS impacts on biodiversity, ecosystem services, and human health in the Mediterranean Sea. Based on Tsirintanis et al. (2022). IAS, invasive alien species.

extinctions were not marine (e.g., invasive rats). In many reported extinctions, IAS were not the sole driver, and their contribution was often unknown, introducing uncertainty about their actual role as the cause of extinctions. The Mediterranean-endemic fan mussel *Pinna nobilis* is an example of IAS-related local extinctions in Europe. It experienced extensive local extinctions due to infection by the newly described protozoan *Haplosporidium pinnae* (likely introduced by shipping), putting the species at risk of global extinction (Katsanevakis et al., 2022). It is now critically endangered in the Red List (Kersting et al., 2019).

Although complete species extinction due to biological invasions is rare in the marine environment, dramatic declines in populations caused by predation or parasitism can lead to functional extinction (Boero et al., 2013). For instance, in the Baltic Sea, the invasion of the round goby *Neogobius melanostomus* resulted in a significant decline in the population of blue mussels (*Mytilus edulis trossulus*), leading to the disappearance of the mussel-created biotope, which served as a crucial habitat for wintering bird populations (Skabeikis et al., 2019).

The predatory impacts of IAS are often focused on, with most studies emphasizing the top-down predatory effects of invaders on native prey, although many species play both predator and prey roles in the ecosystem. The prey role is particularly interesting since nearly all NIS eventually become subject to predation by native predators, which can even lead to the control of IAS populations (e.g., Hunt and Yamada, 2003; Jensen et al., 2007), a process that often takes time (Santamaría et al., 2022). For example, in the Chesapeake Bay, USA, native blue crabs exert predation pressure on the invasive green crab to the point where there are no green crab populations left (DeRivera et al., 2005). In many cases, native predators may even benefit from the new prey (Crane et al., 2015; Pintor and Byers, 2015). Conversely, there are instances where the increased invasive resource leads to an increase in predator populations and results in increased predation on native species (Noonburg and Byers, 2005).

Prey naivety toward invasive predators has been extensively studied and documented (e.g., Sih et al., 2010; Anton et al., 2020). However, less focus has been given to the naivety of predators, although similar naivety may occur, especially toward novel prey (Reid et al., 2010; Santamaría et al., 2022). This can be particularly noticeable during the early stages of invasion, resulting in lower predation pressure on the novel species compared to native, more familiar prey (e.g., Carlsson et al., 2009; Santamaría et al., 2022).

7 Management options: lessons learned from the implementation of management measures

7.1 Prevention: pathway management

Prevention of IAS introductions is the first line of defense (Olenin et al., 2011; Katsanevakis, 2022). According to Article 13 of the IAS Regulation, EU Member States need to "carry out a comprehensive analysis of the pathways of unintentional introduction and spread of invasive alien species of Union concern" in their marine waters and "establish and implement one single action plan or a set of action plans to address the priority pathways".

To prevent introductions through shipping (Transport-stowaway), the most important pathway of marine introductions in the EU (Figure 3), a critical development was the entry into force of the IMO BWMC in 2017. The BWMC mandates all ships to adopt a ballast water management plan and, by September 2024, treat their ballast waters with an approved ballast water treatment system to diminish the survival probabilities of ballast water-transferred marine organisms. Although enforcement of the BWMC is challenging, it is expected to substantially reduce new introductions *via* ballast waters. In contrast, biofouling is currently regulated only voluntarily. The IMO's Biofouling Guidelines (Resolution MEPC.207(62)2011) aim to establish a globally

consistent approach to biofouling management. However, there is growing support for a new Biofouling IMO Convention, with intensive research focusing on efficient biofouling systems, including surveillance optimization (e.g., Abdo et al., 2018; Luoma et al., 2022) and hull cleaning (e.g., Morrisey and Woods, 2015; Zabin et al., 2016).

Corridors, particularly the Suez Canal, rank as the second-most significant introduction pathway in Europe (Figure 3). However, managing the Suez Canal to control invasions (e.g., implementing a salinity barrier or establishing locks to reduce current movement) falls beyond EU jurisdiction, and there is no political will from Egypt or the Barcelona Convention to undertake such measures (Galil et al., 2017). Nonetheless, there are arguments that consider climate change impacts in the eastern Mediterranean, Lessepsian species may not pose the primary threat to biodiversity and ecosystem services; instead, they could potentially play a role in securing ecosystem functions and services (see Box 1).

Regulation 708/2007 "concerning the use of alien and locally absent species in aquaculture" (European Union (EU), 2007) has been an important instrument for reducing aquaculture-introduced species. It was implemented well before the IAS Regulation, based on the ICES Code of Practice on the Introductions and Transfers of Marine Organisms (ICES, 2005), and resulted in a noticeable decline in new introductions (Katsanevakis et al., 2013). In contrast, the aquarium trade, a lesser but growing pathway (Zenetos and Galanidi, 2020), lacks EU-level regulation, leading to continued risks of new introductions. Numerous potentially invasive marine species are traded in EU markets (e.g., Mazza et al., 2015; Vranken et al., 2018).

7.2 Implemented eradication and control measures for marine IAS (physical, chemical, and biological approaches): lessons learned

In a recent systematic review of implemented species-specific eradication and control measures for marine IAS, only 31 studies covering 40 cases were found, of which 11 failed to achieve eradication or control targets (Table S2; Katsanevakis, 2022). These studies mainly focused on macroalgae (10), ascidians (7), and fish (seven; all related to lionfish). Physical methods were most commonly used (e.g., removal by divers, mechanical removal by trawling, dredging, or suction, jute matting, heat treatment, using traps, or promoting targeted fisheries), followed by chemical (using various chemicals such as bleach, herbicides, salt, acetic acid, copper sulfate, and sodium hypochlorite) and biological methods (using native predators or parasites).

Only six successful eradication cases have been reported in the global literature (Table S2): sodium hypochlorite used to eradicate the green alga *Caulerpa taxifolia* from California, USA (Anderson, 2005); physical removal by divers to eradicate the brown alga *Ascophyllum nodosum* from Redwood City, California, USA (Miller et al., 2004); a combination of physical removal by divers and heat treatment to eradicate the brown alga *Undaria pinnatifida* from a sunken trawler in Chatham Islands, New Zealand (Wotton et al., 2004); eradication of the sabellid polychaete *Terebrasabella heterouncinata* from an intertidal site in California, USA, by removing its main native host (Culver and Kuris, 2000); extensive chemical treatment with 187 tonnes of liquid sodium hypochlorite and 7.5 tonnes of copper sulfate to eradicate the mussel *M. sallei* from three sheltered marinas in the Darwin Harbour Estuary (Northern Territory, Australia) (Bax et al., 2002); and dredging to eradicate the invasive mussel *Perna perna* from a subtidal soft-sediment habitat in central New Zealand (Hopkins et al., 2011). Remarkably, successful eradication efforts have been reported only from the USA, New Zealand, and Australia; no successful eradication of a marine IAS from the EU has been reported.

In the EU, only four related studies appear in the literature (Uchimura et al., 2000; Žuljevic et al., 2001; Mancinelli et al., 2017; Kleitou et al., 2021). The first three are experimental investigations or proposals of control approaches, lacking large-scale implementation. Only the latter (Kleitou et al., 2021) made an effort to control lionfish populations in Cyprus, with partial success; lionfish removals significantly decreased its density and biomass (by >50%) in the short term, but long-term suppression requires repeated removals due to rapid population recovery. Another unpublished control effort in the EU (also from Cyprus) is the case of the silver-cheeked toad-fish *Lagocephalus sceleratus*, a toxic predatory fish with serious impacts on fisheries and human health. A targeted fishery by the small-scale fleet was promoted through fishers' compensation based on the fished and incinerated biomass (Table S3). Although there has been no targeted monitoring to assess the measure's effectiveness, empirical evidence from fishers supports its success in reducing the species' biomass and mitigating its impacts; food web modeling indicates that *L. sceleratus* populations could have been higher without any measures, and continuous management is necessary to prevent the population's rebound at high levels (Michailidis et al., 2023).

The only two species for which large-scale control efforts have been implemented in the EU (*Pterois miles* and *L. sceleratus*) have not been included in the IAS list of Union Concern of the IAS Regulation. Both species were proposed, but their inclusion in the latest (2022) update of the list was not approved. Conversely, there are no known successful control efforts for the only two marine species included in the Union List, i.e., the fish *P. lineatus* and the alga *R. okamurae* (Supplementary Text 1; Table S4). This highlights an inconsistency between the criteria for inclusion in the Union List (which may secure EU or national funding for management efforts) and existing applicable management options for specific marine IAS.

Reported successful eradication or control efforts globally (Katsanevakis, 2022) have highlighted several best practices (Table S2). The most critical factor for eradication success is a rapid response after detection (e.g., Bax et al., 2002; Miller et al., 2004; Anderson, 2005; Hopkins et al., 2011); delayed responses compromised many eradication efforts (e.g., Read et al., 2011; Sambrook et al., 2014). Developing rapid response mechanisms among EU member states (largely missing) is essential for successful eradication. Missing the critical time window for a

rapid response makes eradication from the marine environment practically impossible. Once an IAS is established, alternative management strategies beyond eradication should be explored, essentially focusing on control (see Section 7.3) or considering the option of non-intervention (ignore).

Other best practices for successful eradication or control include flexibility in amending existing legislation (Bax et al., 2002); good coordination among local, regional, and national authorities and stakeholders (Anderson, 2005); effective communication with stakeholders and the local community to gain public support (Bax et al., 2002; Wotton et al., 2004); adequate and continuous funding (Wotton et al., 2004; Anderson, 2005; Hopkins et al., 2011; Sambrook et al., 2014); continuous monitoring (Culver and Kuris, 2000; Miller et al., 2004; Wotton et al., 2004; Anderson, 2005; Kleitou et al., 2021); and a good knowledge of biology and ecology of the IAS and underlying ecological theory to select appropriate eradication/control methods (Culver and Kuris, 2000; Wotton et al., 2004; Anderson, 2005; Hopkins et al., 2011; Green et al., 2014; Harris et al., 2020).

7.3 Management options for established IAS populations

Managing marine IAS is more challenging than terrestrial and freshwater species due to the increased functional connectivity of the oceans (Kinlan and Gaines, 2003; Katsanevakis, 2022). Nevertheless, several management measures have been implemented (Section 7.2; Table S2), and potential additional options have been investigated (e.g., Thresher and Kuris, 2004; Giakoumi et al., 2019; Katsanevakis, 2022) (Table 6). The applicability of these measures depends on factors, such as effectiveness, technical feasibility, social acceptability, side impacts on native communities, and cost (Giakoumi et al., 2019). Some options, such as biological control using alien predators, parasites, or viral diseases, are strongly opposed by experts and stakeholders due to fears of irreversible detrimental side effects on native biodiversity. Despite their low expected effectiveness, soft measures like "education and awareness" or "environmental rehabilitation", and inaction were ranked high by experts (Thresher and Kuris, 2004; Giakoumi et al., 2019). Commercial utilization of IAS has been widely suggested as a means of turning mitigation costs into profits for local populations (Mancinelli et al., 2017). Targeting and eating invaders, such as the lionfish (Kleitou et al., 2022), offers several supplementary advantages, such as raising public awareness about IAS and encouraging citizen participation in identifying new populations and engaging in other control measures (Nuñez et al., 2012).

A striking result reported by Thresher and Kuris (2004) was that the perceived likelihood of success of management options was negatively correlated with their acceptability. This suggests the need to enhance the effectiveness of existing techniques or increase the acceptability of potentially effective techniques (e.g., biological control and genetic technology to decrease pest viability) or develop new techniques that are both acceptable and effective (Thresher and Kuris, 2004).

TABLE 6 Management options for controlling established marine IAS populations.

Physical measures
Physically remove IAS—culling efforts.
Encourage targeted removal and commercial or recreational utilization (excluding trading of live individuals).
Chemical measures
Deploy pest-specific biocides, reproductive inhibitors, etc.
Deploy non-specific biocides, tactically applied.
Biological/ecological measures
Rehabilitate the environment in the belief that resistance to IAS impacts will increase.
Promote native consumers (predators or grazers) that attack the IAS.
Promote native diseases and parasites that attack the IAS.
Apply biological control using alien consumers (predators or grazers).
Apply biological control using alien parasites and/or diseases.
Apply biological control using alien viruses.
Genetically modify native species (i.e., to use them as vectors for physiological inhibitors).
Genetically modify disease/virus to increase pathogenicity against pests.
Apply genetic approaches that affect only the IAS.
Other
Education and public awareness.
Do nothing in the belief that the problem might go away.

Adapted from Thresher and Kuris (2004); Giakoumi et al. (2019), and Katsanevakis (2022). IAS, invasive alien species.

8 IAS and climate change

Climate change, primarily ocean temperature increases, may facilitate the introduction and establishment of thermophilic NIS. It can also amplify the impacts associated with IAS, reducing the fitness of thermally sensitive species and thereby decreasing the resilience of native species, habitats, and ecosystems (Birchenough et al., 2015). The Mediterranean Sea, a semi-enclosed basin experiencing rapid warming compared to other marine regions (Schroeder et al., 2016), is a hotspot for bioinvasions by thermophilic Red Sea species (Costello et al., 2021; Box 1). In the Mediterranean, it was shown that an alien intertidal gastropod is much more resilient to warming than three native gastropod species, which may disappear in the future, leaving it the only large mollusk grazer in the region (Rilov et al., 2022).

Higher rates of between-continent dispersal events due to increasing international trade and human traveling are expected (Hewitt et al., 2018; Sardain et al., 2019; Roura-Pascual et al., 2021).

For marine ecosystems, trade/transport and climate change are considered by invasion scientists as the primary drivers of IAS impacts until 2050 (Essl et al., 2020). The combined effects of climate and rapid transport could result in large-scale biotic homogenization, potentially exceeding the impact of either climate change or IAS acting alone due to context-dependent interactions (Gissi et al., 2021). Despite global climate change often facilitating IAS (Dukes and Mooney, 1999), these two issues are mostly treated independently (Pyke et al., 2008).

Climate change may affect IAS introduction pathways and vectors (Robinson et al., 2020). Melting Arctic ice caps have already facilitated new, faster shipping routes, connecting previously isolated ports and regions and increasing the chances of propagules surviving transit (Pyke et al., 2008; Miller and Ruiz, 2014; McCarthy et al., 2022). Climate change can also alter shipping connectivity by affecting trading patterns and tourism destinations, leading to increased propagule pressure in some locations and decreased pressure in others.

The effects of ocean climate change and acidification on NIS introductions and impacts are frequently discussed in the literature (Occhipinti-Ambrogi, 2021). However, causal effects are not well-documented. Studies that aimed to elucidate the influence of climate change on NIS tend to focus on the impact of increasing ocean temperature, with less attention to non-thermal factors associated with climate change (e.g., ocean acidification, salinity, dissolved oxygen, weather events, and hydrodynamic changes). Furthermore, limited research evaluates the effects of multiple factors and their interactions (Gissi et al., 2021), restricting our ability to robustly predict future IAS impacts.

Marine species are expected to undergo a general poleward expansion due to seawater warming (Pinsky et al., 2013; Poloczanska et al., 2016; Essl et al., 2019). Some evidence suggests that climate-related changes are increasing IAS abundances in marine systems (Sorte et al., 2010; García-Gómez et al., 2020; Stæhr et al., 2020). Among the different pathways of NIS introductions, the poleward expansion linked to ocean warming would be most relevant for secondary introductions. This is because southern seas, as hotspots of NIS introductions, could serve as source populations for further introductions to northerly regions as temperature conditions gradually become favorable there.

The rate of new NIS has significantly increased since the early 1980s (e.g., Zenetos et al., 2022; Jensen et al., 2023) possibly influenced by climate change-induced warming of the sea. Recent studies suggest a higher rate of new NIS arrivals in southern seas (Tsiamis et al., 2018; Tsiamis et al., 2019; Zenetos et al., 2022), with up to 76% of all NIS primary introductions in Europe originating from the Mediterranean Sea. This suggests the importance of secondary non-assisted dispersal for many observed NIS species in northern regions. In the OSPAR regions, secondary introductions accounted for only 5% of NIS introductions (Stæhr et al., 2022). The influence of climate-related warming on NIS introductions is not generally strongly supported by data and requires targeted species-specific analysis for the different European regions.

Climate change can alter the effectiveness of IAS management. Temperature dictates the life cycle of many IAS, influencing maturation, reproduction, establishment, and persistence (e.g., King et al., 2021; Teixeira Alves et al., 2021), with implications for eradication and population control under climate change. Some studies suggest that mechanical control of IAS becomes less efficient under climate change pressure (Hellmann et al., 2008; Pyke et al., 2008; Kernan, 2015), necessitating increased management efforts to achieve the same management goals (Teixeira Alves and Tidbury, 2022). Further research is needed to understand how both thermal and non-thermal factors of climate change influence IAS management.

In climate change hotspots, particularly in land-locked basins, such as the Mediterranean Sea, native biodiversity decline due to climate change may compromise ecosystem functioning and services (see Box 1). In such cases, thermophilic NIS could play a significant role in sustaining ecosystem functioning and services. As a result, a change in conservation goals has been proposed, moving from protecting native biodiversity to protecting functions and services (Rilov et al., 2019a; Rilov et al., 2020). Similarly, Reise et al. (2023) highlighted that some NIS in the Wadden Sea positively contributes to sediment stabilization, mud accretion, and diversification of lower food web levels, potentially benefiting foraging birds. They argued that these NIS have raised the tidal ecosystem's capacity to adapt to environmental change rather than degrade it.

9 Recommendations: how to improve the management of IAS in Europe

9.1 Costs of biological invasions and funding

Global damage and management costs associated with biological invasions have exponentially increased in the last 50 years (Diagne et al., 2020). However, the allocation of economic resources toward invasive species prevention, control, research, long-term management, and eradication measures needs a substantial increase to offset the economic losses caused by direct and/or indirect impacts of invaders (Diagne et al., 2021).

The extensive economic impacts of invasions, reaching beyond administrative and national scales, highlight a clear discrepancy between the implementation of international agreements (Table 1) by local authorities and the achievement of broad policy objectives. Enhancing governance, encompassing the capacity to implement policies through expertise and resources, is crucial for preventing and managing biological invasions and their impacts. International initiatives and European Institutions play a critical role in supporting and expediting measures that require local implementation but rely on effective global and regional coordination. Strategic planning and securing adequate funding will be central to addressing many of the challenges raised in this review.

9.2 Inadequate coverage of marine biological invasions by the IAS Regulation

Currently, only two marine species (*P. lineatus* and *R. okamurae*) are included in the List of Invasive Alien Species of Union Concern, which does not reflect the status of marine biological invasions in the EU. Marine NIS thrive in the European seas, with EASIN listing 1,602 alien or cryptogenic species, while globally, WRiMS and AquaNIS currently report 2,781 and 2,028 species, respectively. The Mediterranean Sea, in particular, is a hotspot of biological invasions, harboring more NIS than any other sea globally (Costello et al., 2021). Many of these species are invasive, significantly impacting biodiversity, ecosystem services, and human health (Katsanevakis et al., 2014b; Tsirintanis et al., 2022). An EU horizon scanning exercise identified 18 marine species absent from or with a limited distribution in EU marine waters as potential candidates for inclusion in the list based on their impacts and management feasibility (Tsiamis et al., 2020). However, it seems that member states hesitate to include marine species in the list of IAS of Union Concern, assuming that management of marine IAS is impossible. As indicated in previous sections, managing marine IAS is more challenging than terrestrial or freshwater species, but it is not impossible. Hence, the current list of IAS of Union Concern does not fully acknowledge the threat marine IAS pose to the EU marine environment, and it needs to be supplemented based on current scientific advice and risk assessments (as per Article 5 of the IAS Regulation).

9.3 Learning from countries with high biosecurity: take stock of good practices

Ideally, a robust biosecurity system should encompass all three steps of the invasion process (pre-border, border, and post-border) and implement effective and timely interventions, drawing from countries with established cutting-edge biosecurity programs (Carvalho et al., 2023). New Zealand, Australia, and the USA have well-established biosecurity systems, as evidenced by their successful cases of marine IAS eradication or control (Table S2). For example, New Zealand's Marine Biosecurity Team, operating under the Ministry of Fisheries since 1998, conducts various activities such as quarantine, surveillance, response to incidents, long-term control of established pests, and enforcement of legislation (Hewitt et al., 2004). Europe could benefit from the experience, learning from both successes and failures in managing IAS in these countries. Organizing workshops and meetings involving high-level policymakers, marine scientists, managers, and officials from various countries can promote collaborative knowledge sharing and mutual learning to enhance global marine IAS management.

9.4 Creating an EU funding mechanism to secure the sustainability of important information systems

Adequate EU funding is crucial to sustain key databases and online information systems. EASIN plays a central role in harmonizing and integrating information on NIS in Europe. It primarily acts as an aggregator that gathers data from various sources and provides efficient tools and services for access to harmonized datasets. However, the foundation of the European infrastructure relies on national institutions, local and regional networks, and online databases and initiatives. These entities are essential data suppliers to centralized systems like EASIN. Therefore, it is critical to financially support and sustain national institutions and scientific networks to ensure the continuous flow of information, knowledge, and expertise to EASIN and the scientific community.

NIS information systems should be multipurpose, following the principle of "gather data once, utilize it many times". In addition to operational usage, these systems should continuously accumulate data for analysis and forecasting. Ideally, this should not only include information on species occurrences but also offer search functions for NIS biological traits, environmental tolerance limits, and their impacts on native biodiversity, ecosystem functioning, economy, and public health.

9.5 Improving monitoring and early warning systems

Continued efforts to increase the spatial and temporal coverage of marine IAS monitoring, as well as transboundary cooperation, are required. Aligned with the ethos of "take once, use many" and driven by the application of novel techniques such as eDNA, automated monitoring, and even citizen science, integration of NIS monitoring with other biodiversity monitoring programs, where applicable, is an opportunity to balance data collection against increasing costs/declining budgets. Automated eDNA monitoring (Hansen et al., 2020; Preston et al., 2023) and using citizen science for monitoring eDNA also have associated difficulties (Agersnap et al., 2022; Knudsen et al., 2023), and the eDNA metabarcoding itself (Fonseca, 2018) and species-specific eDNA detection are not without pitfalls and problems with interpretation (Klymus et al., 2019). The data analysis required when eDNA is to be interpreted is often complicated and is better off being aided by taxonomic experts who are familiar with the organisms known to inhabit the sampled area. Further, streamlining marine NIS data flow and reducing data time lags will enhance early warning systems and facilitate rapid response. Understanding introduction pathways is also crucial for implementing effective prevention measures and reducing new introductions.

Several studies have considered how man-made structures (offshore wind farms, wrecks, and oil and gas platforms) could act as *de facto* MPAs, facilitating colonization by both native and NIS (Birchenough and Degraer, 2020). It is important to highlight that the presence of these man-made structures will alter the species pool, with repercussions for trophic interactions (Mavraki et al., 2019) and secondary production, and may also serve as stepping stones for range-expanding (sometimes non-indigenous; Kerckhof et al., 2011) species altering population connectivity patterns (Henry et al., 2018; Coolen et al., 2020).

9.6 Improving predictions

Accurately predicting the potential distribution of invasive species is crucial for global marine conservation. To improve

predictions, it is imperative to consider the biological characteristics and distribution of the species, biotic interactions, and environmental conditions. Incorporating intrinsic traits in modeling can prove advantageous, as these traits can either facilitate higher adaptation rates or impose limitations on the invasion process (Gamliel et al., 2020). More data from both native and invaded ranges enhance prediction accuracy, allowing for a better assessment of the role of environmental factors in distribution and expansion potential. Removing noisy or uncertain predictors can further increase model accuracy. Integrating invasion dynamics like biotic interactions, dispersal limitations, and adaptation potential can inform potential niche conservatism violations (D'Amen and Azzurro, 2020b; Liu et al., 2020). As a final note, when selecting modeling approaches (e.g., correlative, mechanistic, and process-oriented), careful consideration of available input data accompanied by rigorous validation is essential (Melo-Merino et al., 2020).

9.7 Improving integrated impact assessments: cumulative impact mapping to prioritize actions

Cumulative impact assessments of invasive species are valuable for several reasons. They offer a comprehensive understanding of the combined effects of multiple IAS on marine ecosystems, aiding policymakers and managers in understanding the extent and severity of ecological disturbances. This knowledge is crucial for devising effective strategies to prevent new invasions and mitigate existing impacts. As marine management shifts toward ecosystem-based spatial approaches, cumulative impact assessments become essential tools. They facilitate the integration of spatial information into environmental decisions and the setting of specific operational objectives. By identifying highly impacted areas, resources can be directed toward priority zones or targeted management actions for IAS.

Comprehensive large-scale analyses of the impacts of all alien marine species are urgently needed. Policymakers and managers, particularly in regions like the European Union, require a better understanding of invasive species' impacts to meet environmental protection goals. Despite limitations and uncertainties in impact assessments, the adaptive management approach, involving monitoring, filling data gaps, and learning from management actions, offers a way to address and manage IAS impacts over time. In a limited-funding environment, decision-makers can efficiently allocate resources by focusing on sites, pathways, and species with high impacts and low uncertainty, increasing the chances of success in mitigating IAS effects. These initial successes can motivate further efforts to address biological invasions.

9.8 Assessing positive impacts and exploiting NIS

NIS have become a permanent component of contemporary ecosystems, and their potential benefits on ecosystem services, human wellbeing, and biodiversity should be thoroughly investigated (Schlaepfer et al., 2011; Vimercati et al., 2020; Vimercati et al., 2022). Many invasion studies are biased toward perceiving alien species as harmful due to their history of detrimental effects on ecosystems. Some reported negative impacts supported by limited strength of evidence may be influenced by this bias (Katsanevakis et al., 2014b; Tsirintanis et al., 2022), affecting impact assessments (e.g., compare Figures 5 and Figure S1). Scientists should adopt holistic approaches, considering both the negative and positive consequences of IAS on recipient ecosystems, relying on substantial evidence. The role of NIS in marine conservation, restoration, and securing ecosystem functioning and services, particularly in climate change hotspots, deserves serious consideration (see Box 1) (Mačić et al., 2018; Rilov et al., 2019a; Rilov et al., 2020).

In such regions heavily impacted by climate change, such as the eastern Mediterranean, IAS commercial exploitation becomes not merely a management choice but an essential measure to ensure the fishing industry's viability and safeguard seafood supply from the ocean (Katsanevakis, 2022). However, in other regions, there are risks associated with promoting commercial utilization of IAS, and initiatives aimed at controlling IAS through human consumption should be carefully evaluated, as they could produce unintended outcomes contrary to their goals (Nuñez et al., 2012; Katsanevakis, 2022). This shift in perception could lead to illicit attempts to spread IAS to new areas, ultimately exacerbating their invasive potential (Mancinelli et al., 2017). Furthermore, it might create pressure to maintain and sustainably exploit these problematic species (Nuñez et al., 2012), as has happened in the cases of *Rapana venosa* in the Black Sea (Demirel et al., 2021) and the invasive red (Kamchatka) king crab (*Paralithodes camtschaticus*) fishery in the Barents Sea (Spiridonov, 2018).

Bioprospecting involves identifying and extracting new bioactive compounds with various potential applications, such as biomedicine, human health, food provision, nutraceuticals, cosmeceuticals, and the search for anti-fouling and antimicrobial agents. Managing IAS through prospecting can turn a threat into a resource, as demonstrated by growing research on invasive species, e.g., alien or native jellyfish (see Leone et al., 2015; Leone et al., 2019; De Domenico et al., 2023, and references therein), alien macroalgae (Misal and Sabale, 2016; Vitale et al., 2018; Cherry et al., 2019; Meinita et al., 2022), and even the poisonous *L. sceleratus* (Çavaş et al., 2020).

Author contributions

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Writing – review & editing. KT: Visualization, Writing – original draft, Writing – review & editing. SB: Conceptualization, Writing – original draft, Writing – review & editing. HJ: Conceptualization, Writing – original draft, Writing – review & editing. SWK: Writing – original draft, Writing – review & editing. AL: Data curation, Writing – original draft, Writing – review & editing. AM: Writing – original draft, Writing – review & editing. SP: Writing – original draft, Writing – review & editing. HTi: Writing – original draft, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

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New tools and recommendations for a better management of harmful algal blooms under the European Marine Strategy Framework Directive

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Marine harmful algal blooms (HABs), caused by various aquatic microalgae, pose significant risks to ecosystems, some socio-economic activities and human health. Traditionally managed as a public health issue through reactive control measures such as beach closures, seafood trade bans or closure of mollusc production areas, the multifaceted linkages of HABs with environmental and socio-economic factors require more comprehensive ecosystem-based management approach tools to support policies. This study promotes a coordinated understanding and implementation of HAB assessment and management under the Marine Strategy Framework Directive (MSFD), targeting the achievement of Good Environmental Status (GES) in European marine waters. We introduce two novel tools: GES4HABs (GES for HABs) decision tree, and MAMBO (environMental mAtrix for the Management of BlOoms), a decision support matrix. These tools aim to streamline HABs reporting and prioritize resource allocation and management interventions. The GES4HABs decision tree defines a sequence of decision steps to identify HAB management strategies according to their state (evaluated against predefined baselines) and causes (anthropic or natural). MAMBO is proposed to address different HABs and their interaction with human and environmental pressures. The matrix utilizes two axes: natural trophic status and level of human influence, capturing major aspects such as nutrient supply. While acknowledging the limitations of this simplified framework, MAMBO categorizes marine regions into quadrants of varying management viability. Regions with high human influence and eutrophic conditions are identified as most suitable for effective management

intervention, whereas regions with minimal or mixed human influence are deemed less amenable to active management. In addition, we explore and describe various indicators, monitoring methods and initiatives that may be relevant to support assessments of HAB status and associated pressures and impacts in the MSFD reporting. Finally, we provide some recommendations to promote the consideration of HABs in ecosystem-based management strategies, intensify efforts for harmonizing and defining best practices of analysis, monitoring and assessment methodologies, and foster international and cross-sectoral coordination to optimize resources, efforts and roles.

KEYWORDS

decision support tools, ecosystem-based management, indicators, marine monitoring, eutrophication, marine biotoxins, environmental assessment, pressures and impacts

1 Introduction

The term "harmful algal blooms" (HABs) refers to ecologically, socio-economically or health-related detrimental events caused by a wide range of taxonomically, physiologically, and ecologically distinct microalgae and macroalgae. Focusing on microalgae, of the approximately 3,400 to 4,000 known species worldwide, only a mere 1–2% are categorized as harmful (Shumway et al., 2018).

Although HABs are best known for their adverse impacts on public health, aquaculture, fisheries, infrastructure, and recreational and tourism activities (Anderson et al., 2012; Brown et al., 2019; Kouakou and Poder, 2019; Young et al., 2020; Karlson et al., 2021; Lenzen et al., 2021), several adverse effects on marine organisms, including molluscs, fish, seabirds, reptiles and marine mammals, are increasingly documented (Landsberg, 2002; Zohdi and Abbaspour, 2019; Rattner et al., 2022). All these impacts significantly contribute to changes in marine ecosystems, their associated services, and human wellbeing (Masó and Garcés, 2006).

HABs are typically classified into three broad categories based on their "mechanisms of harm": (i) low biomass toxin-producers, which can contaminate seafood, water, and generate aerosols even at low biomass levels, (ii) high-biomass toxin-producers, which can produce similar harmful effects when reaching high concentrations, and (iii) high-biomass non-toxic species, that can cause either hypoxic/anoxic conditions or unpleasant/nuisance foam or gelatinous masses, among other effects (Anderson et al., 2017; Karlson et al., 2021). A comprehensive list of the most frequently described adverse effects (impacts) of HABs on ecosystem services has been compiled in the Supplementary material (Supplementary Table S1).

Identifying the causative factors behind HAB events is a complex endeavor. Most HABs are natural phenomena that have historically occurred in various regions worldwide before human activities altered coastal and marine ecosystems (Hallegraeff et al., 2003). HABs involve a change of phytoplankton assemblages, which can arise are in response to chemical, biological or habitat alterations (Smayda, 2008). Various ecological mechanisms have been suggested to elucidate HABs, including biological life strategies such as mixotrophic behavior, swimming ability, allelopathy effects, multi-resource competition, and prey avoidance (Choi et al., 2023). In some instances, certain types of HABs from across the globe have been associated with distinct anthropogenic pressures, such as nutrient loads (Riegman et al., 1992; Glibert et al., 2005; Heisler et al., 2008; Harrison et al., 2012), intensified human activities (e.g., aquaculture and navigation, see Hallegraeff et al., 2021), habitat modifications (Garcés and Camp, 2012), and climate change (Anderson, 2014; Wells et al., 2015; Glibert and Burkholder, 2018; Glibert, 2020).

The first legislations on HABs appeared in the mid-1990s: for instance, the local Galician Government legally established the monitoring network for marine biotoxins in bivalve molluscs grown in rafts in the Galician Rías (NW Spain) in 1995 (Pazos and Maneiro, 1999), and the US *"Harmful Algal Bloom and Hypoxia Research and Control Act"* was enacted in 1998. In Europe, HABs are currently managed primarily as a public health issue (Food and Hygiene Regulations [Regulation (EC) 853/2004, 2004; Regulation (EC) 2074/2005, 2005; Regulation (EU) 2019/627, 2019; Regulation (EU) 2021/1709, 2021]), Bathing Water Directive (BWD) (European Commission, 2006), but are also considered within the Water Framework Directive (WFD) (European Commission, 2000). These regulations mandate the monitoring of marine biotoxins and toxic phytoplankton while establishing specific thresholds to trigger control measures, such as beach closures or seafood trade bans (European Food Safety Authority (EFSA), 2009; Serret et al., 2019). Nevertheless, the significant interconnections between HABs and various environmental and socio-economic issues (see Supplementary material 1) highlight the need of a holistic, ecosystem-based approach to manage HABs through appropriate instruments and policies. Furthermore, neglecting HABs management in environmental policies may lead to future environmental challenges if affected socio-economic actors resort to unregulated mitigation measures such as algicide application, ultrasound, clay disposal or biological treatment (Silliman, 2022).

In this context, the European Marine Strategy Framework Directive (MSFD; European Commission, 2008) represents a significant milestone by introducing an ecosystem-based management approach (EBMA) for the sustainable utilization of marine resources and ecosystem services across Europe. The MSFD aims to ensure that, through its implementation by the EU Member States, in coordination with the Regional Sea Conventions (RSCs), a "Good Environmental Status" (GES) of the EU's marine waters is achieved by 2020 (now, 2026) (European Commission, 2020).

In practice, the MSFD is implemented through a six-year adaptive management cycle, starting with (i) an initial assessment

of the status of the marine environment and its essential features and characteristics, (ii) an analysis of the prevailing pressures and impacts, and (iii) an economic and social analysis of the sea use (Art. 8 MSFD). In parallel, the determination of GES (Art. 9 MSFD) and a set of environmental targets and associated indicators (Art. 10 MSFD) was established. GES is defined by eleven descriptors that elucidate the conditions indicative of GES attainment. The indicators and reference values are used to assess compliance with GES and to establish adapted monitoring programmes (Art. 11 MSFD) and programmes of measures (Art. 13 MSFD) for preserving or restoring GES conditions. The six-year management cycle allows Member States to periodically review the suitability and effectiveness of their GES determination, environmental targets, indicators, and measures.

HABs received limited attention in the 2012 MSFD initial assessments (Palialexis et al., 2014). In the 2018 reporting phase, only few Member States initiated reporting on HABs (cyanobacteria in the Baltic Sea and southern North Sea, *Noctiluca scintillans* in the Black Sea, and *Phaeocystis* spp. in the southern North Sea) (Tornero Alvarez et al., 2023). Although progress is being made, the diverse array of environmental and socio-economic problems associated with HABs in European coastal and offshore waters is inadequately reflected in the reporting (Tornero Alvarez et al., 2023). Indeed, in the European Seas, abiotic conditions such as nutrient availability and hydrodynamics vary significantly between the open sea and coastal areas. This leads to differences in the types of phytoplankton species present and the frequency of their blooms, which can range from seasonal to unpredictable (Garcés and Camp, 2012). The nearshore zones, covered by the WFD assessment, frequently exhibit signs of eutrophication due to substantial nutrient inputs are often sites of phytoplankton blooms and the presence of harmful algal (HA) species (Bricker et al., 2008). Although most of the potential HAB impacts are expected to occur in nearshore areas designated under the WFD and MSFD, some may extend and impact to offshore regions exclusively covered by MSFD.

In this context, the aim of this study is to pave the way for the integration of HABs into EBMA, with a specific focus on the MSFD (without forgetting lessons learnt from WFD). The main objective is to provide policy- and decision-makers with technical guidance and tools that can enhance the monitoring, assessment and management of HABs in marine environments.

The study outcomes include the proposal of two new conceptual decision support tools (a decision tree and a conceptual matrix), an exploration of existing and alternative indicators and monitoring methods potentially useful for HABs, and recommendations for fostering EBMA strategies.

2 Proposed conceptual decision support tools for guiding HAB management

Within the MSFD framework we found the following principles as most relevant for contextualizing HABs (European Commission, 2017, 2020, 2022):

- The **MSFD** primarily focuses on assessing the overall environmental status of marine ecosystems, with a particular emphasis on evaluating the impacts of human activities.
- **GES is not conceived to reflect a pristine status but should encompass prevailing environmental conditions,** including natural variability, climate change, past human activities, their pressures and impacts as well as the ecosystem's resilience and capacity for recovery (Claussen et al., 2011).
- **Climate change should be regarded as a "shifting baseline" to be integrated into GES determination** (Elliott et al., 2015). Even if climate change is acknowledged as a significant pressure across all European marine regions (European Commission, 2020), assessing climate change effects is not a specific objective of the MSFD. Thus, it is important to distinguish wider climate-change impacts from more localized effects caused by other anthropogenic pressures.
- Member States can, based on risk analysis**, focus their efforts on the main problems and areas**. The exclusion of low-risk areas and issues does not preclude the maintenance of surveillance monitoring for early detection of future deviations.
- The new MSFD framework requires the setting of **quantitative "threshold values"** grounded in the best available science, aiming for consistent and comparable outcomes among Member States (European Commission, 2017).
- The **(re)use of existing monitoring, standards, and methods stipulated in other EU legislation** is recommended to avoid redundant processes and unnecessary reporting burden on member states (European Commission, 2020).

Considering these requirements, we have developed a **decision tree**, hereafter referred to as **GES4HABs**, and a **decision support matrix**, hereafter referred to as **MAMBO** (environMental mAtrix for the Management of BlOoms). GES4HABs breaks down complex decisions into a sequence of more manageable steps, rendering the decision-making process easier to understand and follow (Figure 1). MAMBO is nested within GES4HABs and assists in identifying HABs that are more amenable to management actions, thereby directing efforts and resources efficiently (Figure 2). Hereafter, the consecutive steps and criteria encompassed in GES4HABs, and MAMBO are described.

2.1 GES4HABs entry point: the initial assessment

Although reactive local control measures and regulatory limits will always be necessary to mitigate the impacts and risks of HABs [e.g., Food and Hygiene Regulations [(EC) 853/2004; (EC) 2074/2005; (EU) 2019/627; (EU) 2021/1709], Serret et al. (2019); Bathing Water Directive (European Commission, 2000)] (Figure 1), upstream management based on EBMAs, such as the MSFD, can assist in identifying the causes and impacts of HABs, assess their status against the expected prevailing conditions, and define appropriate management measures. Ultimately, EBMA aims

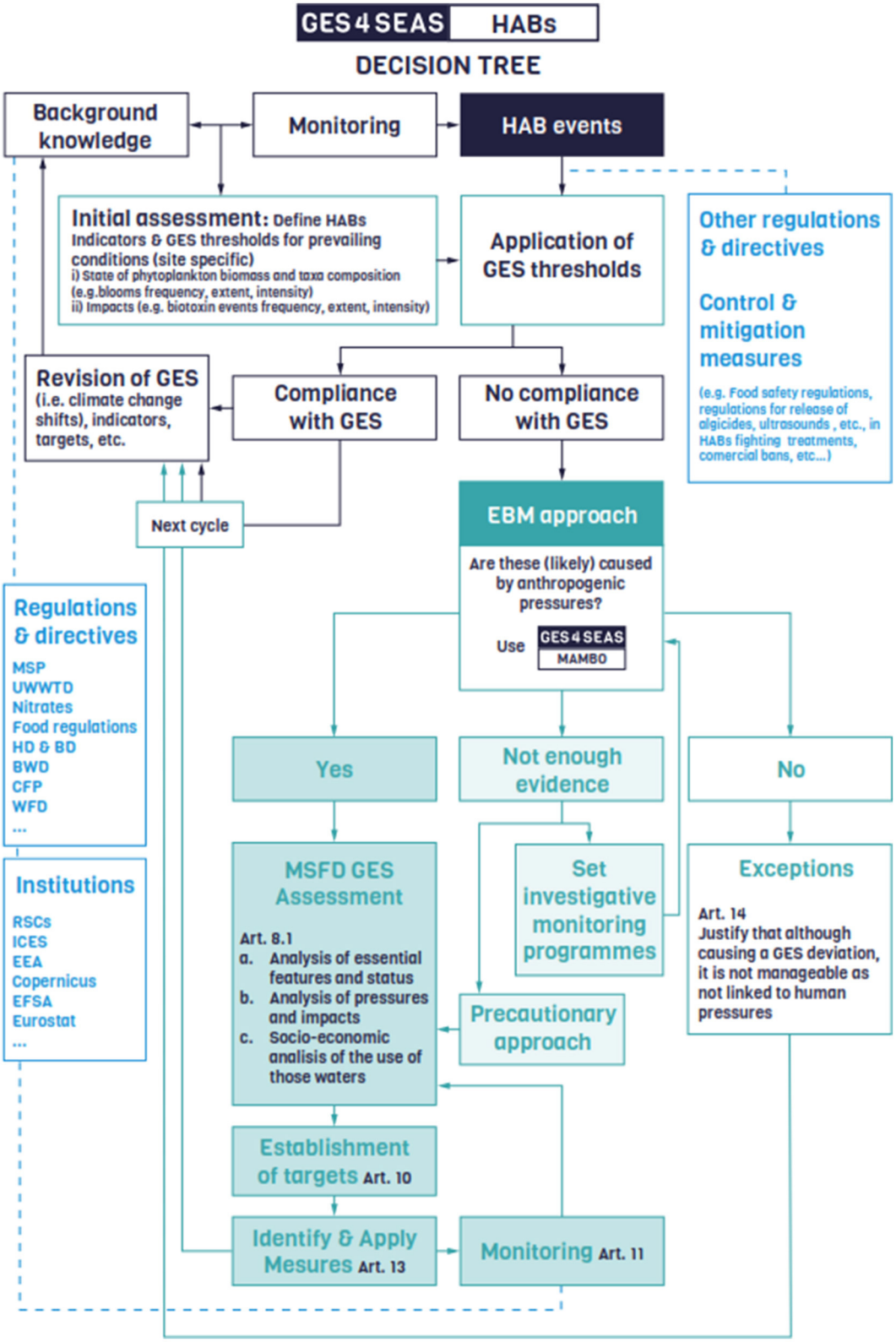

FIGURE 1
GES4HABs Decision tree to guide policy makers and Marine Strategy Framework Directive (MSFD) stakeholders on the steps and decisions to support management and MSFD reporting actions related to different Harmful Algal Blooms (HABs) in their jurisdiction areas. GES, Good Environmental Status; EBM, Ecosystem-Based Management; RSC, Regional Seas Conventions; ICES, International Council for the Exploration of the Sea; EEA, European Environment Agency; EFSA, European Food Safety Authority; Eurostat, Statistical office of the European Union; MSP, Maritime spatial planning; WFD, Water Framework Directive; UWWTD, Urban Waste Water Treatment Directive; Nitrates, Nitrates Directive; HD and BD, Habitats Directive and Birds Directive; BWD, Bathing Water Directive; CFP, Common Fisheries Policy; MAMBO, environMental mAtrix for the Management of BlOoms (see Figure 2).

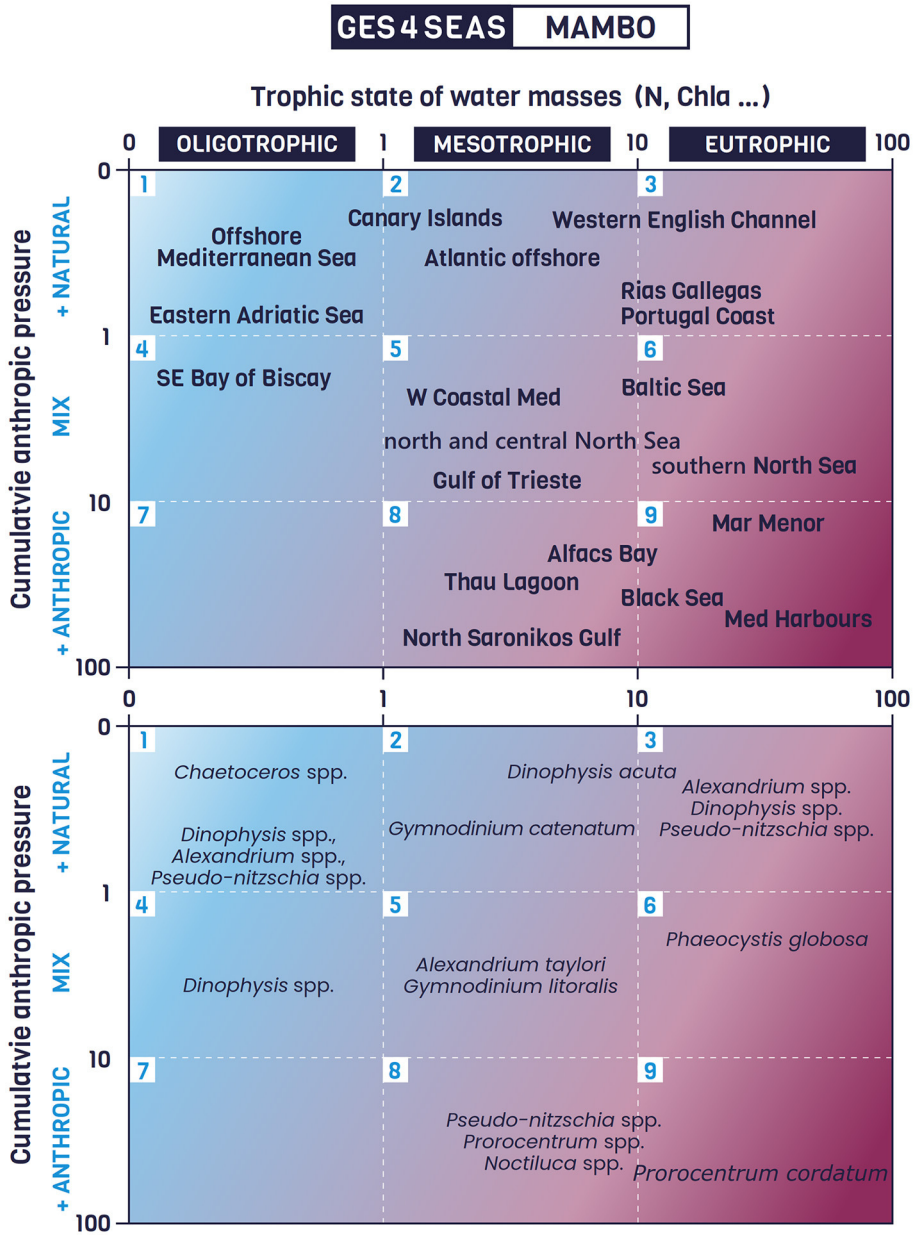

FIGURE 2
Top: Representation of some marine geographical regions in the MAMBO (environMental mAtrix for the Management of BlOoms) matrix according to their associated trophic state (X axis) and anthropic influence level (Y axis). **Bottom**: Representation of some examples of Harmful Algal species occurrences in relation to the European marine geographical regions previously represented **(Top)**. The examples added are not meant to hold a comprehensive list of HAB events in European seas but to provide different examples of harmful algae presence and/or events in Europe and exemplify their position in the MAMBO matrix. More examples can be found in Supplementary Table S2.

to preserve or enhance ecological integrity, resilience, the provision of ecosystem services, stakeholder engagement and accountability, and transdisciplinary integrated management (Delacámara et al., 2020).

The first **step** in implementing this approach involves leveraging the local experts' background knowledge of HABs, along with existing monitoring data and infrastructure, to conduct an initial/preliminary assessment (Figure 1). During this initial assessment, appropriate indicators, reference conditions (e.g., those corresponding to the prevailing environmental conditions that determine GES), and thresholds (e.g., those indicating the boundaries between GES and non-GES) should be established to assess HAB events in a given area (WG GES, 2011).

This initial phase could also serve to identify inadequate or inconsistent monitoring efforts and techniques needed to establish effective indicators and reference points (Zampoukas et al., 2014). This may be particularly relevant in the context of rapidly changing conditions due to climate change and the expanding and intensifying human footprint in the assessed areas (e.g., due

to aquaculture, coastal modifications, shipping, mining, fishing, and recreation).

The required indicators for this initial assessment can focus on the status of HABs (e.g., phytoplankton biomass, taxa composition, frequency, extent, and duration of blooms) or their impacts (e.g., biotoxin concentrations, frequency and number of closed mariculture sites, and organism mortality) (Figure 1). This choice should be driven by the characteristics of the HABs occurring in the area, the available monitoring networks, and possibilities for inter-comparison (see Section 3 for further information on HAB-related indicators).

While this initial assessment is challenging and resource-intensive, it is essential to (i) identify and account for HAB occurrences in the assessed areas, (ii) determine whether HABs deviate from prevailing conditions, and (iii) anticipate potential new HABs or shifts in baselines due to global change.

The second **step** commences with a new reporting phase, during which the HABs recorded in the reporting period should be compared to the reference values for prevailing conditions (GES thresholds) set in the initial assessment (Figure 1). If HABs fall within these thresholds, reporters can confirm compliance with GES, justify the lack of need for additional management measures, and maintain the existing surveillance monitoring and response control measures. Conversely, if the assessment indicates a departure from GES, a potential concern arises, leading to the next question: Are these HABs (likely) linked to anthropogenic causes and therefore manageable within the policy framework? (Figure 1).

2.2 Use of MAMBO to address the complexity of environmental factors and human influence in the management of HABs

At present, establishing clear links between HABs and anthropogenic pressures is challenging due to several factors: (i) the complexity of the mechanisms that trigger HABs, (ii) the interaction of multiple pressures, both human and natural, and their cumulative effects (additive, synergistic, or antagonistic), and (iii) changing conditions due to climate change.

In this context, MAMBO is proposed to pragmatically delineate the manageable environment within which policy makers and environmental managers can direct their efforts and resources. MAMBO intersects the natural trophic status of marine waters, ranging from oligotrophic to highly eutrophic systems (X axis), with their level of anthropic influence (Y axis) (Figure 2). For the quantitative application of MAMBO, these axes can be customized with different metrics. The 'trophic state' axis could be determined by average chlorophyll *a* concentration values or any other metric deemed appropriate to represent prevailing conditions. Similarly, different metrics could be chosen for the cumulative anthropic pressure axis. This choice may be based upon user preferences, data availability, and regional characteristics (e.g., freshwater content, land use indices, or other anthropic indicators).

These axes were chosen because most connections between human activities and HABs are related to nutrient status. Although the link with over enrichment of nutrients is more often associated with high-biomass HABs, the effect of nutrients in promoting HABs (including toxic HABs) is neither uniform nor straightforward (Masó and Garcés, 2006; Smayda, 2008; Gowen et al., 2012). Establishing a direct link between trophic status and HABs is challenging, especially when attributing this status to either natural or anthropogenic sources is required. In addition, this link is often context dependent with the co-occurrence of other factors or pressures (Smayda, 2008; Davidson et al., 2014). For instance, nutrient reduction policies leading to oligotrophication could increase Paralytic Shellfish Poisoning (PSP) events in warm shelf systems (Walsh et al., 2011) and Mediterranean lagoons (Collos et al., 2009). Additionally, changes in nutrient stoichiometry may favor some harmful species, as observed in areas of intensive bivalve cultivation (Brown et al., 2019) or after dam construction (Humborg et al., 1997). Apart from climate change, other anthropic pressures may also contribute to HABs, such as the transmission of species via ballast waters (Brown et al., 2019; Karlson et al., 2021), the decline of top predators due to fishing (Walsh et al., 2011), the introduction of cysts in the water column due to dredging operations (Carrada et al., 1991; Feki et al., 2022), and the construction of structures that affect hydrodynamics, such as harbors and dikes (Garcés and Camp, 2012; Karlson et al., 2021). These pressures may even interact to produce larger effects (Ferreira et al., 2011).

Recognizing that the selected axes do not fully capture the complex interactions between different pressures and HABs but only the most relevant ones, MAMBO can depict different quadrants associated with different levels of management viability. When different geographical marine regions and different HAB species occurrences are represented in MAMBO (Figure 2), those falling within highly anthropized and eutrophic quadrants (quadrants numbered 5, 6, 8 and 9) have the potential for effective management intervention. In the remaining quadrants (1, 2, 3, 4 and 7), active management interventions would be less viable because HABs are more likely to be driven by natural phenomena occurring in areas with mixed or no anthropogenic pressures.

Several examples of HABs in European geographical areas, found in the reviewed literature, have been placed within the MAMBO matrix quadrants (Figure 2) and briefly described in Supplementary Table S2 to illustrate MAMBO functionality. For example, in quadrants 2 and 3, where HABs have a natural origin, there is the occurrence of *Gymnodinium catenatum* blooms in Portugal and the Galician Rias in Spain. The *G. catenatum* blooms are triggered at the end of the coastal upwelling seasons when nutrient-depleted, warm surface water is found offshore, while coastal upwelling keeps the nearshore waters cold, nutrient-rich, and with a rich community of diatoms. When the upwelling subsides, warmer offshore waters move toward the coast, resulting in a temperature increase that favors the blooms of *G. catenatum*. In some cases, an inshore poleward current may transport populations of dinoflagellates to the Rias from waters off northern Portugal (Sordo et al., 2001; Pitcher and Fraga, 2015). These natural triggers place these blooms outside the scope of management, making monitoring and early warning systems the most appropriate tools for mitigating their impacts.

Alexandrium taylori and *Gymnodinium litoralis* blooms, which are influenced by both natural and anthropogenic factors, are illustrative examples of quadrant 5. These are common in

Mediterranean coastal waters, and result from a combination of factors, including nutrient enrichment, enhanced growth, and limited water renewal. Nutrients are mainly supplied by groundwater, rivers and seasonal Mediterranean streams, while local summer winds maintain high cell densities in coastal waters (Garcés et al., 1999; Basterretxea et al., 2005; Reñé et al., 2011; Garcés and Camp, 2012). Both increased growth rates and reduced wind-driven water renewal are critical in modulating these blooms. While nutrient inputs can be controlled, hydrographic mechanisms cannot.

In quadrant 9, the harmful algal species *Prorocentrum cordatum* has traditionally been associated with eutrophication, mainly from riverine nutrients exported to the coast (Glibert et al., 2008). The authors demonstrate that the species is prevalent in regions with high levels of dissolved inorganic nitrogen and phosphorus significantly originated from anthropogenic sources, such as fertilizers and manures.

It is worth highlighting that a single HAB species or groups may appear in different quadrants. For example, *Pseudo-nitzschia* is a genus of diatoms that exhibits remarkable adaptability, thriving in a variety of environmental conditions (Hasle, 2002; Hubbard et al., 2023). Even if commonly found in upwelling systems, such as the Galician Rias, it also thrives in eutrophic areas where excess nutrients from human activities create favorable conditions for its growth, such as Alfacs Bay in the Mediterranean. This diatom genus even appears in open waters with an oligotrophic status, demonstrating its ability to bloom in diverse environments. This adaptability illustrates MAMBO's effectiveness in defining manageable conditions for the same microalgae involved, emphasizing that the bloom's origin is often more pertinent than the species involved.

Moreover, the ecosystem positions in MAMBO are dynamic. For example, European assessments of eutrophication indicate that phosphorus levels in rivers are decreasing, thereby reducing fluxes to coastal areas such as the Mediterranean and southern North Sea (Ludwig et al., 2009). Therefore, as WFD measures take effect, the trophic status of areas within the MAMBO matrix may shift away from anthropogenic influences. However, the gaps of knowledge on these changes hinder our ability to predict what will be the trends of the trophic status and generation of HABs in the European seas. For example, in the offshore Mediterranean Sea, oligotrophication is expected to continue due to reduced continental inputs and increased water column stability under global change. However, the extent to which these processes will be influenced by extreme weather events or increased atmospheric deposition is not known.

Anyhow, the outcomes from MAMBO will define the next steps in the GES4HABs decision flow (Figure 1): HABs identified as manageable should be included in a comprehensive assessment informing on their status, their related pressures and impacts (MSFD Article 8.1b) and the human activities involved (Article 8.1c). This assessment will support the designation of appropriate measures to restore GES conditions (Articles 10, 13, 11). For HABs located in quadrants 1 to 3, an exception (Article 14) could be considered for the implementation of new management measures, justifying the likely natural and unmanageable nature of the identified GES deviation. In cases with insufficient evidence to rule out or confirm HAB linkages with anthropogenic pressures, additional investigative monitoring should be supported to clarify these questions. Alternatively, a precautionary approach can be adopted, assuming probable linkage to anthropogenic causes, and initiate a full assessment and management cycle as in the first case. The following sections provide a list and brief descriptions of the indicators and monitoring methods that can be used to achieve this.

3 Currently used indicators and alternatives

For both initial assessment and the subsequent reporting cycles, it is essential to identify suitable indicators under the relevant MSFD descriptors and criteria that evaluate the state, associated pressures and impacts of HABs. Although the MSFD currently addresses HABs solely within the eutrophication descriptor (D5C3 criterion) and their potential impacts on the "D1C6-pelagic broad habitat" state criterion (European Commission, 2017), it formally omits HABs unrelated to anthropic eutrophication (European Commission, 2022). This omission occurs despite their evident connections with other ecological challenges (e.g., mass mortalities or disruption of ecosystem services). Further details on these connections between HABs and the MSFD descriptors are provided in Supplementary Table S3.

In addition to the thematic context, **indicators should be defined alongside quantifiable metrics or indices and their associated thresholds** to ensure operational, transparent, and efficient assessments.

Criteria for indicator selection within a normative framework should: (i) have limited sensitivity to natural variation (Heink and Kowarik, 2010), (ii) reflect pressure-state-impact linkages with other indicators (Dale and Beyeler, 2001; Niemeijer and de Groot, 2008; Marques et al., 2009; Birk et al., 2012), (iii) consider the feasible/required sampling and analysis capabilities, (iv) account for the temporal, spatial, and taxonomic resolutions of underlying data and their associated uncertainties (Racault et al., 2014), and (v) allow for intercomparison and intercalibration at the pan-European level (Poikane et al., 2014). Threshold values, Ecological Quality Ratios (EQRs), trends, or supplementary information are crucial for properly interpreting the indicator results (Cusack et al., 2008).

3.1 Indicators for pressures causing HABs

The main abiotic pressures identified to cause HABs, as for phytoplankton in general, are nutrients (both macronutrients and micronutrients), light, temperature, water column stability (Anderson et al., 1998; Litchman and Klausmeier, 2008; Facey et al., 2019), pH (Shapiro, 1984; Raven et al., 2020) and oxygen concentration (Heisler et al., 2008; Ryan et al., 2009; Kudela et al., 2010; Pitcher and Fraga, 2015; McCabe et al., 2016; Xiao et al., 2019). The conditions that trigger HABs can result from changes in the seabed and hydrography, as well as species translocations caused by human activities. Thus, criteria and indicators used under MSFD descriptors other than D5 (e.g., D2, non-indigenous species; D4, food-webs; D6, seafloor integrity; and D7, hydrography) could be relevant for assessing the pressures contributing to HABs. However, currently used indicators may require adaptation to appropriately assess HAB causes.

For instance, many HABs are associated with certain inorganic nutrient ratios, forms or composition regardless of the total nutrient availability (Glibert and Burkholder, 2006; Heisler et al., 2008). Some mixotrophic or heterotrophic harmful algal species, seem to be stimulated by the availability of organic forms of nitrogen or phosphorus (Herndon and Cochlan, 2007; Cochlan et al., 2008; Kudela et al., 2008, 2010; Loureiro et al., 2011; Davidson et al., 2014), whereas other HAB forming species consume predominantly particulate rather than dissolved nutrients (e.g., Jeong et al., 2005). Another example is the ability of some harmful algal species to fix and convert gaseous nitrogen, enabling them to succeed and grow in nitrogen-depleted conditions (Litchman, 2023).

The development of HABs is often also related with the dynamics of the whole ecological system and the adaptive strategies of certain species (e.g., against predation) (Flynn, 2008). Therefore, multiparametric indicators or methods have been also proposed based on the multitrait characteristics associated with different HABs (Litchman, 2023), the combined mixing-irradiance-nutrient conditions (Smayda and Reynolds, 2003), or interestingly, indicators focusing on other ecological groups like zooplankton to improve forecasting of biotoxins from harmful algae blooms (Trapp et al., 2021).

Other abiotic indicators on irradiance levels (at the surface or reaching the seabed), or on the dissolved oxygen profiles, could be interesting if linkages between particular conditions and certain HABs are revealed. Finally, to report on hydrographical or seabed alterations potentially promoting HABs, indicators reflecting these changes (anomalies, inflection points) or special conditions (extreme events, stratification or upwelling indices, residence times, etc.) could be eligible.

3.2 Indicators for HAB state

These indicators parallel those used to assess phytoplankton, but are specialized to address potentially harmful phytoplankton taxa. They also take into account the frequency or probability of their associated occurrence (e.g., seasonal, occasional, potential). The commonly used indicators for phytoplankton and phytobenthos provide information on their composition, structure or functions, as detailed in Supplementary Table S4.

Indicators addressing composition commonly rely on metrics such as presence, abundance or biomass of phytoplankton and phytobenthos taxa, often quantified as the cell counts per volume or weight. For certain toxigenic HABs, the identification to species level is required to differentiate between toxic and non-toxic species within the same genus (e.g., *Alexandrium* and *Pseudo-nitzschia*). However, the mere presence of a HAB species does not necessarily indicate an outbreak, or a toxic event. Moreover, if the HABs anthropogenic origin is inconclusive, the indicator may not suffice to trigger management actions, according to GES4HABs (Figure 1).

The presence and abundance of phytoplankton toxic species are currently reported under various regulatory frameworks such as Food Regulation (EU) 2019/627, Bathing Water Directive, as well as in OSPAR assessments from 2003, 2008 and 2017 (OSPAR Commission, 2003, 2008, 2017). Some Member States also reported data for abundances of noxious taxa, such as *Phaeocystis* spp. and *Noctiluca* spp., under the MSFD, while HELCOM assessments include data on bloom-forming cyanobacteria genera. Most of these abundance indicators have associated thresholds, sometimes established at the national level (e.g., Chorus, 2012; Funari et al., 2015; Serret et al., 2019), which are periodically revised for accuracy and relevance. These thresholds serve as benchmarks for initiating regulatory actions and are adaptable to align with updated scientific knowledge and environmental conditions.

Indicators related to phytoplankton structure include information on the coexistence of different phytoplankton groups. These groups can be structured either taxonomically (i.e., diatoms/dinoflagellates), by size (microplankton, nanoplankton, picoplankton, etc.), based on their pigment signatures (Bustillos-Guzmán et al., 2004; Havskum et al., 2004; Not et al., 2007; Hayward et al., 2023), or according to their functional traits such as autotrophs-to-heterotrophs ratios or ecological assemblages (Nogueira and Figueiras, 2005; Weithoff and Beisner, 2019; Lehtinen et al., 2021; Litchman, 2023). This structuring of indicators offers a multifaceted approach to understanding phytoplankton communities and their ecological roles.

A high variety of multi-metric indices that incorporate phytoplankton community information are utilized in eutrophication assessments, including national WFD reporting (Tett et al., 2008; Devlin et al., 2009; Giordani et al., 2009; Spatharis and Tsirtsis, 2010; Lugoli et al., 2012; Facca et al., 2014; Ní Longphuirt et al., 2019), and HELCOM, OSPAR, or UNEP-MAP assessments. These indices often come with established thresholds and are linked to nutrient levels and other eutrophication pressures.

Finally, indicators focusing on bloom frequency, amplitude, peak, spatial extent, and phenology are rarely used because the high temporal resolution required for phytoplankton data. However, such indicators do exist for variables like chlorophyll *a*.

Chlorophyll *a* (chl-*a*) concentration, due to its ease of sampling and measurement, as well as its correlation with nutrient inputs, is the most used proxy of phytoplankton biomass. While it may be unsuitable for determining the abundance at species level, this indicator can be useful in depicting the extent and frequency of phytoplankton blooms and contextualizing the relation between widespread coastal eutrophication and the increase of HABs (Heisler et al., 2008; Xiao et al., 2019).

3.3 Indicators for HAB impacts

The indicators addressing the impact levels of different HABs should clearly address the corresponding types of impacts they produce (see Supplementary Table S1).

3.3.1 Impacts on ecosystems and marine wildlife

Indicators addressing impacts on ecosystems can only be efficient if the occurrence and extent of HAB events are directly connected with the ecosystem status. On a global scale, there have been numerous wildlife mortality events associated with HABs (Rattner et al., 2022) but only in a few cases, robust evidence of direct causation has been provided (e.g., domoic acid:

Fritz et al., 1992; Work et al., 1993; microcystin: Miller et al., 2010; aetokthonotoxin: Breinlinger et al., 2021). So far, there is no historical evidence of lasting population level consequences associated with persistent HABs (Rattner et al., 2022).

The controlled studies of algal toxin effects in wildlife have focused on acute impacts such as mass mortality events involving marine mammals, seabirds and charismatic megafauna, but far more data and studies are needed to assess the hazard of various algal toxins to wildlife. In this context, diagnostic guidance or protocols (toxic doses, target organs, molecular biomarkers, microscopic lesions, signs of intoxication, etc.) for linking algal toxin exposure to morbidity and mortality of different species or groups, would be a valuable resource to define suitable indicators and thresholds. It is noteworthy that such information (e.g., tissue residues, molecular biomarkers, histopathological lesions, behavioral effects, delineation of various intoxication syndromes) is available for domoic acid and other toxins in marine mammals (Lefebvre et al., 2012; Cook et al., 2015; Broadwater et al., 2018). In the interim, toxin content in water or seafood vectors might be employed to predict risk to wildlife. Analyses of toxins on stranded dead animals or ongoing stomach content analyses for litter assessments [OSPAR Ecological Quality Objective (EcoQO)] could be an opportunity for that.

Using indicators addressing the abundances of some vector species serving as "sentinels" or "bio-indicators" like filter-feeding invertebrates, top predators or confined fishes could also help to support early detection of toxic HAB episodes or record the cumulative effects of their occurrence given their often ephemeral and local frequency (Backer and Miller, 2016).

For eutrophication impacts, some phytoplankton species have also been tested as bio-indicators in the Baltic Sea, due to their positive linear relationship with nutrient concentration (Höglander et al., 2013), e.g., *Cyclotella choctawhatcheeana* and *Cylindrotheca closterium* (Jaanus et al., 2009), and *Planktothrix agardhii* (Carstensen and Heiskanen, 2007).

Impacts on biodiversity may also be caused by high biomass and mucilage/foam producing HABs, by reducing water column oxygenation, light penetration and viscosity inducing mass mortalities to benthic communities and species like gorgonians, corals, and sponges. In these cases, the status of the potentially affected species may be assessed to monitor these impacts (Özalp, 2021).

3.3.2 Impacts on human health

Most of the monitoring and management efforts on HAB impacts are related to human health either by direct exposition or toxic seafood consumption. The European Commission has already established specific laws for the toxin content of bivalves of planktic origin entering the market for human consumption and the marine toxin limits allowed before legal sale [Regulation (EC) 853/2004, 2004]. These regulations are applicable by seafood producers and by food security administrations.

The detection of marine biotoxins in other seafood vectors (rarely covered by the monitoring programs) is already being done in European countries such as Portugal, UK, Croatia and Spain (Ben-Gigirey et al., 2012, 2020; Silva et al., 2013, 2018, 2020; Dean et al., 2020), to prevent further seafood intoxications. For example, the possible presence of PSP toxins in cephalopods, echinoderms and tunicates and the increased interest in the exploitation of marine live resources other than bivalves have promoted a revision of monitoring strategies introducing non-traditional vectors [Regulation (EC) 853/2004, 2004]. These regulations also include the maximum PSP toxin concentrations allowed in echinoderms, tunicates and marine gastropods. However, more studies are needed to evaluate the potential risks they could pose for human health as well as their impacts on food webs. On top of that, more data on the presence of emerging marine toxins in the EU marine invertebrates are also necessary for risk assessment studies on these non-traditional vectors (Ruiz-Villarreal et al., 2022).

The impacts of HABs on human health can also be evaluated as societal costs that in precedent studies (Sanseverino et al., 2016) have focused on medical costs (medical cares and medical investigations) and individual expenses (lost wages, lost vacation time, transportation of patients to the hospital, etc.).

3.3.3 Impacts on socio-economic activities

Indeed, while substantial research is directed toward understanding, quantifying, and forecasting HAB occurrences (HAB state indicators), less attention has been given to understanding, quantifying, and preparing for the socio-economic impacts that these events generate each year (Trainer, 2020). There are some examples of comprehensive assessments of the economic losses due to HABs (including direct and indirect costs) (Hoagland and Scatasta, 2006; Sanseverino et al., 2016; Martino et al., 2020; Karlson et al., 2021). While reasonable estimates are often possible for harvest and job or wage losses associated with decreased yields of seafood products (direct losses), as well as the medical costs associated with acute poisonings (induced losses), other, often much larger costs are more difficult to assess. These include impacts on associated industries, which may turn to alternate sources or activities to partially compensate for HAB-related losses in revenue, changes in seafood availability including losses of subsistence harvest potential, losses in recreational and tourism revenues, and losses of consumer confidence in the safety or quality of the product that undercuts demand and thus the price (Trainer, 2020).

Many articles analyzed the consequences of seafood trade bans at different scales (Basti et al., 2018). Dyson and Huppert (2010) used an Input-Output model to estimate the detrimental impact of beach closures on recreational razor clam fisheries. Díaz et al. (2019) studied the economic loss of the salmon farming industry in South Chile caused by HAB events, where the economic damage was deemed particularly strong in PSP outbreaks. Red tides are also largely studied through their economic impacts on different industries, using monitoring data (Larkin and Adams, 2007). More recently, Theodorou et al. (2020) evaluated the consequences of HAB-related mussel farming site closures in the Mediterranean Sea and concluded that the risk depends on the season (summertime being the most critical) when it occurs, with a limited financial risk at certain non-critical periods. Park et al. (2013) studied the economic impact and mitigation strategies of HABs in Korea, where the aquaculture industry suffered a total

loss of USD $121 million from the early 1980s to the early 2010s, with a predominance of *Cochlodinium polykrikoides* events since 1990. In Southern Europe, Rodríguez Rodríguez et al. (2011) looked at mussel cultivation in Galicia in the presence of red tides. They estimated the correlation between the time length of area shutdowns and the quantity of unsold output. They showed that there was no systematic effect: losses depend on specific market circumstances and authors highlighted the importance of organizational solutions to mitigate commercial risks. More recently, Martino et al. (2020) used a production function to investigate the effect of HABs on the Scottish shellfish market. They showed a significant but non-linear relationship between DSP and shellfish production.

Most of the available studies on socioeconomic losses on tourism caused by HABs are found in the US (Sanseverino et al., 2016). However, indicators like the number of beach closures, the expenditures on foam cleaning or barriers deployments in recreational waters, or the decrease of visitors may be useful to assess these impacts. Some of this information is already collected by public national or European statistical agencies (i.e., EUROSTAT) and/or other stakeholders like civil protection servants. On the contrary, information on damages caused by HABs on infrastructures like pumping systems or desalination plants may be more difficult to gather.

Considering the need for further monitoring and research to fill research gaps and assessment requirements related with HABs (Guillotreau et al., 2021) an evaluation of monitoring costs could evidence the benefits of such investments when compared to the accumulated costs of their negative impacts. Often, when considering the total costs of environmental management, from monitoring to management programs, monitoring costs constitute only a small proportion that becomes even smaller when adding the benefits achieved from efficient management (Nygård et al., 2016).

4 Current and novel monitoring programs and methods

The selection of indicators related to HABs will be highly reliant on the monitoring methods employed (including sampling and analysis procedures), and the required/feasible spatio-temporal extents and resolutions. Anderson et al. (2019) examined several regional programs in the USA, European Union, and Asia and concluded that there is no one-size-fits-all approach.

HABs occur in sunlit pelagic oceans, at the surface or at subsurface in open seas, coastal and upwelling regions and estuaries. Traditional phytoplankton sampling employs discrete *in situ* water samples, collected using Niskin bottles or nets at various depths that are filtered and preserved for laboratory analysis through multiple analytical techniques (Karlson et al., 2010). In their guidelines for monitoring the toxin-producing phytoplankton in bivalve mollusc harvesting areas, Serret et al. (2019) recommend sampling the full range of depths where shellfish are grown.

Non-motile resting cysts of HAB species that settle and accumulate in seabed, are collected using devices like sediment grabs, cores or pumps. Comprehensive guidelines for HABs and cyst sampling can be found in Hallegraeff et al. (2003). Such cysts are often found in finer grain sediments, with low wave and wind exposure like protected harbors and bays. Recent formed cysts are found in the surface sediment layers with progressively older cysts, sometimes, decades older, found with increasing depth.

No standard procedures exist for benthic HAB sampling due to the diversity of substrates that cells grow on (macroalgae, seagrass, sand, pebbles, rocks, coral, and coral rubble). Tracking their growth is challenging due to planktonic/benthic alternation stages and high spatio-temporal variability (Berdalet et al., 2017). Commonly, cells are shaken off the substrates and filtered to collect detached cells (Yasumoto et al., 1980; Hoppenrath et al., 2023). The use of artificial substrate to recruit benthic cells over 24 hours followed by counting as a proxy measurement of benthic HAB species abundance has been recommended (Tester et al., 2014; Jauzein et al., 2016; Mangialajo et al., 2017).

Samples are processed in the laboratory for the identification and abundance quantification of different taxa. Currently, the most prevalent technique employs morphological identification through optical microscopy, conducted by expert microalgae taxonomists. This method is time-consuming, expensive, and limited to identifying larger phytoplankton species (>5μM). Additionally, there is a declining pool of expert taxonomists, further complicating the process (McQuatters-Gollop et al., 2017). In this sense, advanced open international training courses and certificates in phytoplankton taxonomy, such as those organized by the IOC-UNESCO, are essential to promote the availability of qualified taxonomists and interlaboratory intercalibration exercises.

In any case, new approaches for more rapid, cost effective and precise microalgae cell counting and identification are being continuously developed and proposed to support HAB monitoring.

4.1 Analyses for HAB identification and cell abundance estimation

There are extensive reviews for the established detection methods for harmful microalgae found in Anderson et al. (2001), Hallegraeff et al. (2003), and Liu et al. (2022), and detailed methodological guide by Karlson et al. (2010). The described methods include **morphological structure-based detection methods** (optical microscopy, inverse optical microscopy and scanning electron microscopy, automated image identification and classification), **analytical detection techniques** (high-performance liquid chromatography, absorption spectral analysis and fluorescence spectral analysis), **immunofluorescence assay**, immunosensing assay, enzyme-linked immunosorbent assay; and **nucleic acid-based detection** methods (fluorescence *in situ* hybridization, sandwich hybridization assay, polymerase chain reaction techniques, metabarcoding, isothermal amplification technology, and microarrays). Liu et al. (2022) also provided information on the principles, advantages, weaknesses and suitability of these methods for the detection and identification of harmful microalgae.

The **analytical detection or chemotaxonomic analysis** may contribute to study the distribution and composition of different phytoplankton classes with specific pigment signatures (Schlüter et al., 2000; Henriksen, 2002). It is rarely used now for HABs

monitoring as pigment signatures do not specifically relate to taxonomic identity. However, Bustillos-Guzmán et al. (2004) found that 76% and 84% of dinoflagellate and diatom cell density was explained by their specific pigment signature variation suggesting that pigment analysis could be very useful in delineating taxa or potential toxin-producing groups, particularly in combination with remote sensing near real-time or predictive models.

FlowCAM (Sieracki et al., 1998) is an automated identification device that includes a flow cytometer with a camera and a microscope which is widely used in several studies for analyzing fixed and fresh phytoplankton samples both in the laboratory or onboard ships. It is effective at detecting some harmful algae by image, often using an imaging training set (Buskey and Hyatt, 2006). For toxigenic *Alexandrium catenella*, it was shown that mean abundances as defined by FlowCam were comparable to those defined by molecular-probe and microscopy (Ayala et al., 2023). However, it is limited to microscopic-level species distinction. This method is still in development for harmful algae detection, so there is much heterogeneity in methodological reporting (e.g., FlowCam unit, sample preparation, run settings, improved post-processing of images). Harmonized protocols and guidelines are needed to enhance the quality, interpretability, and repeatability of FlowCam results (Owen et al., 2022).

Molecular methods are frequently used for quantifying marine organisms including toxin-producing microalgae via species-specific qPCR/droplet digital PCR (dPCR) methods, or to determine phytoplankton community biodiversity (with metabarcoding or amplicon sequencing methods) (Scorzetti et al., 2009; Pearson et al., 2021). This trend is likely to continue thanks to improved standardization and technological development (Goodwin et al., 2016; Medlin and Orozco, 2017; Jerney et al., 2023), lower sample processing costs, and relatively straightforward sample collection and preservation from water filters (Jerney et al., 2023) or phytoplankton net or sediment samples. Species-specific PCR or dPCR based methods are relatively accurate and sensitive but require specialist knowledge of the relevant species (or toxin genes), and assays (primer pairs) targeting these species (or genes). Extensive public sequence databases exist from Genbank, PR2, BOLD, Midori or Phyto (Murray et al., 2011; Casabianca et al., 2014; Pearson et al., 2021; Yarimizu et al., 2021). Routine monitoring using qPCR or dPCR is already used in the French Atlantic and Mediterranean coasts, the Bay of Biscay, UK, Ireland, the US and New Zealand to provide HAB early warnings (Drouet et al., 2021; Pearson et al., 2021). Metabarcoding methods have also been already widely used to study the dynamics of HAB species and their spatial distribution (Dzhembekova et al., 2022; Gaonkar and Campbell, 2023). Both qPCR/dPCR (Perini et al., 2019) and metabarcoding (Wang et al., 2022) can also be successfully applied to assess the distribution and abundance of toxic dinoflagellate cysts (Perini et al., 2019).

Biosensor technology is applied to all these methods to miniaturize platforms for the detection of multiple targets, for *in situ* rapid detection to increase detection frequency and reduce manual costs (Medlin et al., 2020; Chin Chwan Chuong et al., 2022; McNamee et al., 2023).

Most of the above methods, in addition to the requirement for high-tech equipment and trained staff, depend on (i) the development/availability of ancillary data (like libraries of genes, taxonomic images, or pigment signatures), (ii) powerful algorithms/models to reliably identify microalgae species based on the features analyzed, (iii) standardized protocols or guidelines [e.g., Karlson et al., 2010; U. S. Integrated Ocean Observing System (IOOS), 2017; Serret et al., 2019] and (iv) intercomparisons of results from different methods (e.g. Not et al., 2007; McNamee et al., 2023).

4.2 Analysis methods for HAB toxin detection and quantification

In Europe, an official Standard Operating Procedure (SOP) exists for the determination of several biotoxins in live bivalve molluscs: the amnesic shellfish poisoning toxin (Commission Regulation, 2005), the okadaic acid, as well as some azaspiracids and yessotoxins (Commission Implementing Regulation (EU) No 2019/627), and the PSP toxins ordered by the Commission Implementing Regulation (EU) 2021/1709. The SOP establishes the reference methods to use by official authorities for seafood at any stage of the food chain and for internal checks by food business operators (FBO). These methods were validated under the coordination of the European Union Reference Laboratory for marine biotoxins (EU-RL) in an inter-laboratory validation study carried out by the Member States. However, the recent findings of the presence of emerging azaspiracids, spirolides, pinnatoxins, gymnodimines, palitoxins, ciguatoxins, brevetoxins, and tetrodotoxins in European coastal seas require additional monitoring, analytical guidelines and regulatory guidance to face new potential risks caused by these substances (Otero and Silva, 2022). There are already ongoing activities to develop and validate workflows for the identification and characterization of emergent marine toxins, and the organisms producing them, in environmental samples based on the next-generation sequencing (NGS), shotgun metagenomic sequencing and computational analysis for OneHealth surveillance and food safety risk assessment (García-Cazorla and Vasconcelos, 2022).

Other non-bivalve marine organisms such as echinoderms, tunicates and marine gastropod species may act as toxin vectors in the marine food web (Ben-Gigirey et al., 2020) and have already been responsible for some past poisoning incidents (Costa et al., 2017). Regulation (EC) 853/2004, 2004 stipulates that testing requirements for live bivalve molluscs should apply equally to live echinoderms, live tunicates and live marine gastropods. However, the accumulation of toxins in marine food web is incomplete, and there is still a need to revise which animals act as toxin vectors, and improve recommended guidelines for toxin determination across a wide range of complex variable matrices, including the required sample size and sampling frequency, the highest toxin levels per group, etc.

Emerging studies are also investigating the analysis of concentrations of marine biotoxins in seawater (Bosch-Orea et al., 2021), in aerosols (Ciminiello et al., 2014) and in sediments (Liu et al., 2019) as a toxin reservoir and potential accumulation paths for benthic organisms. Recent advances have been made for portable toxin sensing and biosensing assays for on-site rapid

detection of different chemicals including some marine biotoxins (Sohrabi et al., 2021).

4.3 Automated sampling methods and platforms

Significant progress has been made in the development of automated sampling devices that can increase spatial coverage and frequency of sampling (Boss et al., 2022; Nichols and Hogan, 2022) required for an indicator-based assessment of GES on the number, extent, and duration of HABs.

Automated (discrete or continuous) sampling and sensing technologies can be mounted on scientific survey ships, ships-of-opportunity, moored platforms and buoys, land based, remotely operated aerial and underwater platforms, or in autonomous surface or underwater vehicles (Ruiz-Villarreal et al., 2022).

For instance, the **Continuous Plankton Recorder** (CPR), although originally designed for zooplankton sampling (~270 μm mesh) in 1931, filters 3 m^3 of water that retain high densities of phytoplankton trapped in the mesh (Batten, 2003; Richardson et al., 2006). Although there are very few HAB genera that can be effectively sampled using the CPR, a recent study has demonstrated its value in characterizing changing temporal and spatial patterns of *Pseudo-nitzschia* species using high- throughput sequences from DNA of CPR samples in the North Pacific (Stern et al., 2018). Six decades of data from the CPR have revealed distinct North Sea phytoplankton community events (Bresnan et al., 2013), showing Atlantic-scale decline in harmful dinoflagellates and stable or increasing harmful diatoms, in line with overall dinoflagellate and diatom trends linked to ocean temperature and wind (Hinder et al., 2012). The limitations of CPR data include its collection only of subsurface samples at 4–10 m with poor taxonomic resolution of some harmful algae taxa. However, samples collected by the CPR Survey since 1958 are stored and carefully curated, providing a bank of samples available for future analysis using new and innovative methodologies.

The **MBARI Environmental Sample Processor (ESP)** (Moore et al., 2021) collects and analyses seawater samples to identify the presence of organisms and/or biological toxins. The instrument uses an electromechanical fluidic system to autonomously collect and filter water samples. Then it either preserves and archives the sample for use after the ESP is recovered or directly applies molecular detection technology to investigate the biology of the sample in near real-time. ESP was deployed in the Pacific Northwest to provide near real-time surveillance of growth and toxicity of *Pseudo-nitzschia* (Scholin et al., 2009), as well as *Alexandrium catenella* and Domoic acid by ELISA (Ryan et al., 2011). The ESP device can now be deployed on long-range AUVs for extended spatial sampling and post-collection eDNA sequencing (Truelove et al., 2022).

The **Imaging FlowCytobot (IFCB)** is an *in situ* automated submersible imaging flow cytometer that generates high resolution images of particles in-flow taken from the aquatic environment. An IFCB deployed in Rhode Island has been recently used to generate a daily-resolution time series of *Pseudo-nitzschia spp*. and *Dinophysis spp*. (Agarwal et al., 2023). Other flow cytometers and Imaging Flow Cytometers have been deployed in US (Fischer et al., 2020), Scandinavia (Kraft et al., 2021), Hong Kong (Guo et al., 2021), France, and Scotland (Davidson et al., 2021; Ruiz-Villarreal et al., 2022).

The **Scripps Plankton Camera system**[1] is an underwater microscope with real-time image processing and object detection, A classifier has been developed to find potential HABs. Seven potential HAB formers were detected with an image classifier model (Orenstein et al., 2020).

Autonomous Surface Vehicles (ASVs) or Autonomous Underwater Vehicles (AUVs) encompass a wide range of surface and subsurface platforms but suffer from limited payload space for complex instruments required to process samples although there are some new prototypes proposed for sample collection (e.g., Zhang et al., 2019; Truelove et al., 2022). These ASVs typically include sensors to acquire physical and/or chemical data, and/or aggregated biological variables such chl-*a*, phycocyanin pigments, UAVs can also be equipped with multispectral (Becker et al., 2019) or hyperspectral sensors (Shang et al., 2017), digital cameras (Cheng et al., 2020; Chan et al., 2022) or echosounders (Benoit-Bird et al., 2018). AUVs and ASV have been tested for surficial water sampling in continental and marine waters (e.g., Hanlon et al., 2022; Ruiz-Villarreal et al., 2022). These data can be eligible to support indicators related with some abiotic and biotic pressures on HABs.

However, although very promising for high frequency data, these complex systems have significant constraints related to the acquisition and maintenance costs, staff training, and data management and subsequent data processing notably:

- *In situ* deployed systems may require two or three equipment units for continuous monitoring including maintenance, calibration or training. Land based systems exist, with seawater being continuously pumped with easier access for maintenance (Ruiz-Villarreal et al., 2022).
- Real-time analysis options require a physical link to land (cables) or a wide bandwidth network or radio connection and access to significant data processing capability.
- The sensors onboard these autonomous platforms need to be light (miniaturized) and low power demanding. While performant probes are already available for some physical parameters (Sun et al., 2021) like temperature, pressure, light, and fluorescence (Roesler et al., 2017), challenges remain to produce accurate, long-range, and sensitive data for salinity (Gu et al., 2022), dissolved oxygen (Wei et al., 2019), or pH (Okazaki et al., 2017). Finally, measurement of nutrients is the most challenging to be measured by *in situ* sensors (even when not miniaturized), due to their low stability. Sensors for marine nutrients are classified into colorimetric, optical and electrochemical devices. However, most of these devices present several weaknesses as the low accuracy, short duration, narrow detection concentration range and poor repeatability (Liu et al., 2023), Many novel and higher performance sensors are under development to overcome the above-mentioned weaknesses. For instance, Beaton et al. (2022) propose low-cost nutrient analyzers that during the tested in-field profile

1 https://spc.ucsd.edu/

measurements yielded results comparable to laboratory-based analyses.

Despite all these challenges, technological innovation and product development are advancing very rapidly to make these technologies more reliable and widely accessible to users.

Besides the *in situ* sensing devices, **remote sensing technologies** on board aerial and satellite platforms can also provide useful information for indicators or drivers related to HABs. These include Sea Surface Temperature (SST) from infrared sensors, and ocean-color based products such as chl-*a* and turbidity (Groom et al., 2019; Nichols and Hogan, 2022). These parameters are measured over large areas at higher temporal ranges and frequencies, that can assess temporal dynamics (seasonality, anomalies, extreme events, trends, etc.), and spatial distribution and evolution (i.e., blooms and river plumes extensions). The main limitation of remote sensing is that cloud or ice coverage obscuring image acquisition in some areas and seasons (above all in winter and in northern and equatorial latitudes), and lack of subsurface data. Whilst parameters like SSTs are reliable, the estimation of chl-*a* and other ocean-color metrics are often uncertain in optically complex waters found mainly near the coast. New algorithms and processing methods are continuously being proposed to overcome these difficulties and provide improved products not only for chl-*a* but also for the identification of HAB risk areas. For instance, a web alert system to track the development, magnitude and spread of HABs (*Karenia mikimotoi, Phaeocystis globosa, Pseudo-nitzschia* spp.) in the French-English Channel with satellite data has been developed within the INTERREG-VA FCE project S-3 EUROHAB[2] Preliminary results indicate that HAB risk maps of *Karenia mikimotoi* and *Phaeocystis globosa* from the NASA satellite MODIS-Aqua are comparable to *in situ* cell abundances, whereas the *Pseudo-nitzschia* risk maps are less accurate. Similar studies using satellite data for HAB risk identifications have been proposed for *P. globosa* and *K. mikimotoi* in the southern North Sea and western English Channel (Kurekin et al., 2014), for *Pseudo-nitzschia* in the Galician upwelling area (Torres Palenzuela et al., 2019), for *Karenia brevis* in the Gulf of Mexico (Stumpf et al., 2003; Cannizzaro et al., 2008; Carvalho et al., 2011), for *Cochlodinium polykrikoids* in the Persian Gulf (Ghanea et al., 2016), for diatom blooms in the East China Sea (Tao et al., 2015), and for distinct phytoplankton assemblages (Smith and Bernard, 2019, 2020), and cyanobacterial-dominance blooms (Matthews et al., 2012) in the Benguela upwelling area. Remote sensing data is used for calculating the cyanobacterial bloom index pre-core indicator in the HELCOM region of the Baltic Sea for reporting GES status (HELCOM, 2018).

Besides physico-chemical parameters, other remote sensing products can be useful to support indicators on human print like coastline changes (Murray et al., 2019) or location of aquaculture sites (Themistocleous, 2021) from high resolution true-color images, or vessel densities and fishing effort from Automatic Identification Systems (AIS) (Robbins et al., 2022).

2 https://www.s3eurohab.eu/portal/

4.4 Integrated approaches: models and early warning systems

Many of the above monitoring approaches are often included or complemented in more complete monitoring and research frameworks to integrate information on different biological and environmental features related to HABs. Often this information is integrated in modeling tools than can help to (i) investigate, characterize and quantify the links between different parameters, HABs and their impacts, (ii) discern the contribution of natural vs. anthropogenic causes, (iii) delineate areas with higher risks for HABs based on historical data, (iv) predict, in real- or near real-time, the risk of HABs, and (v) make climatic projections.

There are a multitude of different **model types** and approaches potentially useful to support HAB research and management, such as ecological and food web models, biogeochemistry models, statistical and machine learning models, physical numerical models, Lagrangian particle tracking models, spatial plan models, etc. (Glibert et al., 2010; Fernandes-Salvador et al., 2021). These models can, at different reliability levels, assess areas with the highest risk likelihood of HAB events over short periods, help to optimize monitoring plans (e.g., with less sampling effort in situations of low probability of HABs), assess/manage the compatibility of different marine uses, aid the preparedness for contingency responses, or extrapolate *in situ* observations/indicators within the grid to better depict the spatio-temporal variability of the pelagic habitat (Magliozzi et al., 2023).

Although models can be very practical tools, it is important to bear in mind that they cannot substitute monitoring data, especially when public health is compromised. Models are a form of secondary monitoring that use multiple data sources. Their reliability depends on accurate and representative data for their development and calibration, implementation, and validation.

Ralston and Moore (2020) provide a large review of statistical and process-based models that have been developed for different HAB species in different areas of the world. An example of benthic harmful algae model comes from Asnaghi et al. (2017), using Quantile Random Forests model to predict the concentration of *Ostreopsis ovata* in the Ligurian Sea. Valbi et al. (2019) developed a Random Forest model trained with molecular data to predict the presence of *A. minutum* in the NW Adriatic Sea. Cheng et al. (2021) developed an iterative Random Forests along the California coast to identify phytoplankton abundance and microbial community structure in response to coastal conditions and land-sea nutrient fluxes.

Early warning systems (EWS) incorporate region-specific knowledge of HAB risk, observations and/or models, which are operationalized (nowcast or forecast modes) to provide communication, by an official source, of authoritative, timely, accurate, and actionable warnings on the likelihood of HAB occurrence and the risk of potential HAB-related impacts of concern. These should consider preparedness protocols at all relevant levels to respond to early warnings with timely actions (FAO, 2023).

Different EWS for HABs exist in Europe (Ireland, Scotland, England, France, Spain and Portugal) ranging from weekly bulletins based on expert analysis and identification systems. EWS can

involve particle tracking models and/or remote sensing data (Lin et al., 2021), statistical (e.g., Generalized Additive Models, GAMs) and machine learning models, or mechanistic full-low trophic ecosystem models (Fernandes-Salvador et al., 2021). One such example is ShellEye[3] that combine remote sensing, modeled hydrographic data, local algae and biotoxin modeled data to forecast water quality for Scottish shellfisheries that can benefit science-based development of harmful algae indicators.

Very recently, FAO (2023) published a Technical Guidance for the Implementation of Early Warning Systems for HABs that includes examples of several case studies of HABs and EWSs, but mostly provides a complete roadmap for authorities and institutions in countries or regions to commence building an EWS or expand the existing ones.

4.5 International cooperation, monitoring synergies and data management

The information collected in the former sections evidence that there are already several scientific studies and monitoring programs related to HABs that involve different stakeholders (scientists, regulators, managers, industry, and general public) and organizations (European Commission, EFSA, RSCs, ICES, FAO, IOC, etc.). Nevertheless, the resources and initiatives are still quite disconnected among the three main foci of concern for marine HABs: seafood toxins and aquaculture, cyanobacteria and eutrophication, and recreational water quality. Bridging these areas could serve to optimize monitoring efforts and plans, analysis methods and protocols, and information exchange and maintenance (raw data, indicators and metadata).

So far, collective databases with relevant data for HABs can be found in:

- The IOC-ICES-PICES **Harmful Algal Event Database (HAEDAT)**[4] (Bresnan et al., 2021). Developed in the 1990s it contains more than 8,000 entries on harmful algal events associated with monitoring programmes and *ad hoc* reports from across the globe. It is a part of the IOC International Ocean Data exchange (IODE), and collects, harmonizes, stores and publishes HAB events reported on a voluntary basis by a variety of scientific working groups including the ICES-IOC Working Group on Harmful Algal Bloom Dynamics (WGHABD). The "harmful algal events" considered in HAEDAT must be associated with a negative impact or management action. This information is sensitive to monitoring and reporting effort and efficiency and requires expert interpretation.
- To complement the records of HAEDAT, in 2017, international HAB experts were trained to report on occurrences of toxic algae from scientific publications in the OBIS (Ocean Biodiversity Information System), which now supports **HAB OBIS**[5], a global database with 18,864 harmful algae occurrences reported incorporating databases mentioned in this review. Such data address questions on the probability of change in HAB frequencies, intensities, and geographic ranges. HAEDAT and HAB OBIS data supported the first Global HAB Status Report (Hallegraeff, 2021). While the results and conclusions are likely to be modified as more data become available, these databases encourage reporting and further contribute to these initiatives.
- Databases for **RSCs' assessments** (HELCOM, OSPAR, UNEP-MAP, BSC) collect and harmonize data provided by different contracting parties. These are made publicly available alongside supporting indicators. In addition to the raw data, some regional sea conventions have made progress in harmonizing indicators and assessment metadata and documentation including guidelines for monitoring, analysis, data processing, quality control, and thresholds. Zampoukas et al. (2014) provide details on phytoplankton monitoring programs (among other elements), related to RSCs (HELCOM, OSPAR, UNEP-MAP) and other marine related EU legislation. All the monitoring guidelines of HELCOM are public[6].
- There are currently 120 marine **LTERs (Long-term Ecological Research Sites)** in European seas measuring key microscopic phytoplankton and *in situ* chl-*a* on a regular basis among other environmental parameters. The data collected in these LTERs conform to LTER European data policy, of which one of the guiding principles is to "focus on Open Source products as well as to foster an Open Access policy wherever possible and useful" (Kunkel et al., 2019). As such, LTER data can be of inestimable value also for HAB characterization. Phytoplankton, Zooplankton, ocean hydrography and nutrients for Northern European countries are compiled and available at ICES[7], including historic data.
- The **Coastal and Oceanic Plankton Ecology, Production and Observation Database (COPEPOD)**[8], developed by the US National Marine Fisheries Service provides quality-reviewed, globally distributed plankton (phytoplankton, zooplankton and microbial) data with co-sampled environmental hydrographic and meteorological data. Although it includes 193,696 worldwide observations on phytoplankton since the mid-nineties, it was last updated in 2019 and, moreover, much of the historical phytoplankton data is only qualitative ("absent/present/rare/common"). However, it has the great advantage of discovering many phytoplankton historical surveys and monitored sites and providing time series visualizations of phytoplankton and concurrent environmental conditions. Access to raw data often needs to be requested to contributors.
- **EMODnet Biology**[9] provides open and free access to interoperable data and products on marine species (angiosperms, benthos, birds, fish, macroalgae, mammals,

3 https://www.shelleye.org/

4 http://haedat.iode.org/

5 https://obis.org/node/33dec23c-af65-4fb1-a437-79543c562ef0

6 https://helcom.fi/action-areas/monitoring-and-assessment/monitoring-guidelines/

7 https://www.ices.dk/data/dataset-collections/Pages/Plankton.aspx

8 https://www.st.nmfs.noaa.gov/copepod/about/databases.html

9 https://emodnet.ec.europa.eu/en/biology

reptiles, phytoplankton, zooplankton). It also includes nutrient data. Although EMODNET collects data from different providers (RSCs, research institutes, OBIS, etc.), it also releases maps on the temporal and spatial distribution of species/taxa and species traits in European regional seas.

- Toxin datasets from Food Operators could be very valuable to support assessments and scientific studies beyond their primary objectives for seafood controls especially if combined with phytoplankton counts. In many cases the food operators are reluctant to release these data, especially in real-time, and in some member states toxin data is not available. These hampers investigations linking harmful algae and toxin production. Moreover, toxins are not measured by agencies during the closing periods for cost reasons and because public health is already guaranteed. As a result, information on new appearing toxins, toxin maxima values or detoxification kinetics is not available.
- Phytoplankton and toxin data reported for the BWD in bathing waters with HAB risks are made publicly available through different national portals on recreational water quality.

Besides the effort needed to collect HAB related data, it is important to think on coordinated work for finding common data models and formats, distribution mechanisms and repositories, metadata content (quality controls, lineage, authorship, etc.) and formats, etc. All these best practices should be in line with the Open Science and FAIR (Findable, Accessible, Interoperable, Reusable)[10] principles meant to optimize the reuse of data. To meet these demands, the data management efforts should benefit from the participation of professional data management and IT experts, and sustained resources to ensure the good continuity of these collaborative initiatives.

Minelli et al. (2021) concluded from their study on open access to research projects and data that, despite the initial and still existing mistrust, it is more than just a best practice because it improves the transparency of research (thus increasing the credibility of researchers, the reproducibility of science and the re-use of products), supports many international initiatives and regulations, and encourages collaboration between scientists from different fields and laboratories. However, the (re)use of these data in a regulatory context needs to be carefully evaluated for relevance and reliability, ideally by using the same criteria for the different studies producing them (Brock et al., 2021).

5 Conclusions and recommendations to move forward

HABs (like pests or storms) are natural phenomena, but their changing patterns are often a reflection of an ecosystem alteration. Therefore, HABs cannot be eliminated, but only prevented or mitigated. While conventional management focuses on mitigating local impacts, a shift toward EBMAs is essential to prevent to some extent and counteract HAB crises more effectively and cost-efficiently.

10 https://www.go-fair.org/fair-principles

The MSFD stands as a milestone in ecosystem-based marine management in Europe, with the aim of achieving GES. Despite its holistic approach and two concluded reporting cycles, HABs have so far received limited attention from Member States (Palialexis et al., 2014; Tornero Alvarez et al., 2023). However, current efforts aim to build on the lessons learned from the WFD and the two reporting cycles of the MSFD, and to promote best practices for integrating HABs into MSFD assessments, recognizing their relevance to marine ecosystems and socio-economic issues.

To improve HAB monitoring, assessment, and management, we have developed new tools and compiled several key recommendations.

5.1 Local tailored solutions with harmonized best practices

There are many different cases of HABs, with different impacts on socio-economic and/or ecosystem components and triggered by different and often combined causes. Therefore, there is no one single solution for the assessment and management of marine HABs in different affected areas, and specific tailored solutions are needed.

Indeed, most of the proposed phytoplankton indicators for eutrophication are site-specific due to the heterogeneous response of marine phytoplankton to nutrient loads and the different monitoring approaches used by Member States. This heterogeneity poses a challenge for comparing results across regions (Garmendia et al., 2013), as demonstrated in the WFD intercalibration exercise (Poikane et al., 2014), where only chl-*a* was found suitable for biomass-based indicators in coastal and transitional waters by most member states (European Commission, 2018).

However, this does not preclude the need for international and cross-sectoral coordination to (i) share knowledge and data, and (ii) define harmonized or standardized best practices to support joint large-scale assessments and synergistic and optimized strategies. These best practices may relate to monitoring programmes, monitoring methods, analysis protocols, indicator metrics, assessment methods, data management and flows, division of responsibilities, etc.

5.2 Monitoring needs for better understanding HABs, their causes and their impacts

Although the understanding of HABs has increased rapidly over the last two decades, there are still many gaps in our knowledge of their specific causes, toxicity triggers, frequency, extent, duration, impacts on biodiversity, etc.

To meet these knowledge needs, sustained long-term monitoring programmes with appropriate strategies are essential. Monitoring of HABs should have appropriate temporal, spatial and taxonomic resolution, and the spatial distribution of monitored areas should be designed/adapted to avoid: (i) over-representation bias due to the concentration of monitoring sites (e.g., in aquaculture areas), and (ii) spatial gaps in under-monitored areas with potential risk of HABs. The data generated must be long-term

(10-year horizon), quality controlled and stored according to international data and metadata standards.

In addition to the detection of HABs, sustained monitoring efforts will enable the establishment of baselines of environmental factors and biodiversity components, the rate and extent of environmental change, the detection of hazards and environmental disturbances, and the estimation of recovery times.

Traditional methods of monitoring HABs, involving *in situ* sampling and taxonomic identification and cell counting in laboratories, are currently the best available option but remain costly, time-consuming and inadequate for the vast geographical scope of the MSFD. New technologies are being developed to provide more cost-effective solutions, such as genomic methods, automated samplers, remote sensing, early warning systems, artificial intelligence models, etc. The future use of the results of these novel techniques will need to undergo intercalibration processes in order to be reliably used in the assessment and management processes (Stauffer et al., 2019).

5.3 Integration with the MSFD framework

To consider the principles of the MSFD, this study proposes a GES4HABs decision matrix to assist MSFD reporters in deciding whether to include HABs in the MSFD and adopt management decisions. Within this process, the MAMBO matrix helps to distinguish between manageable and unmanageable circumstances around HAB outbreaks. If HABs are found suitable for inclusion in the MSFD assessment cycles, then the full assessment procedure should be engaged. In this context, it is extremely important to identify, demonstrate and quantify the links between HABs, the pressures causing them and their impacts on public health and on the different components of the ecosystem and socioeconomic activities, and to select the most appropriate indicators and thresholds to reflect these links. This remains an important prerequisite for targeting the best management measures to effectively reduce the occurrence of HABs and their impacts.

To date many of these management measures proposed by European environmental instruments (like MSFD, WFD, ND, UWWTD, etc) have focused on nutrient reduction objectives but have largely overlooked measures to counter habitat degradation in coastal areas. This oversight contributes to the simplification of European coastal habitats and ecosystems, allowing harmful algal blooms to persist.

5.4 International and cross-sectoral cooperation to increase synergies and optimize resources and efforts

Cooperation fora and roles need to be better defined to integrate new knowledge on different HABs and scale up from multiple national assessments to regional or global observing system for HABs (Anderson et al., 2019). To this end, the complementarities between the resources and organizations currently dedicated to HAB management (food safety and public health authorities, environmental managers, scientific organizations, food producers, marine spatial planners, etc.) should be closely examined to build bridges of cooperation, avoid duplication, optimize efforts, and focus new resources to fill the identified gaps.

5.5 Preparedness and anticipation for adaptability and sustainability of ecosystems

Although the general perception of a global increase of HABs needs further and more refined substantiation (Hallegraeff et al., 2021), the rapidly changing environmental conditions due to climate change and the expansion of the human footprint in European coastal and marine waters strongly support the need to actively intensify efforts toward ecosystem based management strategies that although complex and challenging can provide solutions to avoid increasing vulnerability to future changes, and reinforce our preparedness and anticipation capacities for adaptability.

Author contributions

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Conflict of interest

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

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Supplementary material

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Management of jellyfish outbreaks to achieve good environmental status

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Jellyfish and gelatinous zooplankton (GZ) in general, fulfill important ecological roles with significant impacts, although they are often oversimplified or misunderstood. This paper reviews the impacts, pressures, monitoring methods and current management strategies for various GZ groups. It also introduces potentially applicable indicators for their assessment in ecosystem-based management approaches, such as the European Marine Strategy Framework Directive (MSFD). This multi-faceted review is primarily envisioned to serve as a state-of-the-art document for scientists and policymakers to foster a holistic assessment and management of GZ across European regional seas. The systematic review on global impacts of GZ shows a notable increase in the number of studies since the early 2000s. Stings were the main cause of human health impacts. Mechanisms that impact biodiversity included direct predation, modification of trophic flows or competition for resources. Several GZ taxa may be beneficial to biodiversity acting as biological regulators and provide societal ecosystem services such as food provision or medical applications. The systematic review on monitoring techniques outlined a variety of methods, such as nets (the most common technique), continuous plankton recorder (CPR), polyp and jelly-fall monitoring, acoustic methods, remote aerial and underwater imaging, molecular methods, and citizen science. Furthermore, several currently employed management strategies were enumerated, including the use of anti-jelly nets, bubble curtains, chemical compounds, or the introduction of GZ predators. This study highlights the pressing need for enhanced GZ-dedicated monitoring, assessment, and anticipatory management of GZ populations to address future GZ crises more effectively and

cost-efficiently. Moreover, exploring GZ ecosystem services unveils opportunities to harness marine resources while mitigating adverse effects, thereby supporting sustainable blue economies.

KEYWORDS

Cnidaria, Ctenophora, pelagic tunicates, impacts, monitoring, ecosystem based management approach (EBMA)

1 Introduction

The term "jellyfish" collectively encompasses gelatinous zooplankton (GZ) from diverse metazoan taxonomic groups, including Cnidaria (cnidarian jellyfish or medusozoans: the planktonic life stages of Hydrozoa, Scyphozoa and Cubozoa), Ctenophora (comb jellyfish), and pelagic Tunicata (e.g., larvaceans, salps, and doliolids) (Boero, 2013; Jaspers et al., 2023). GZ can exhibit complex life cycles. Several medusozoan species frequently comprise an alternation or coexistence of asexual (often benthic) polyp and sexual medusa stages (Russell, 1953, 1970). Non-metazoan gelatinous organisms are not considered here.

Jellyfish have long been associated with stinging risks to bathers and adverse impacts on diverse socioeconomic activities at sea (Bosch-Belmar et al., 2021b; Lee et al., 2023). In recent years, there seems to be a public perception of a global increase of jellyfish outbreaks, which is often attributed to climate change. This perception is enhanced by media reports portraying historically documented jellyfish outbreaks as novel phenomena (e.g., mass fish kills in the UK and Ireland caused by *Pelagia noctiluca* outbreaks). However, there are few long-term data and insufficient reference baselines to substantiate this claim (Condon et al., 2012) and the available long-term data document large fluctuations without understanding the underlying causes (see Decker et al., 2023).

It is now scientifically acknowledged that gelatinous zooplankton play a vital role in marine ecosystems and may provide a range of benefits to humans (Doyle et al., 2014; Graham et al., 2014; Culhane et al., 2019; Jaspers et al., 2023). However, despite their importance, the ecological roles of GZ are often grossly oversimplified or misunderstood, and GZ taxa remain poorly monitored compared to other zooplankton groups (Templeman et al., 2021). Managers limit resources for monitoring GZ based on the assumption of their unpredictable nature (Aubert et al., 2018) and some monitoring difficulties, such as sample damages during collection, preservation difficulties, or scarcity of taxonomic expertise on surveys.

Currently, jellyfish management is mainly focused on responsive control and mitigation of local impacts (Dong, 2019). Nevertheless, as marine ecosystems continue to be altered by climate change and human activities, and the abundance and frequency of some GZ species increases in some coastal waters (Brotz and Pauly, 2012; Lee et al., 2023), approaches such as ecosystem-based management strategies can help anticipate GZ outbreaks, rather than simply respond to emergencies, which have greater costs and societal impacts (Brodeur et al., 2016).

In Europe, the Marine Strategy Framework Directive (MSFD, European Commission, 2008), marked a significant milestone in adopting an ecosystem-based management approach for sustainable supply of marine goods and services across Europe. The initial MSFD's objective was to achieve Good Environmental Status (GES) in European seas by 2020 (now, by 2026) (European Commission, 2020). Implemented through a 6-year adaptive management cycle, the MSFD includes assessing the status of the marine environment and its essential features, analyzing their predominant pressures and impacts, and considering economic and social aspects of sea use (Art. 8 MSFD, European Commission, 2008). For assessing the status of European Seas, determining GES (Art. 9 MSFD), environmental targets and associated indicators (Art. 10 MSFD), leads to the development of monitoring programs (Art. 11 MSFD), and programs of measures (Art. 13 MSFD) to maintain or restore GES (Palialexis et al., 2021).

In 2010, the Joint Research Centre - MSFD Task Group 4 on Food Webs recommended assessing the abundance and distribution of key taxa with fast turnover rates, such as jellyfish. These taxa can serve as early warning indicators of food web functioning in response to environmental changes (Rogers et al., 2010). Despite this recommendation, GZ were almost absent in the 2012 and 2018 assessment reporting cycles (Tornero Alvarez et al., 2023). Nonetheless, past and ongoing initiatives continue to propose "cost-effective" monitoring and assessment strategies and tools to include GZ information in MSFD assessments (Aubert et al., 2018; Magliozzi et al., 2021, 2023).

This study reviews the main impacts, pressures, and management options described in the literature, as well as current and upcoming monitoring methods and indicators applicable to assess GZ. This paper aims to serve as a practical state-of-the-art document for scientists and policymakers to foster the assessment and management of GZ across European regional seas and contribute to the achievement of GES.

2 Methods

This work includes one traditional literature review based on comprehensive, critical, and objective analysis of the current knowledge for pressures, indicators, and management sections, and three systematic literature reviews for the sections on impacts and monitoring techniques. The systematic reviews followed the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (Moher et al., 2009) and the detailed search criteria were the following ones:

For the **systematic review on impacts**, the search string used, combining keywords, Boolean operators and wildcards, was: (*"gelatinous *plankton" OR jellyfish OR cnidaria* OR scyphozoa* OR hydrozoa* OR cubozoa* OR medusozoa OR medusa* OR ctenophor* OR salp* OR tunicat* OR thaliacea* OR appendicularia**

OR doliolid OR urochordat* OR siphonophor*) AND (impact* OR effect* OR consequence* OR damag* OR loss OR sting OR econom*) AND (bloom* OR outbreak* OR swarm* OR proliferation* OR aggregation* OR accumulation* OR "mass occurrence").* The search was conducted on the 5th of April 2023, it was limited to the title, abstract, and keywords, and was not restricted by publication year. The initial search yielded 2,382 and 1,378 articles from Scopus and Web of Science online databases, respectively (Supplementary Figure S1). Screening of additional publications identified by experts or within the references of assessed articles or reviews was carried out (n = 151 articles). Following the removal of duplicate entries, 2,596 articles remained for the initial screening stage. Four reviewers assessed the articles for eligibility and inclusion in the second-stage full-text screening, based on the titles and abstracts. Inclusion criteria was based on a GZ relative population level being assessed for potential negative impacts on biodiversity, ecosystem services or human health at global scale, without any geographical restriction. Exclusion criteria included the manuscript's language (only English, Spanish, Italian, Portuguese, Greek, or French were considered), and the publication type encompassing only published research documents with primary evidence of GZ impacts. Review studies that did not provide primary knowledge on impacts were removed to prevent the inclusion of duplicate records of impacts. It is important to note that all relevant review articles underwent full-text screening, and additional relevant references missing in the literature search were added for screening. To ensure inter-rater reliability, the reviewers independently evaluated a randomly selected sample of 50 retrieved articles, subsequently discussing any discrepancies. This validation process involved the four participant reviewers of the first stage screening. The first stage screening of title and abstract for eligibility against the inclusion criteria resulted in 306 articles selected for the second stage full-text screening (the full process can be tracked in PRISMA flow diagram Supplementary Figure S1). In this subsequent phase, eight reviewers were engaged in examining the full text of retrieved articles to determine their eligibility and extract pertinent information from the included studies. Finally, 212 articles were included for data extraction and 94 articles were excluded as they did not meet the above-mentioned inclusion criteria.

The relevant information extracted from the selected articles included: (1) year of publication; (2) marine realm and province (based on Spalding et al., 2007); (3) species identified as having an impact; (4) type of evidence classified into six categories (Katsanevakis et al., 2014): manipulative or natural experiments, experiments, direct observation of impacts, modeling, non-experimental based correlations, and expert judgment (definitions of each type of evidence category are provided in Supplementary Table S1), (5) mechanisms of impacts on biodiversity, ecosystem services, and human health, (6) magnitude of the impact on biodiversity categorized as minimal, minor, moderate, major, or massive according to Blackburn et al. (2014) (definitions of each magnitude category are provided in Supplementary Table S2), and (7) any indication of benefits from GZ.

For the **systematic review on monitoring methods**, the search string used was: (*"gelatinous *plankton" OR jellyfish* OR cnidaria* OR scyphozoa* OR hydrozoa* OR cubozoa* OR medusozoa OR medusa* OR ctenophor* OR salp* OR tunicat* OR thaliacea* OR appendicularia* OR doliolid* OR urochordat* OR siphonophor*) AND (monitor* OR survey* OR sampl* OR detect*) AND (bloom* OR outbreak* OR swarm* OR proliferation* OR aggregation* OR accumulation* OR "mass occurrence"*). The search was implemented on Scopus and Web of Science online databases, covering peer-reviewed literature from 2008 (year of the MSFD publication) to 20th April 2023. The initial search yielded 1,113 and 665 articles from Scopus and Web of Science online databases, respectively (Supplementary Figure S2). Screening of additional publications identified by experts was carried out (n = 8 articles). Following the removal of duplicate entries, 1,171 articles remained for the initial screening stage. Three reviewers assessed the articles for eligibility to be included in the second-stage screening, based on title and abstract. The inclusion criteria applied was based on (1) the mention of GZ identification techniques; and (2) the use or development of monitoring tools. Exclusion criteria considered (1) the specific language of the manuscripts (only English, Spanish, Italian, Portuguese, Greek, or French were considered), (2) publication type and (3) if monitoring method referred to modeling approach to forecast GZ occurrence, not to a direct and currently applied technique for monitoring. Each reviewer independently evaluated a third of the total articles, and subsequently the other two reviewers checked for agreement/disagreement with the original decision and discussed any discrepancies. This validation process occurred during various virtual meetings involving the three reviewers. After the first screening regarding the appropriateness of each article to be included as a monitoring technique paper, 282 articles were selected for the second-stage screening. In this subsequent phase, eleven reviewers were engaged in examining the full text of retrieved articles to determine their eligibility and extract pertinent information from the included studies. Ultimately, 212 articles were included for data extraction.

An additional **systematic search was performed specifically for monitoring on medusozoan polyps**. In this case the search string was: (*polyp* OR scyphopolyp* OR cubopolyp* OR scyphistoma*) AND (monitor* OR survey* OR sampl* OR detect*) AND ("gelatinous *plankton" OR jellyfish* OR cnidaria* OR scyphozoa* OR hydrozoa* OR cubozoa* OR medusozoa OR medusa*).* The initial inventory of 291 (Scopus) and 181 (Web of Science) papers published from 2008 to 19th June 2023 was reduced to 302 after removing duplicates (Supplementary Figure S3). These papers were consecutively screened by title, abstract and full text by three reviewers, resulting in 73 articles that mentioned marine polyp identification techniques (excluding freshwater species and benthic hydrozoan), the use or development of monitoring tools, and were written in English, Spanish, Italian, Portuguese, Greek, or French. Out of these, 72 articles were selected for the second-stage screening. In this subsequent phase, four reviewers were engaged in examining the full text of retrieved articles to determine their eligibility and extract pertinent information from the included studies. Ultimately, 19 articles were included for data extraction.

From both sets of selected articles on monitoring techniques, relevant information was retrieved, including: (1) year of publication, (2) survey temporal coverage (year/month), (3) survey

spatial coverage (country, site name, geographical coordinates, and marine realm and province, based on Spalding et al., 2007), (4) monitoring methodology used, (5) GZ species considered, (6) monitoring objectives, and (7) results related to stressors present in the area of GZ proliferation, predictions, geographical or phenological changes, abundance/biomass (and units used), outbreak periodicity, and shifts in species composition.

The list of articles obtained in the three searches, as well as the row data extracted are publicly available as Supplementary material (see Data availability statement). The figures were created using the open-source software R 3.6.0 (R Core Team, 2020) and the "ggplot2" package (Wickham, 2016).

3 Results

3.1 Impacts caused by gelatinous zooplankton

Most adverse impacts caused by GZ on maritime activities and ecosystems result from mass occurrences that can range from small, localized spots to large patches detectable for kilometers. GZ aggregations can form due to passive drift by wind or currents, or because of active swimming, by which they form swarms, often in association with sudden population increases or "outbreaks" (Alldredge, 1982; Hamner and Dawson, 2009). The high reproductive and growth potential for outbreaks is observed in a limited number of Cnidaria genera, belonging to the Rhizostomeae and Semaeostomae scyphozoans, in hydrozoans (Hamner and Dawson, 2009; Fernández-Alías et al., 2021; Leoni, 2022), in some ctenophore species (Jaspers et al., 2018a; Shiganova et al., 2019), and in most pelagic Tunicata (Jaspers et al., 2023). In cases of highly venomous species (e.g., *Chironex fleckeri*, *Physalia physalis*), only a few individuals may adversely impact human health (e.g., Lippmann et al., 2011; Cegolon et al., 2013).

The systematic review on global impacts of GZ revealed that most of the studies were conducted in the temperate Northern Atlantic (57%) (Figure 1A). The number of studies on negative GZ's impacts notably increased after the early 2000s (Figure 1B). Most of these studies focused on GZ's impacts on biodiversity, food provision, or human health, and few addressed impacts on recreation and tourism, ocean nourishment and water storage (Figure 1C). The term "biodiversity" is used hereby in accordance with the definition of "biological diversity" proposed by the Convention on Biological Diversity (CBD, 1992) and taken up in the MSFD - Task Group 1 report (Cochrane et al., 2010).

Impacts on biodiversity and ecosystem services were investigated mostly in the northern European Seas and the Mediterranean Sea (Figures 2A, B). GZ were frequently reported to impact aquaculture facilities through both stings (Baxter et al., 2011a; Bosch-Belmar et al., 2016a,b, 2017; Marcos-López et al., 2016; Powell et al., 2018; Mitchell et al., 2021) and disease transmission to farmed fish (Ferguson et al., 2010; Delannoy et al., 2011; Clinton et al., 2021). Impacts on human health were less frequently reported and mostly found along temperate and tropical coasts. Stings were the primary cause of human health impacts, and only three articles identified GZ as potential vectors of pathogens (Basso et al., 2019; Stabili et al., 2020, 2022) (Figure 2C).

Among the species frequently cited for negative impacts on biodiversity, *Mnemiopsis leidyi* ($n = 28$ articles), *Aurelia aurita* ($n = 19$), and *P. noctiluca* ($n = 10$) were the most prominent. For impacts on ecosystem services, the most cited species were also *P. noctiluca* ($n = 15$), *A. aurita* ($n = 15$), and *M. leidyi* ($n = 6$). In contrast, impacts on human health were mainly associated with *P. physalis* ($n = 11$), *P. noctiluca* ($n = 9$), *Carukia* spp. ($n = 9$), *C. fleckeri* ($n = 6$), and *Rhopilema nomadica* ($n = 4$). Fatal cases involved mostly box jellyfish, such as *C. fleckeri* (Currie and Jacups, 2005), but also scyphozoans, such as *Nemopilema nomurai* (Fenner and Williamson, 1996; Kim et al., 2018). A detailed enumeration of the reported species associated with different adverse impacts is included in Supplementary Table S3. It is important to note that some GZ taxa are formed by a complex of cryptic species, often misidentified and typically referred to as a single, most popular species (e.g., the moon jellyfish *A. aurita*; see Scorrano et al., 2017; Lawley et al., 2021; Moura et al., 2023).

Impacts on biodiversity were suggested to be caused through various mechanisms, such as direct predation (Yilmaz, 2015; Wang et al., 2020; Báez et al., 2022; Vineetha et al., 2022), modification of trophic flows (West et al., 2009b; Dinasquet et al., 2012b), competition for resources (Lynam et al., 2005; Báez et al., 2022), transmission of pathogens (Basso et al., 2019; Stabili et al., 2020, 2022), reduction of light penetration (Zaitsev, 1992; Stoner et al., 2014), behavioral changes of species in order to avoid GZ (Carr and Pitt, 2008; Chittenden et al., 2018), and envenomation (Helmholz et al., 2010) (Figure 3A). "Modification of trophic flows" (Dinasquet et al., 2012a; Tiselius and Møller, 2017) may occur through indirect predation (Schneider and Behrends, 1998; Dinasquet et al., 2012a; West et al., 2009a), accumulation of decaying organic matter (i.e., *jelly-falls*) (Tinta et al., 2012; Chelsky et al., 2016: Dunlop et al., 2018; Lebrato et al., 2019), and mucus and nutrient excretion altering abiotic parameters such as nutrients and oxygen concentrations (West et al., 2009b; Condon et al., 2011; Dinasquet et al., 2012b; Manzari et al., 2015; Marques et al., 2021).

Most studies on GZ impacts on biodiversity drew conclusions primarily from non-experimental correlations (39%), followed by manipulative experiments and expert judgment (both 20%), direct observations (16%), and modeling (5%) (Figure 3B). Hence, the strength of evidence was low for a substantial portion of the reported impacts.

Stronger evidence provided by manipulative experiments demonstrated impacts on biodiversity through predation or modification of trophic flows (Sullivan and Gifford, 2004; West et al., 2009a; Dinasquet et al., 2012a,b; Pereira et al., 2014; Zoccarato et al., 2016; Wang et al., 2020). *Aurelia aurita* and *M. leidyi* were the most frequently studied species through manipulative experiments (7 and 6 studies respectively). Other mechanisms of impacts on biodiversity, such as competition were primarily reported through non-experimental correlations, modeling and expert judgment.

Concerning GZ effects on ecosystem services, manipulative experimental studies revealed impacts on farmed fish (Baxter et al., 2011b; Bosch-Belmar et al., 2016a,b; Powell et al., 2018) and alterations in nutrient cycling and carbon flow (Chelsky et al., 2016; Sweetman et al., 2016; Tinta et al., 2016). Additionally, studies based on direct observations addressed GZ impacts on fishing (Kim et al., 2012; Mianzan et al., 2014; Conley and Sutherland, 2015; Diciotti et al., 2016; Mghili et al., 2022), aquaculture (Ferguson et al., 2010;

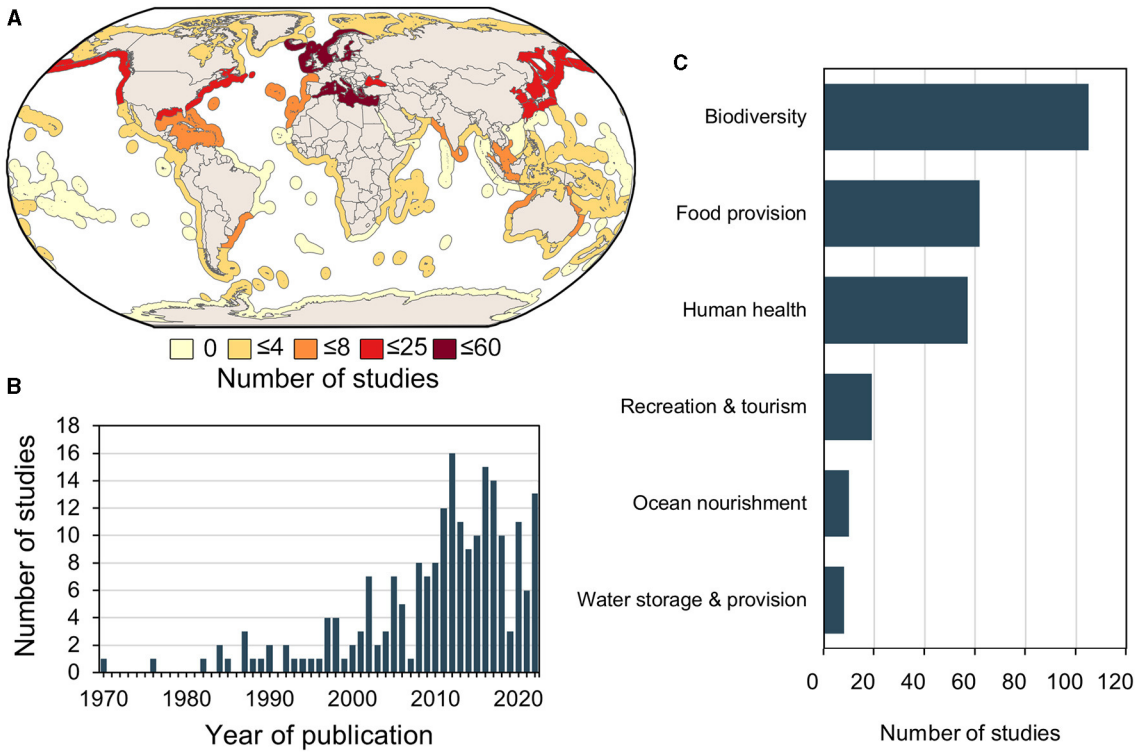

FIGURE 1
(A) Spatial distribution of studies investigating negative impacts of gelatinous zooplankton (GZ) on biodiversity, ecosystem services and human health, **(B)** number of studies published per year investigating GZ impacts, and **(C)** number of studies investigating GZ impacts on biodiversity, ecosystem services categories (food provision, recreation and tourism, water storage and provision, and ocean nourishment) and human health.

Marcos-López et al., 2016; Mitchell et al., 2021), and desalination and coastal power plants through clogging or ingress (Mianzan et al., 2014; Graham et al., 2014; Angel et al., 2016; Kumar et al., 2017).

According to the categories of the magnitude of the impact on biodiversity *sensu* Blackburn et al. (2014) (see Supplementary Table S2), "moderate" impacts inducing population declines in other species (e.g., though predation on copepods, pteropods, rotifers, cladocerans, chaetognaths, hydromedusae, or fish larvae and eggs) were prevalent ($n = 77$ reports) and followed by "minor" impacts ($n = 43$). "Major" impacts resulting in the local extinction of at least one prey species were less abundant ($n = 21$) and "massive" impacts have not been documented for GZ species. "Minimal" impacts were infrequently reported in the literature ($n = 11$), although this category may be under-represented, as non-significant results are less likely to be published (Jennions and Møller, 2002).

Probably one of the most notable examples of a "major" impact is the invasion of *M. leidyi* in the Black Sea in the mid-1980s, causing significant reductions in zooplankton abundances, primarily by predation (Shiganova, 1998), as documented for other invaded areas as well (e.g., Riisgård et al., 2012). This intense predation caused changes in the community structure of the Black Sea, with some species becoming virtually absent (Zaitsev, 1992; Shiganova, 2005). However, in the late 1990s, a new non-indigenous species (NIS) of ctenophore, *Beroe ovata*, was introduced in the Black Sea. This species preyed exclusively on GZ including *M. leidyi*, leading to reductions of *M. leidyi* population densities (Finenko et al., 2003). Since then, impacted species have been recovering (Finenko et al., 2003; Shiganova, 2005). The reduction of other ecosystem pressures, such as eutrophication and fishing pressure, along with changes in large-scale atmospheric conditions, also contributed to the changes observed in the Black Sea food web (Bilio and Niermann, 2004).

Therefore, GZ can have positive impacts on biodiversity: they are an important food source for various top predators and threatened species like sea turtles, birds and fish (Cardona et al., 2012; Jarman et al., 2013; Mianzan et al., 2014; Sato et al., 2015; Smith et al., 2016; Hays et al., 2018; Thiebot and McInnes, 2020; Jaspers et al., 2023) and some species can act as biological regulators of invasive species, such as the arrival of *B. ovata* in the Black Sea (Shiganova et al., 2001; Finenko et al., 2003; Bilio and Niermann, 2004). Additionally, certain GZ species, especially scyphomedusae provide shelter and trophic resources to juvenile fish, thereby improving their survival rates (Lynam and Brierley, 2007; Masuda et al., 2008; Mianzan et al., 2014; D'Ambra et al., 2015; Tilves et al., 2018). In some quite exceptional cases, GZ may also play a role in maintaining water quality and preventing dystrophic crises through a top-down control process (Pérez-Ruzafa et al., 2002, 2019; Fernández-Alías et al., 2022).

Furthermore, GZ can provide several societal ecosystem services (Doyle et al., 2014; Leone et al., 2015). Up to 35 species of jellyfish have been reported to be consumed by humans (Brotz et al., 2017). For millennia, GZ (mostly scyphomedusae) have been

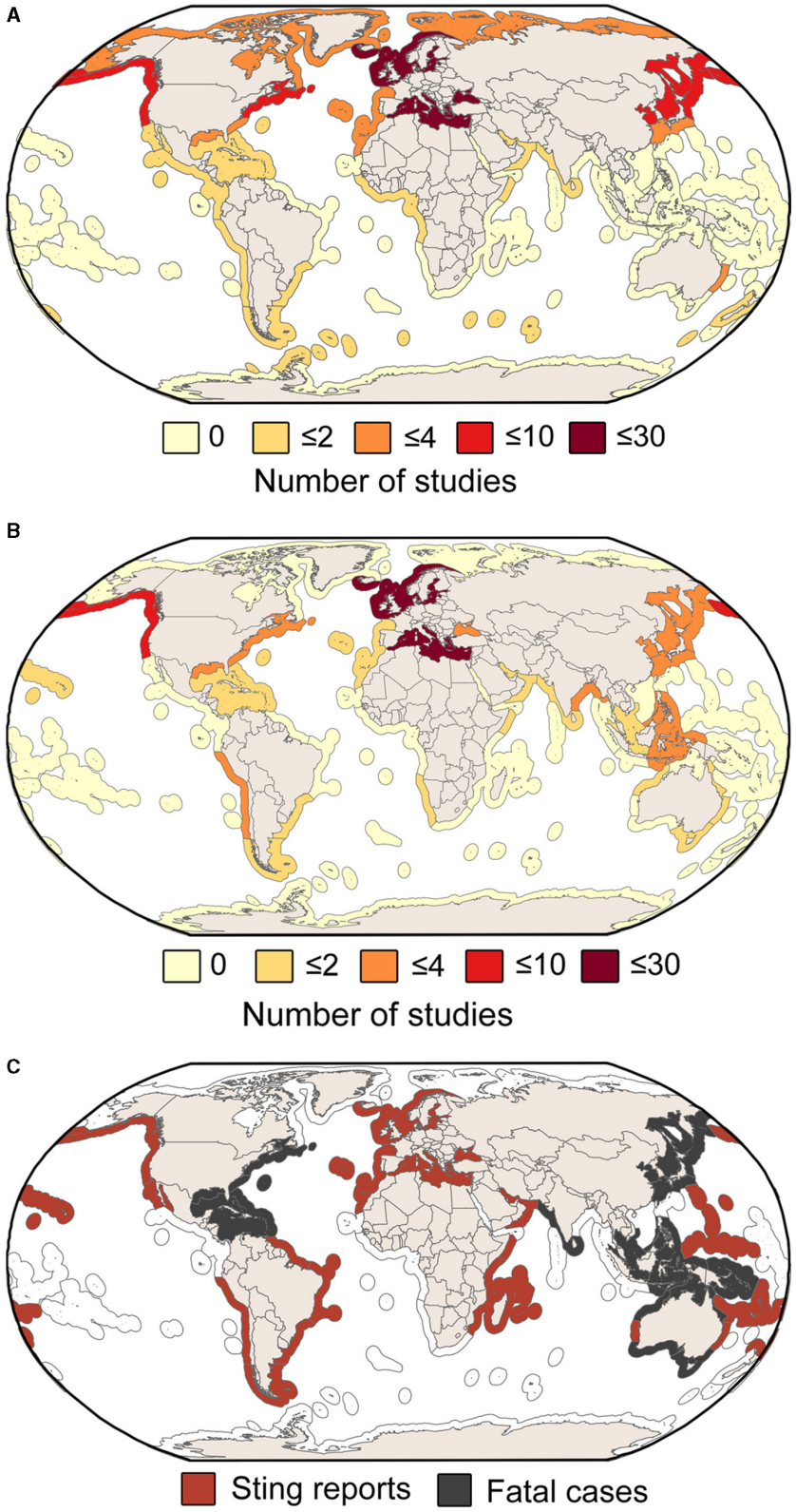

FIGURE 2
Spatial distribution of studies investigating gelatinous zooplankton impacts on **(A)** biodiversity and **(B)** ecosystem services. **(C)** Marine provinces where stinging events were reported from the retrieved studies and fatal cases.

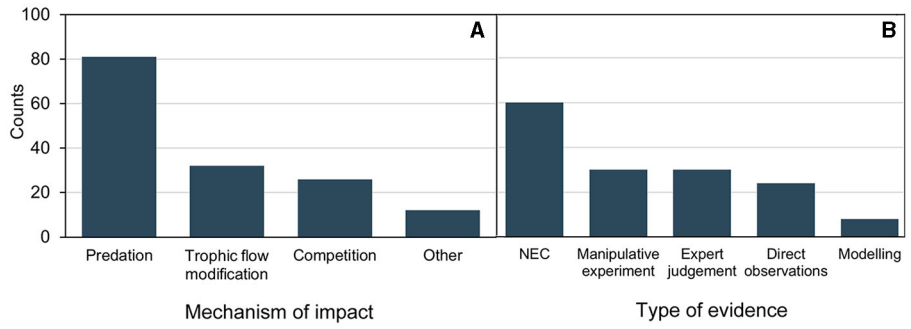

FIGURE 3
(A) Counts of the reported mechanisms of impacts of gelatinous zooplankton (GZ) on biodiversity. "Other" includes reduction of light penetration, disease transmission, envenomation, and behavioral changes to other species. **(B)** Counts of types of evidence for the reported impacts of GZ on biodiversity. "NEC" stands for non-experimental based correlations.

consumed in Asia, where they are considered delicacies (Omori and Nakano, 2001; Brotz and Pauly, 2017; Syazwan et al., 2020) and recently, there has been growing interest in Western countries considering jellyfish as a sustainable food resource (Brotz et al., 2017; Pedersen and Vilgis, 2019; Ramires et al., 2022a,b). Since the 1970s−80s there have been attempts to establish *Stomolophus meleagris* fisheries in the United States (Page, 2015), and in Mexico (Cruz-Colín et al., 2021), mainly where commercial fishing crises occurred due to overfishing of finfish and shrimps. However, the product was primarily exported to Asia, due to low consumer acceptance and neophobia in western countries (Torri et al., 2020), as well as its health- and cost-effective processing (Brotz, 2016; Raposo et al., 2022). In Europe, several species have the potential to support jellyfish fisheries (Brotz, 2016; Brotz et al., 2017; Bleve et al., 2019; Leone et al., 2019; Youssef et al., 2019; Edelist et al., 2021; Duarte et al., 2022; Raposo et al., 2022). The target species are particularly large-sized Rhizostomeae, with low stinging potential and recurring annual blooms, such as *Rhizostoma pulmo* and *Rhizostoma octopus*. In the absence of significant consumption, jellyfish have been labeled as "novel foods" under the current European regulation (European Union Regulation 2015/2283) and some innovative processing tests have already yielded new patented jellyfish-based foods that overcome the limitations of traditional Asian processes (Bleve et al., 2019, 2021; Leone et al., 2021; Ramires et al., 2022a,b). Jellyfish harvesting from by-catch of finfish fisheries may also offer novel resources to diverse industries and economic activities, as organic fertilizers (Hussein et al., 2015; Emadodin et al., 2020; Borchert et al., 2021), insecticides (Yu et al., 2005, 2014, 2016, 2021), animal feed for terrestrial or aquaculture farming (Miyajima et al., 2011; Wakabayashi et al., 2012; Liu et al., 2015; Duarte et al., 2022), or bait for fishermen (Mianzan et al., 2014).

GZ may also provide important biomaterial for medical applications and research (Ahn et al., 2018; Rastian et al., 2018; Widdowson et al., 2018; Felician et al., 2019). In the early 1900s, Charles Richet won the Nobel Prize in Medicine for his groundbreaking research on anaphylaxis, uncovered by studying *P. physalis*. From the serendipitous discovery of green fluorescent protein (GFP) in the hydromedusa *Aequorea victoria* (Shimomura et al., 1962), the biotechnological potential of cnidarians started to attract the attention of researchers for their well-documented ability to produce venoms (Turk and Kem, 2009). Other bioactive compounds obtained from various GZ species have been examined for their antioxidant, anticancer, antihypertensive, and antimicrobial properties, suggesting potential use in the pharmaceutical sector (Leone et al., 2013, 2015; Amreen Nisa et al., 2021; De Rinaldis et al., 2021; Ranasinghe et al., 2022; De Domenico et al., 2019, 2023). Furthermore, in the fields of biotechnology and biomedicine, GZ biomass has been explored for designing cell-scaffold devices to address non-healing skin wounds (Nudelman et al., 2019; Fernández-Cervantes et al., 2020).

Other GZ provisional services, include the contribution to the aquarium trade (Duarte et al., 2022), and more recently GZ material was proposed as a potential alternative for replacing fossil-based plastics (Steinberger et al., 2019). Moreover, it has been proposed that cnidarian GZ mucus might be used as bio-flocculation material for trapping and sequestrating plastic micro- and nanoparticles from contaminated waters of factories (Patwa et al., 2015; Lengar et al., 2021) and wastewater treatment plant effluents (Ben-David et al., 2023).

Further, pelagic tunicates, especially salps (Décima et al., 2023) and larvaceans (Jaspers et al., 2023) as well as cnidarian jelly-falls (Lebrato et al., 2019) have a significant capacity to fuel carbon sequestration, highlighting a crucial role amidst the ongoing climate crisis.

3.2 Potential pressures causing gelatinous zooplankton outbreaks and aggregations

Attributing GZ outbreaks to specific causes, whether natural or anthropogenic, is often challenging and accompanied by uncertainty (Lee et al., 2023). Increases in GZ populations appear often to be influenced by a combination of human activities, which might interact synergistically to trigger outbreaks of certain species (Richardson et al., 2009). A critical review by Pitt et al. (2018) contended that there was weak evidence that anthropogenic stressors trigger GZ outbreaks, because such claims were mostly based on two highly invasive (and often cryptic) taxa (*A. aurita* and *M. leidyi*) and relied on correlative investigations or circumstantial evidence that cannot establish causation (e.g., Duarte et al., 2015). However, the increase of human activities and uses of the marine

ecosystems suggests, that regardless of "natural" global increases of GZ populations, their interactions with human activities are expected to increase, particularly in coastal waters (Gibbons and Richardson, 2013).

Several GZ have specific functional attributes that enable them to thrive in disturbed marine ecosystems and capitalize on ecological opportunities presented by anthropogenic activities. These include a broad diet (Purcell, 1992; Lilley et al., 2009; Fleming et al., 2015; Nagata et al., 2015), rapid growth rates (Marques et al., 2015; Jaspers et al., 2023), tolerance of harsh conditions (Purcell, 2012), or the ability to shrink and channel body carbon into reproduction during food-shortage to keeping up high reproduction rates (Lilley et al., 2014; Jaspers et al., 2015).

Various human-related causes of GZ outbreaks have been reported in the literature (Supplementary Table S4):

- **Overfishing**. The removal and decline of fish populations, which compete with certain carnivorous GZ for prey or predate on them, has allowed certain GZ taxa to exploit available resources more effectively and has led to abnormally large and long-lasting outbreaks of some jellyfish in certain areas (Lynam et al., 2006; Richardson et al., 2009; Boero, 2013). These declines may be reversible if new ecological components control these outbreaks or if the fishing pressure is reduced (Daskalov et al., 2007).
- **Eutrophication**. It has been hypothesized that excessive nutrients from fertilizer runoff and sewage into coastal waters, rich in nitrogen and phosphorus but poor in silica, promotes the dominance of non-siliceous phytoplankton, such as flagellates, and can create conditions that are more suitable for certain GZ than for fish to thrive. Various reasons have been suggested for this. Some GZ have the ability to feed on these protists directly (e.g., Parsons and Lalli, 2002; Richardson et al., 2009); further, GZ are reported to be more competitive than other metazoans including finfish to thrive under hypoxic conditions, that often occur in eutrophic environments (e.g., Purcell et al., 2001; Breitburg et al., 2003; Purcell, 2012).
- **Climate change**, with its associated sea surface warming, altered water column stratification, and increased climate variability, can also influence GZ population dynamics (Boero et al., 2016; Jaspers et al., 2023; Lee et al., 2023). Increased sea surface temperatures can create more favorable conditions for GZ by favoring their prey abundances (Jaspers et al., 2023) and/or accelerating their growth (Purcell, 2005). Fernández-Alías et al. (2021) showed that large species living in temperate, shallow waters appear to have a high outbreak potential, with temperature appearing to be the main environmental factor regulating the onset of population outbreaks, and food availability, enhanced by bottom-up eutrophication, being key to maintaining large biomass. Furthermore, the expansion of venomous tropical jellyfish species to subtropical and temperate latitudes due to warming, poses potential threats to the colonized ecosystems and local economies.
- **Species translocation**. The human-assisted movement of species in new marine regions through ballast water exchange, fouling on ship hulls, aquaculture, and the opening of corridors connecting previously isolated seas (such as the Suez Canal) has translocated many outbreak forming GZ species such as the hydrozoans *Blackfordia virginica* (Marques et al., 2017), *Maeotias marginata*, *Nemopsis bachei* (Nowaczyk et al., 2016), or *Gonionemus vertens* (Marchessaux et al., 2017) which can reach remarkably high abundances and cause significant ecosystem impacts on invaded habitats. Although we are still far from understanding the true number of NIS of gelatinous zooplankton, especially small sized hydrozoan jellyfish species, examples of non-indigenous GZ in European waters include *R. nomadica* (Galil et al., 1990; Spanier and Galil, 1991; Deidun et al., 2011) and *Cassiopea andromeda* (Mammone et al., 2021; Cillari et al., 2022) in the Mediterranean Sea, *G. vertens* in the northern European coasts (Marchessaux et al., 2017) as well as multiple independent invasions of *M. leidyi* into other European seas (Jaspers et al., 2018b, 2021).
- **Habitat modification**, such as an increase in suitable benthic habitat, either natural or artificial (ocean sprawl), could contribute to the proliferation of jellyfish polyps by providing additional substrates for polyp attachment and growth (Duarte et al., 2013).

3.3 Management measures and strategies

Despite the numerous and heterogeneous known impacts of GZ outbreaks and the studies dedicated to identifying their triggering causes, current GZ management strategies are based on reactive strategies that primarily focus on controlling and mitigating the adverse impacts caused by cnidarian jellyfish populations at local scales (Lucas et al., 2014; Dong, 2019). Their main objective is to reduce health risks and loss of revenue for the affected coastal and marine activities (Ghermandi et al., 2015). Some of the control methods that are used nowadays are enumerated below.

Jellyfish cutters are used in Japan and Korea to remove aggregated jellyfish like *Nemopilema* spp. or *Aurelia* spp. (Kim et al., 2013; Lucas et al., 2014). However, cutting and/or grinding jellyfish do not affect their distribution at sub-surface depths and do not consider the powerful regenerative property of cnidarians such as *Aurelia coerulea*, able to produce new polyps even by few cell debris (He et al., 2015). **Jellyfish-excluding devices** for towed fishing gears (Matsushita and Honda, 2006) have been developed to prevent GZ from entering nets, reducing their bycatch and adverse impacts on fisheries. First adopted in Australia to protect beachgoers against envenomation from lethal cubozoans, **anti-jellyfish nets** are nowadays broadly used throughout the Mediterranean Sea (Piraino et al., 2016) to create enclosed areas for safe swimming and maintain tourism appeal (Ruiz-Frau, 2023). The effectiveness of these nets demands specific design, material and installation procedures (mostly standardized by patents) as well as monitoring and maintenance services, even requiring rapid intervention to remove the nets when required. Other solutions like **protective covers, mesh screens, and bubble screens** are used in the aquaculture industry to safeguard fish production, and in power stations and desalination plants to protect the cooling and pumping systems from GZ infestations (Verner, 1984; Ratcliff, 2004; Lucas et al., 2014; Haberlin et al., 2021).

Chemical compounds are also used for antifouling ship paints to inhibit polyp settlement and attachment in aquaculture facilities and other artificial structures (Guenther et al., 2009, 2010; Feng et al., 2017, 2022). **Introducing natural polyp predators**, like nudibranchs, to habitat areas can also help control some GZ populations with a benthic life-stage such as most cnidarian jellyfish species (Hernroth and Gröndahl, 1985; Hoover et al., 2012). Here, recruitment is reduced and thereby the frequency and intensity of population outbreaks.

Operational early warning systems (EWS) are being developed to inform coastal users about potential GZ presence or predict the outbreak probability or intensity for certain noxious species. EWS may be based on hydrodynamic models, real-time observations, remote sensing techniques and/or unmanned aerial vehicles (UAVs) allied with high resolution imagery and effective image analysis algorithms or deep learning technology (Aznar et al., 2017; Mcilwaine and Casado, 2021; Edelist et al., 2022; Han et al., 2022; Zhang et al., 2023). EWS may also benefit from recent scientific advancements on environmental DNA (eDNA) for detecting rare but life-threatening species (Bolte et al., 2021). EWS are currently employed to detect outbreaks of GZ species such as *N. nomurai* (Uye, 2008; Lucas et al., 2014) *Cyanea purpurea, R. pulmo, Phacellophora camtschatica, Agalma okeni, A. aurita, Phyllorhiza punctata*, and *Rhopilema esculentum* (Gao et al., 2023).

Public education and awareness (i.e., **ocean literacy**) on different GZ groups and their associated risks can also play a significant role in mitigating the impacts of GZ outbreaks on public health and tourism (Gershwin et al., 2010; Lucas et al., 2014). In addition, collaborative **citizen science** approaches (Boero, 2013) involving trained personnel, volunteers, social networks, and media may contribute to gather data on GZ and enhance public engagement (e.g., Pikesley et al., 2014; Gatt et al., 2018; Marambio et al., 2021; Dobson et al., 2023; Levy et al., 2024).

Ecosystem-based strategies including different GZ taxa are uncommon, even though integrating the multifaceted linkages between GZ, human activities and other ecosystem components may help to prevent or reduce outbreaks of harmful GZ species (Lynam et al., 2006; Richardson et al., 2009; Brodeur et al., 2016; Bastardie et al., 2021; Edelist et al., 2021). This is evidenced by the example of the Benguela upwelling region, where historically similar ecosystems (in terms of their structure, species communities, and functions) followed different trajectories after the collapse of small pelagic fish stocks in the 1960/70s. In the northern Benguela system (Namibia), the prolonged absence of fishing regulations after the collapse of stocks, combined with changing environmental conditions, led to the domination of GZ in the mid-trophic level and the depletion of small pelagic fish abundance. In contrast, in the southern Benguela system (South Africa), catch limits and management measures for small pelagic fishes prevented overfishing and succeeded to maintain their ecosystem dominance (Roux et al., 2013).

3.4 Indicators to include GZ in the MSFD's assessments

The MSFD is an ecosystem-based management approach adopted by the European Commission to attain GES across European Seas. In practice, GES is assessed through eleven thematic descriptors and associated criteria related to different ecosystem components (state) and pressures (European Commission, 2017). European Union (EU) member states or Regional Sea Conventions are required to determine indicators and associated thresholds consistent with GES achievement in their marine reporting units. Moreover, the 6-yearly reports must assess the cumulative effects of pressures and social and economic costs of environmental degradation (Tornero Alvarez et al., 2023).

GZ have been considered minimally in the 2012 and 2018 reporting cycles, even though GZ are frequently regarded as sentinels of marine ecosystem health (Schrope, 2012; Lee et al., 2023), offering diagnostic insights to interpret changes across the food web, including higher and lower trophic levels (Bedford et al., 2018). To introduce GZ component in MSFD, an initial assessment would be required to (i) define appropriate indicators and associated thresholds for different GZ taxa and areas, (ii) differentiate between anthropogenic and natural factors driving GZ outbreaks and aggregations ("pressures"), (iii) identify impacts and services of GZ in the ecosystem, and (iv) devise relevant management actions to mitigate/prevent their harmful effects where practical. Such analysis is pivotal for designing and implementing effective monitoring programs that aid GZ-related assessments and establish a robust scientific foundation for crafting efficient management strategies to attain GES. In this holistic approach, various MSFD descriptors (D) and criteria may be of relevance to assess GZ state, their pressures and impacts (see Supplementary Table S5).

The MSFD indicators should include, as a minimum, a measure of the ecological state of an ecosystem component to evaluate change over time (e.g., abundance or biomass of different GZ groups, or the frequency of occurrence of their aggregations). In addition, to understand the changes on GZ populations in the ecosystem, indicators related to the relevant natural and anthropogenic pressures are required (Ndah et al., 2022). Many pressures are already captured in MSFD and regional biodiversity assessments, including temperature increase due to climate change, fishing effort, seabed and hydrological changes, nutrient and contaminant levels and change in the base of the food web through primary production metrics. However, indicators of direct pressure(s) favoring GZ (e.g., provision of artificial settling habitat for polyp stages of cnidarian jellyfish; Duarte et al., 2013) should be included to develop efficient mitigation measures and identify risk of expansion (Foster et al., 2016). Similarly, a measure of GZ as a pressure and their impacts on the ecosystem (e.g., losses in fisheries, aquaculture, or energy generation) would be useful to inform managers of the scale of their effects (Abdul Azis et al., 2000; Doyle et al., 2008; Uye, 2008; Quiñones et al., 2013; Ghermandi et al., 2015; Kennerley et al., 2022).

A few indicators including GZ have been considered in current European biodiversity assessments: the Oslo/Paris Convention's Intermediate Assessment (OSPAR, 2017; Holland et al., 2023a), the Helsinki Commission's coreset of indicators (HELCOM, 2018) and the Black Sea Commission's report on the "State of Gelatinous Plankton" (BSC, 2019) were delivered to assist contracting parties when reporting to the MSFD. While OSPAR, BSC and HELCOM have each developed indicators for NIS, only the BSC mentions GZ explicitly. However, HELCOM acknowledged that GZ were an

important group missing from the indicator: "Trends in arrival of new non-indigenous species" (HELCOM, 2018).

Recently, specific metrics for GZ have been proposed by OSPAR as part of the indicator "Changes in Phytoplankton and Zooplankton Communities" (Holland et al., 2023a; Magliozzi et al., 2023). This indicator is used within MSFD descriptors on pelagic habitats (for D1) and food webs (D4) and adopts the Phytoplankton Community Index approach of Tett et al. (2008). This indicator relies on the concept of "lifeforms" or multiple unrelated taxa that are considered to share a similar functional role within their ecosystem (e.g., primary producers, grazers or carnivores). Once the abundance or biomass of the lifeform groupings are determined from sample data, the ratios of specific pairs of lifeforms are used to evaluate the energy or mass flow through trophic pathways in marine food webs (McQuatters-Gollop et al., 2019; Holland et al., 2023a,b). For GZ, two lifeform pairs indices are considered: (1) GZ vs. fish larvae/eggs and (2) Crustaceans vs. GZ (Supplementary Figure S5). In each case, GZ are considered as a predator (of crustacean plankton and of fish eggs and larvae) directing energy away from fish populations. However, GZ outbreaks may also result from (rather than cause) ecosystem degradation, and metrics of GZ abundance have been proposed as a potential indicator of ecosystem instability (Lynam et al., 2011).

Unfortunately, these assessments are still supported by very little monitoring data on GZ, with all species of Cnidaria and Ctenophora currently grouped together as "Gelatinous zooplankton." Data for GZ were available to OSPAR (2017) from a single sampling site within the western Channel ("L4," Atkinson et al., 2021) and was improved for OSPARs Quality Status Report 2023 (Holland et al., 2023a), with an additional station off north-western Scotland (Loch Ewe) (see Supplementary Figure S5), a station off eastern Scotland (Stonehaven), and Swedish data for the Kattegat and Norwegian Trench in the eastern North Sea. However, these GZ data were insufficient to support additional analyses to determine key environmental pressures (Holland et al., 2023a,b).

In light of the aforementioned considerations and in anticipation of forthcoming assessments, we consider the following to be potentially useful indicators related to GZ:

Pressure indicators driving change in GZ:

- Indicators of water-mass dynamics (e.g., Ndah et al., 2022).
- Provision of artificial habitat (e.g., Duarte et al., 2013; Foster et al., 2016).
- Sea surface temperature and eutrophication (in shallow coastal waters) (Fernández-Alías et al., 2021).

Potential change of state indicators for GZ:

- Estimation of episodic and/or seasonal GZ outbreaks and aggregations as an early warning indicator of climate effects on the marine environment (Van Walraven et al., 2013, 2015).
- Frequency of occurrence of GZ in stomach contents samples of predators (e.g., Smith et al., 2016).
- Polyp presence and abundance in coastal habitats (lagoons, marinas) (e.g., Van Walraven et al., 2016).

Impact indicators due to GZ outbreaks:

- Frequency of occurrence of GZ supporting foraging grounds of dependent predators like leatherback turtles (Houghton et al., 2006).
- Economic losses in fisheries (e.g., Uye, 2008; Quiñones et al., 2013), aquaculture (e.g., Doyle et al., 2008), and coastal desalination or energy installations (e.g., Abdul Azis et al., 2000).
- Social impact indicators, such as number of bathers requiring medical attention due to jellyfish stings (De Donno et al., 2014), or beach closures and loss of tourism (Ghermandi et al., 2015; Kennerley et al., 2022).

The precise selection and definition of GZ-related indicators including their specific metrics, variables and threshold values, remains a pending and challenging exercise which must consider practical aspects, such as feasible/required sampling and analysis capabilities, temporal, spatial, and taxonomic resolutions of underlying data, capacity to reflect pressures-state-impact linkages, inter-indicator connections (Dale and Beyeler, 2001; Niemeijer and De Groot, 2008; Marques et al., 2009; Magliozzi et al., 2023), accumulated uncertainties (Racault et al., 2014), and the potential for pan-European intercomparison and harmonization (European Commission, 2017; Magliozzi et al., 2023). These requisites will heavily rely on the monitoring programs and techniques to be implemented to support the assessment process.

3.5 Current monitoring programs and techniques and new alternatives

Presently there is a growing demand for cost-effective and innovative monitoring approaches to improve research on GZ and integrate them into the MSFD assessment and management framework (Magliozzi et al., 2021, 2023). Technological advancements have introduced new techniques for monitoring GZ outbreaks and aggregations, including sampling approaches more suitable to study these fragile animals.

The findings of our systematic review on monitoring programs and methodologies for GZ are described hereafter.

- **Nets:** WP2 and Bongo nets are the most widely used GZ monitoring tools. They are particularly suited for small, abundant hydromedusae, scyphozoan ephyra and calycophoran siphonophores. Different sampling gears provide complementary insights in GZ populations studies (Hosia et al., 2008; Purcell, 2009). Fish trawl nets are also employed, mainly for sampling larger and more robust gelatinous species (Purcell, 2009). In Europe, night-time ichthyoplankton work conducted during fisheries trawl surveys have been proposed as a cost-saving approach to support GZ monitoring (Aubert et al., 2018). Here, ichthyoplankton sampling gear such as MIK-nets can quantitatively assess the gelatinous macrozooplankton community (Aubert et al., 2018; Køhler et al., 2022). However, these depth integrated nets have the disadvantage of underestimating fragile gelatinous organisms that may break during collection. In addition, true abundances may be underestimated if species are present at very low abundances and low water volumes are processed. Other nets such as MOCNESS or MultiNets may be alternatives for sampling

discrete depth strata where GZ are known to accumulate (e.g., Haraldsson et al., 2013).

- The **Continuous Plankton Recorder (CPR)** is a continuous surface monitoring method (Lynam et al., 2011) that can detect outbreaks of both meroplanktonic and holoplanktonic hydrozoans and scyphozoans. For instance, outbreaks of *P. noctiluca*, recorded by the CPR off Ireland in October 2007, were confirmed by net tows and visual examination (Baxter et al., 2010; Licandro et al., 2010), suggesting that CPR can provide reliable information for identifying regions and periods favorable for GZ outbreaks. The main limitations of this technique are the inability to sample complete specimens of GZ larger than the aperture of the CPR which is only a few centimeters in size, and the difficulties to preserve the GZ morphology, except for rigid calycophoran siphonophores (Gibbons and Richardson, 2009), impairing their taxonomic identification at species level. However, preserved samples can be used for re-analysis and genetic studies (Kirby et al., 2006; Licandro et al., 2010). CPR devices can be mounted on ships of opportunity, enabling periodic surveys covering extensive spatial and temporal scales.
- **Polyp monitoring:** Polyp monitoring ranks as the third most frequently reported monitoring method. Despite their crucial role in cnidarians outbreaks, polyps remain the least known stage in the cnidarians' life cycle, and field investigations of this stage have only recently gained attention. Among Scyphozoa and Cubozoa species (the most conspicuous GZ), 5% are holopelagic, 32% have a benthic stage, whilst the life cycle of the remaining 63% is unknown (estimated from Jarms and Morandini, 2019).

  We observed that polyp species detection in nature is not in accordance with increasing sampling efforts. In only 18.6% of species with benthic stage, polyps have been observed in the natural environment (i.e., 16 of 86 species), with the genus *Aurelia* and *Chrysaora* accounting for almost the half (44%) of these observations (Cargo and Schultz, 1966; Hartwick, 1991; Kikinger, 1992; Dawson et al., 2001 and references in Supplementary Table S6 for reports after 2008). Polyp monitoring and research efforts encompass density estimations, ephyrae production, and the identification of suitable substrates (e.g., Miyake et al., 2002; Van Walraven et al., 2016). In the few occasions when polyps have been observed, monitoring of this benthic stage is usually carried out through visual surveys by SCUBA divers or by employing underwater cameras for recording (Supplementary Table S6).
- **Visual counts:** Although GZ monitoring based on visual observations from ships ranks as the fourth most frequently reported method in the review, this approach is inherently biased toward species of detectable size and relatively straightforward taxonomic identification present on the surface during daytime. Monthly visual surveys from boats have been successfully implemented to monitor five jellyfish species for several years in Irish/UK waters, showing where aggregations tend to occur (Bastian et al., 2011; Purcell, 2012). Additionally, for certain remarkable (dangerous or visually striking) species, visual counts from ferries (Yoon et al., 2018), or boats used for beach surveillance, cleanup, or touristic activities (such as whale watching, birdwatching, and coastal tours) can serve as early warning systems to manage bathing and/or fishing areas and support educational initiatives respectively. In recent years, visual counts have gradually been substituted by aerial and underwater imagery and videos. Visual counts are also sometimes used to ground truth other data collected through other monitoring techniques.
- **Acoustic methods:** Underwater acoustic devices like single-beam and multibeam echosounders, scanning sonars and, hydrophones, have been used in several studies for detecting GZ presence, tracking their movements and vertical diel migrations, and estimating their abundance in the water column (e.g., Han and Uye, 2009). In the past, the use of acoustic systems to detect GZ was disregarded because of their high-water content, resulting in a very low-density contrast at the water–body interface. However, several studies have demonstrated that different species of gelatinous plankton can generate significant levels of sound scattering (Brierley et al., 2005) even at low sound frequencies (38–50 kHz; Colombo et al., 2003). These methods enable faster and broader coverage surveys (including the water column and nighttime), providing continuous count data along transects and accompanying environmental data. Moreover, the acoustic characterization of GZ aggregations from previous recorded acoustic cruises for fish abundance assessment have proved to be valuable in identifying and reconstructing historical scenarios of their abundance and their potential impact on ecosystems (Colombo et al., 2003). However, implementing these methods requires substantial efforts to ground truth species identifications and density estimates, staff training, labor-intensive data processing as well as equipment investment. Acoustic equipment can be mounted on fixed mooring platforms (e.g., for monitoring pumping facilities) on board scientific vessels, or in UAVs and remotely operated vehicles (ROVs).
- **Aerial remote images:** Satellite imagery, aerial photography, and video recording from piloted aircraft or drones are increasingly employed for GZ monitoring. Whereas drones, UAVs, and ROVs may include optical sensors with sufficient resolution for GZ detection, **aerial and satellite platforms** should be equipped with very high resolution or hyperspectral sensors to support GZ monitoring. However, even though this seems to be a straightforward approach, sea state, cloud cover and data processing are major obstacles. Moreover, customized signal processing algorithms must be developed to enable the detection and/or counting of GZ aggregations from the acquired imagery (Raoult and Gaston, 2018; Schaub et al., 2018), e.g., JellyX and JellyNet (Mcilwaine and Casado, 2021). Satellite data from multispectral and infrared sensors are often used to provide environmental data that can be incorporated into GZ prediction models, habitat suitability maps, and early warning systems. An example of this approach can be seen in the multi-platform study of the extreme outbreak of the barrel jellyfish *R. pulmo* in the Gulf of Trieste in April 2021 (Reyes Suárez et al., 2022).

  UAVs and drone platforms allow the collection of larger datasets in less time than those acquired during boat-based

surveys and can also monitor species that are delicate to sample with nets. However, this method requires a sound knowledge of the species present from net-based surveys, as images are often not good enough to allow for species identification. Also, UAVs access is limited, and deployments are costly. Drones could facilitate high spatial coverage (Hamel et al., 2021), however, their usage is constrained by factors such as flight duration, local flight operation regulations, and environmental conditions such as rain and wind speed (Mcilwaine et al., 2022). In addition, remote image quality can degrade due to foggy conditions, sun-glint, or high-water turbidity (Hamel et al., 2021).

Other remote sensing methods such as **airborne LiDAR** have been used to describe the vertical distribution of GZ in the water column (Churnside et al., 2016). However, it is important to keep in mind that some GZ actively modify their position within the water column. For the ctenophore *M. leidyi* it has been shown that sea state and turbulence conditions impact their vertical position, where animals avoid surface waters during high wind speeds (Jaspers et al., 2018b). Furthermore, **electronic tags** have shown that the large scyphozoan jellyfish *R. octopus* spent <10% of their time at the surface (Hays et al., 2012). This data was then used by Elliott et al. (2017) to apply a correction factor to their aerial surface estimates of *R. octopus* abundance.

- **Citizen science:** Active participation from the public in collecting GZ data offers a valuable opportunity to cover larger coastal areas that would be costly or impractical to cover through scientific projects (Marambio et al., 2021; Edelist et al., 2022; Gueroun et al., 2022). However, this information must be verified by experts or requires prior training of the participating volunteers to ensure the quality required for scientific studies, putting a high maintenance demand on this kind of data generation. In addition, data collection often suffers from spatial and temporal bias, as more data is obtained from popular sites during high season for easily detectable species. Therefore, it is advisable to include local communities such as schools, diving or sailing clubs into data acquisition programs and to not restrict these programs to summer seasons and short-term projects.
- **Underwater images and automatic count systems:** Underwater photography and video recording systems (Cillari et al., 2022) acquired by scuba divers (Gibbons et al., 2021) or by underwater platforms like ROVs, AUVs or underwater video profilers (UVPs) (Biard et al., 2016), can facilitate quantitative evaluations from long-lasting and spatially extensive surveys. However, they can bias local fauna's behavior by causing species to escape. In contrast, static systems that are quickly accepted by resident fauna can collect information over longer periods, albeit with lower spatial coverage than mobile systems. Utilizing camera systems in conjunction with computer vision algorithms enables real-time detection and counting of GZ, reducing observer bias and enhancing monitoring efficiency (Gao et al., 2023). Furthermore, specialized bathyphotometer cameras have been employed for the observation and analysis of bioluminescence signals in salps (Melnik et al., 2022).
- **Molecular genetic methods:** The advancement of DNA barcoding, mitochondrial and nuclear DNA and RNA facilitate species detection, including GZ (Créach et al., 2022). Quantitative real-time PCR (qPCR) has also been used to identify GZ by tracing eDNA (Bayha and Graham, 2009; Marques et al., 2019). This emerging method enables the analysis of water and sediment samples to detect extracellular DNA or associated to dead cells (Torti et al., 2015; Minamoto et al., 2017; Ogata et al., 2021). Molecular techniques are limited to detecting the presence or absence of taxa and cannot estimate abundance variability. However, they increase the likelihood of species detection and, in some cases, reduce the time and costs compared to other monitoring and sampling methods. Moreover, marine eDNA is preserved for only 1 day in water, whereas it can persist for at least 1 year in sediments and could therefore be useful to reconstruct past occurrences (Ogata et al., 2021). Furthermore, these techniques can be applied to analyze the gut content of potential GZ predators, contributing to food web characterization (Smith et al., 2016).
- **Jelly-falls monitoring:** Elevated gelatinous biomass may translate into increased transfer of this organic material to the seafloor, providing a food supply to benthic fauna. Monitoring the presence and fate of GZ carcasses has been conducted using various techniques, including sediment traps, photography and video systems, and trawling nets (e.g., Lalande and Fortier, 2011; Sweetman and Chapman, 2011, 2015; Lebrato et al., 2012; Dunlop et al., 2018).

Most GZ monitoring publications were found in Europe, Asia, and the United States (Supplementary Figure S6). Nets were the predominant monitoring method in all Marine Realms (Figure 4), except for the Eastern Indo-Pacific, where citizen science was the only method recorded. Most studies focused on cnidarians and used nets, underwater images, acoustics, and visual counts. Remote images, molecular methods, and jelly-falls have been implemented only for Cnidaria and Tunicata (Figure 5). The number of studies monitoring both the GZ pelagic and benthic stages increased from 2008 to 2022. There was a rise in the number of citizen science publications in 2021–2022 (Supplementary Figure S7).

Articles focusing on polyp monitoring are relatively scarce ($n = 19$). The methods used are summarized in Supplementary Table S6. Among the species considered, 64% belonged to the genus *Aurelia* (e.g., *Aurelia* sp., *A. aurita*, *A. coerulea,* and *A. labiata*), 9% to the genus *Chrysaora* (*C. pacifica* and *C. hysoscella*), and the remaining 27% included four Scyphozoa species (*Atolla* sp., *Atorella sibogae, Cyanea lamarkii*, *Nausithoe* cf. *rubra,* and *N. nomurai*) and one Cubozoa (*Copula sivicksi*). Polyps were found in both natural substrates (shells of clams *Spisula subtruncata* and *Mactra stultorum*, shells of dead clams, hollows of stones, undersurfaces of oysters growing on port pillars, biogenic reefs formed by polychaeta, hidden within the coral substratum, or on barnacles, bivalves, tunicates, sponges, and bryozoan) and artificial substrates (undersides of floating piers, PVC, synthetic rubber, iron oxide, wood, granite, glass, floating docks, and plastic debris).

In several publications, data from direct GZ monitoring techniques (e.g., counting methods and citizen science) have been combined with environmental information (e.g., currents

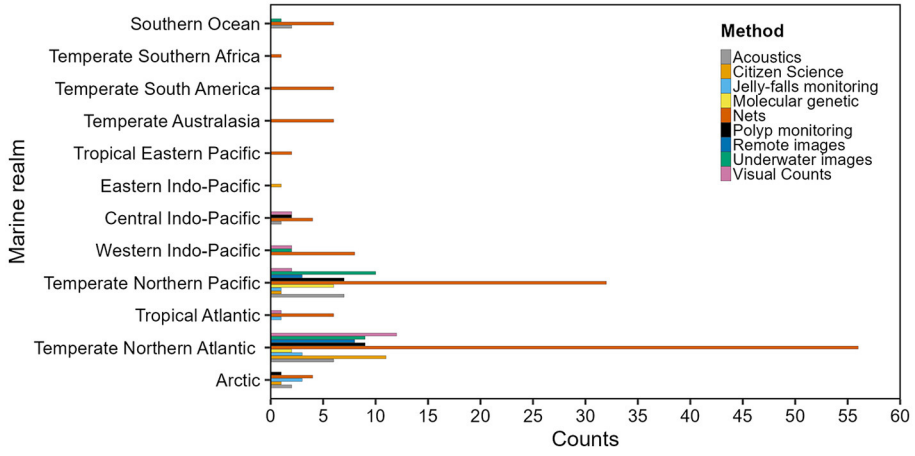

FIGURE 4
Types of monitoring methods used to monitor gelatinous zooplankton outbreaks and polyps (benthic stage of Scyphozoa and Cubozoa) across each Marine Realm, published between 2008–2023.

direction, temperature, and salinity) to develop **ecological models, EWS, or forecast of GZ trajectories** (Ferrer et al., 2015; Ferrer and González, 2021). Ecological modeling approaches used to predict outbreaks and spatial occurrence patterns include trait-based models, mixed models, and ecosystem-functional models (Lamb et al., 2019; Rahi et al., 2020; Ramondenc et al., 2020; Bosch-Belmar et al., 2021a).

4 Discussion: recommendations to move forward

Several key recommendations stem from the present multifaceted review.

4.1 Data representativeness and knowledge bias

The results of the systematic reviews demonstrate a pronounced prevalence of studies conducted in northern Atlantic regions, focusing on Cnidaria, and employing nets as primary monitoring technique. This highlights the need to diversify GZ studies, to publish additional research on non-cnidarian GZ taxa such as ctenophores and tunicates, to diversify monitoring methods, and to include underrepresented marine regions in the Southern Hemisphere.

4.2 Further dedicated and sustained monitoring of GZ is required to support research and management

Despite their important ecological and socio-economic roles in marine ecosystems, monitoring programs focused on GZ are scarce. Currently, there are no coordinated European efforts to monitor GZ, unlike the ICES fishery surveys (e.g., coordinated trawl and beam trawl surveys), or GZ defined monitoring requirements under other EU Directives (MSFD, CFP). Many GZ surveys are dependent on researchers "piggy backing" onboard during fisheries surveys to record "jellyfish bycatch". Certain GZ surveys rely on temporary national or EU funding (such as INTERREG or H2020), which limits their usefulness for assessing changes in GZ populations and distribution. Other monitoring efforts and funding are focused on harmful or noxious GZ species (e.g., *P. noctiluca* research in the Mediterranean in the 1980s) and dry up once abundances return to normal (Boero, 2013). As such, the abundance and distribution of GZ tends to be monitored haphazardly, using an uncoordinated approach.

Often, the implementation of new marine monitoring programs is hindered by their high costs. However, when considering the total costs of environmental management, from monitoring to management programs, monitoring costs constitute only a small proportion that becomes even smaller when factoring in the benefits achieved through efficient management (Nygård et al., 2016). Therefore, one of the most salient recommendations from this exercise is that the GZ research community across Europe needs to work together to design a European-wide monitoring framework supported by European bodies, funding mechanisms and institutes.

In this context, the coordination and GZ-dedicated extensions of existing monitoring programs supporting the Fisheries Data Policy, the Bathing Water Directive, the Water Framework Directive, the Integrated Coastal Zone Management (ICZM) and other monitoring facilities like long term ecological research (LTER) sites or the monitoring of pipelines and aquaculture sites, could help to enhance the coverage and resolution of data and rationalize costs. However, it is important not to forget that to accurately assess GZ, dedicated surveys would require adapted spatial and temporal extensions and resolutions, and adequate sampling gears and analysis methods.

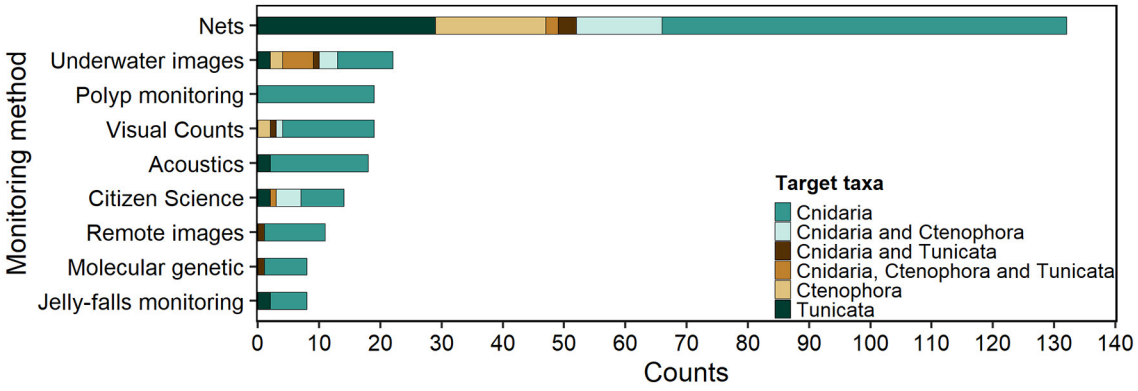

FIGURE 5
Gelatinous zooplankton and polyp (benthic stage of Scyphozoa and Cubozoa) monitoring studies sorted by target taxa based on the methodology used, published between 2008–2023.

4.3 Understanding the onset of GZ outbreaks and the role of the polyp phase

The limited understanding of the interplay between the diversity of pressures that can lead to different GZ species outbreaks, and their complex interaction mechanisms (i.e., additive, synergistic, or antagonistic), highlights the need for further research to comprehend the connections between human-induced stressors with GZ outbreaks.

This entails studying a range of different GZ functional groups, conducting experiments, considering ecosystem dynamics and employing multidisciplinary approaches to detect and quantify factors driving GZ outbreaks: traditional net-based methods and complementary technologies such as automated underwater imaging systems, artificial intelligence-based species detection and calibrated multibeam acoustics can be useful for species detection, abundance estimations, and inference of their interactions and spatial heterogeneity. Molecular techniques can assist in the early detection of potential NIS and problematic species. Remote sensing and modeling activities can cover large spatial scales and upscale local results to a European and global perspective. Standardized global monitoring through citizen science can enhance the availability of *in-situ* observations and increase public awareness of GZ-related issues.

Furthermore, the study of cnidarians' early phases, such as polyps and the first pelagic stages (i.e., ephyrae), is crucial to understand their recruitment and populations dynamics (Kingsford et al., 2000). Many factors determine the timing and magnitude of scypho- and cubomedusae recruitment, such as the polyps' abundance, budding and strobilation rates, and ephyrae survival rates (Pitt and Kingsford, 2003). However, polyps are elusive and efforts to monitor these pivotal stages are still scarce (19 peer-reviewed articles found in the last 16 years). Establishing *in-situ* sampling programs to identify the locations, abundance, and spatial extent of polyps, as well as estimating asexual reproduction, mortality, and growth rates, both *in-situ* and in laboratory experiments, would provide insight into the environmental factors that regulate jellyfish outbreak dynamics.

4.4 Integration of GZ in the MSFD framework

Integrating GZ into the MSFD framework involves starting to define baselines, indicators and thresholds for status, pressures and impacts of relevant GZ taxa across the different European marine and coastal areas. In this challenging context, coordination and complementation of experts, data, methods, and funding are key to achieving consistency and governance efficiency.

GZ can be considered in different descriptors, especially D1 (biodiversity), D2 (NIS), D4 (food-webs), and D5 (eutrophication). Defining relevant indicators and clear thresholds will help to identify when GZ populations exceed natural variability and become a concern for ecosystem health and marine ecosystem services. Moreover, differentiating between anthropogenic and natural factors driving outbreaks is crucial for ensuring that interventions address the manageable causes of GZ outbreaks. Due to the unpredictable and dynamic nature of GZ outbreaks and the current knowledge limitations, it is recommended to implement adaptive management through reassessment of the effectiveness of monitoring and management measures.

4.5 Public awareness, education and engagement

By informing the public about GZ species, risks, and safety/mitigating measures, safer behaviors and proactive preparations can be encouraged, leading to a more supportive and informed community. Therefore, ocean literacy and citizen science can be powerful tools to reduce the impact of GZ outbreaks

on public health, tourism, fisheries, and marine facilities. These initiatives not only provide valuable insights for scientists and managers but also foster a sense of stewardship among the public, making them active participants in observing, reporting, and managing GZ populations and marine health.

4.6 GZ and sustainable blue economy

Finally, GZ provides numerous ecosystem services and potentially new valuable marine resources. However, the exploitation of certain GZ taxa -especially NIS- should undergo scientific safety assessments, and address sustainability issues for massive commercial harvesting. In addition, potential impacts on pelagic food webs, including outbreaks of other non-target GZ or harvesting in sensitive ecological areas such as the leatherback turtle hotspots (Houghton et al., 2006) should be carefully considered before providing incentives for such fisheries (Gibbons et al., 2016; Hays et al., 2018).

To develop a successful blue economy, it is essential to align a healthy and resilient blue natural capital with secure investment and marine uses. This requires the best science, data, and technology, especially to address topics where important fallouts coexist with knowledge gaps, as is the case for GZ.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material. Specifically, the list of articles detected and examined during the PRISMA systematic reviews are provided as in two excel files added as Supplementary Tables 7 and 8. Further inquiries can be directed to the corresponding author.

Author contributions

YS: Conceptualization, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. SP: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. CL: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. VL: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. AN: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. CJ: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. MB-B: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. LF: Formal analysis, Investigation, Methodology, Writing – review & editing. ÁB: Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Writing – review & editing. ES: Writing – review & editing. EA: Writing – review & editing. PB: Writing – review & editing. RA: Writing – review & editing. AL: Writing – review & editing. NM: Visualization, Writing – review & editing. LF: Writing – review & editing. MH: Visualization, Writing – review & editing. TD: Writing – review & editing. GT: Writing – review & editing. SK: Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

EA was employed by International Estuarine & Coastal Specialists (IECS) Ltd.

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.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/focsu.2024.1449190/full#supplementary-material

SUPPLEMENTARY FIGURE S1
Schematic diagram of the screening steps for gelatinous zooplankton (GZ) impacts article selection. Reason 1 = out of scope (e.g., no negative impacts reported or not about GZ species), Reason 2 = language, Reason 3 = publication type (e.g., review; note that all retrieved review articles were screened for citation identification and relevant articles were added for screening as "Other sources").

SUPPLEMENTARY FIGURE S2
Schematic diagram of the screening steps undergone for global gelatinous zooplankton (GZ) monitoring articles selection. Reason 1 = not GZ monitoring, Reason 2 = language, Reason 3 = publication type, Reason 4 = modeling.

SUPPLEMENTARY FIGURE S3
Schematic diagram of article selection on polyp (Scyphozoa and Cubozoa) monitoring through the screening steps. Reason 1 = not polyp monitoring, Reason 2 = Hydrozoans, Reason 3 = freshwater species, Reason 4 = publication type.

SUPPLEMENTARY FIGURE S4
Overview of the different aspects related to gelatinous zooplankton covered by this study. The box sizes of the different impacts and monitoring categories are proportional to the number of articles addressing them within the systematic reviews performed.

SUPPLEMENTARY FIGURE S5
(A) Location of Loch Ewe Site from the Scottish Coastal Observatory. Paired monthly observations of lifeform abundances: **(B)** gelatinous zooplankton versus fish larvae/eggs, and **(C)** gelatinous zooplankton vs. crustacean zooplankton. **(D)** Interannual decreases of gelatinous zooplankton (Marine Scotland Science, 2018; Wells et al., 2022).

SUPPLEMENTARY FIGURE S6
Spatial distribution of studies on gelatinous zooplankton outbreaks and aggregations (n = 200) and polyp monitoring (n = 19) published between 2008–2023.

SUPPLEMENTARY FIGURE S7
Counts of reports of monitoring methods used for gelatinous zooplankton assessment and polyp (benthic stage of Scyphozoa and Cubozoa) monitoring by year, published between 2008–2023 (*articles published in 2023 are not representative as the literature research was performed until June of that year).

SUPPLEMENTARY TABLE S1
Definitions of type of evidence categories considered *sensu* Katsanevakis et al. (2014).

SUPPLEMENTARY TABLE S2
Magnitude of impacts categories *sensu* Blackburn et al. (2014).

SUPPLEMENTARY TABLE S3
Adverse impacts, and the gelatinous zooplankton (GZ) species causing them, identified in this study. Abbreviations for the European regions: GN, Greater North Sea; C, Celtic Sea; B, Baltic Sea; SE, South European Shelf Seas (including Bay of Biscay and the Iberian Coast), MED, Mediterranean Sea.

SUPPLEMENTARY TABLE S4
Potential causes (pressures) of gelatinous zooplankton (GZ) outbreaks reported in the literature.

SUPPLEMENTARY TABLE S5
Marine Strategy Framework Directive (MSFD) descriptors and gelatinous zooplankton (GZ) relevance.

SUPPLEMENTARY TABLE S6
Methods used for Scyphozoa and Cubozoa polyp stage monitoring, published from 2008 to 2023 (n = 19) and the target species.

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The unpredictability of scyphozoan jellyfish blooms

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The study of jellyfish blooms has gained attention in the recent decades because of the importance of forecasting and anticipating them and avoiding their interference with human activities. However, after thirty years of scientific effort (monitoring systems, empirical laboratory and field studies, modeling, etc.), the occurrence of blooms remains unpredictable, and their consequences unavoidable. Climate change, eutrophication, overfishing, coastal construction, and species translocation have been suggested as stressors that increase them, but robust evidence to support these claims is limited. The widespread belief that jellyfish blooms are "increasing in number" has been challenged in recent years. Among the gelatinous zooplankton, the bloom forming species are concentrated in the class Scyphozoa, and the number of species with at least one recorded bloom has increased during the last decade. The analyses of long-term time series show seasonality in the dynamic of each blooming jellyfish species population, but the blooms vary in intensity and there are years of an unexplained absence of jellyfish. In this review, we focus on the current state of knowledge, uncertainties and gaps in the critical points that can strongly influence the intensity of the bloom or even lead to the absence of the medusa population. These points include ephyrae, planulae and scyphistoma natural, predatory or fishing mortality, the molecular pathway of strobilation, benthic population dynamics, planula settlement and ephyra to medusa transition success. Some of these points account for certain empirical laboratory evidence under controlled conditions, and are difficult to be studied on the field, but the different sources of non-typically recorded variability need to be addressed to improve our understanding of jellyfish population dynamics.

KEYWORDS

jellyfish proliferation, life cycle, modeling, predictability, Scyphozoa

1 Introduction

The massive proliferations of jellyfishes, commonly referred to as jellyfish blooms, are usually described in negative terms because of the interference with human activities that results from their appearance. Those interferences include competing with commercial fish species both through predation on fish larvae and through the direct competition for food,

clogging fishing nets, damaging catches, stinging fishermen and swimmers or clogging water intake systems in coastal power plants, among others (Purcell et al., 2007; Richardson et al., 2009; Purcell et al., 2013). The socio-economic impacts of the jellyfish blooms are often neglected in scientific studies (Bosch-Belmar et al., 2020), but some examples can be found. In the case of fisheries, catches can be reduced by up to 25.3%, the catch value can be reduced by up to 33.7%, and the economic loss, in Korean fisheries alone, can exceed US$ 200 million in a single jellyfish season (Kim et al., 2012). For the tourism sector in the United Kingdom, avoiding the areas where jellyfish are present can result in an economic loss of more than 12000 US$ per day for a 10 km^2 tourist area (Kennerley et al., 2022), while in Spain, the average visitor is willing to pay an additional 3.20 € per beach visit if it guarantees a lower risk of encountering jellyfish (Nunes et al., 2015).

However, despite the socio-economic impacts derived from the appearance of jellyfish blooms, the ecosystem services they provide should not be ignored. In eutrophication processes, jellyfish have been linked to the maintenance of water quality through top-down control of the food web (Pérez-Ruzafa et al., 2002; Fernández-Alías et al., 2022; Fernández-Alías et al., 2023), and their use as food has led to the emergence of a fishing and aquaculture industry focused on these organisms (Hsieh et al., 2001; Omori and Nakano, 2001; Purcell et al., 2007; Nishikawa et al., 2015; Khong et al., 2016; Leone et al., 2019). In addition, jellyfish are being studied in search of biomolecules with potential applications in pharmacology and medicine (Zimmer, 2005; Sugahara et al., 2006; De Rinaldis et al., 2021; De Domenico et al., 2023; Sudirman et al., 2023), and as the most energetically efficient swimmers, jellyfish biomechanics are a subject of study in the development of remotely operated swimming vehicles (Gemmell et al., 2013; Gemmell et al., 2015; Costello et al., 2021; Gemmell et al., 2021).

The disturbances and ecological services provided by jellyfish blooms have attracted the attention of the scientific community with increasing interest since the last decade of the twentieth century (Pitt et al., 2018). Along with the scientific community, the general public have also been engaged to participate in the monitoring of jellyfish blooms through citizen science campaigns (Marambio et al., 2021; Dobson et al., 2023). During the years in which this topic has been studied, the perception of a general increase in the frequency, intensity, and extent of jellyfish blooms has become established in the scientific community, and a whole conceptual framework of how ocean degradation favors the occurrence of jellyfish blooms has been developed (Arai, 2001; Purcell, 2005; Purcell et al., 2007; Richardson et al., 2009; Purcell, 2012). Among the ocean degradation factors cited as drivers of jellyfish blooms, overfishing, climate change, species translocation, eutrophication, and habitat modification are commonly highlighted as part of an eventual regression of the ocean state to Cambrian-like assemblages dominated by short-lived organisms such as jellyfish (Figure 1) (Pauly et al., 1998; Parsons and Lalli, 2002; Pauly et al., 2008; Richardson et al., 2009).

The same authors who contributed to the development of the conceptual framework also noted its limitations, highlighting the paucity of reliable baseline data and the short length of the time-series those assumptions were made on (Purcell et al., 2007; Pauly et al., 2008; Richardson et al., 2009). The low availability of data forced scientists attempting to analyze these assumptions to gather all the organisms referred to as jellyfish (Brotz et al., 2012) into a single and generic 'gelatinous zooplankton' group (Condon et al., 2013), despite their taxonomic, genetic and life cycle differences (Hamner and Dawson, 2009; Khalturin et al., 2019). In addition, research efforts have not been equally distributed among all components of the gelatinous zooplankton, with an overrepresentation of the scyphozoan *Aurelia* spp. Lamarck, 1816 and the ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 (Pitt et al., 2018). It should also be noted that bloom-forming species are not evenly distributed throughout the gelatinous zooplankton but are concentrated in the class Scyphozoa (Hamner and Dawson, 2009), with special incidence in the larger species dwelling in temperate, shallow waters (Fernández-Alías et al., 2021). The importance of this class is not limited to a higher number of bloom forming species, as they are also responsible for most of the disturbances in fisheries and aquaculture (Bosch-Belmar et al., 2020), but also collect the highest number of edible species (Brotz et al., 2017).

Despite the controversies and limitations, the conceptual framework is generally accepted by the scientific community, and the number of published papers on the topic increases every year, contributing to the dissemination of the idea of an increase in jellyfish blooms in some areas (Sanz-Martín et al., 2016; Pitt et al.,

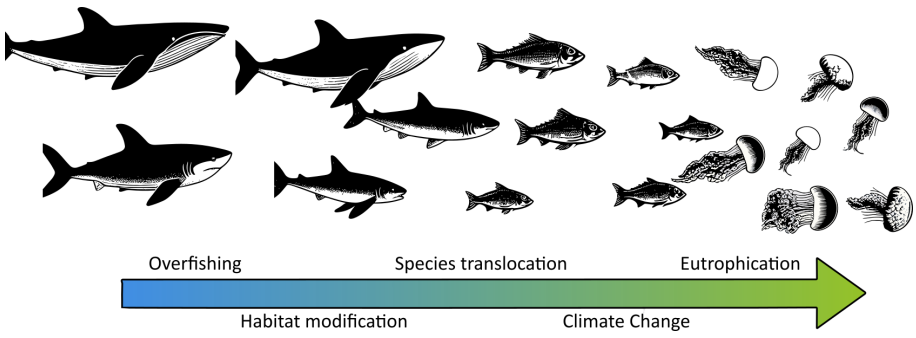

FIGURE 1
Conceptual framework of the change in the key-species controlling marine food webs in a regression to Cambrian-like assemblages because of ocean degradation (based on Pauly et al., 2008).

2018). Considering only the class Scyphozoa, where most of the blooms are concentrated, an increase in the percentage of bloom forming species has been detected in the last decade (Fernández-Alías et al., 2021). However, this increase does not necessarily mean that jellyfish populations are increasing worldwide (Brotz et al., 2012), as it is associated with a higher interest in the topic and more sampling efforts (Pitt et al., 2018).

Of all the variables analyzed within the conceptual framework, temperature is the one that stands out the most (Fernández-Alías et al., 2021), probably reflecting the seasonality that most species exhibit during their life cycle. In the class Scyphozoa, this variable has been shown to control the life cycle, modifying the asexual reproduction rate of the polyp stage, acting as a strobilation trigger and regulating the transition from ephyra to medusa (Prieto et al., 2010; Fuentes et al., 2011; Fuchs et al., 2014; Brekhman et al., 2015; Fernández-Alías et al., 2023). The effect of temperature can also be observed in short-term studies for most ecosystems and species (Fernández-Alías et al., 2020; Gueroun et al., 2020; Leoni et al., 2021a), but becomes blurred when longer time series are considered (van Walraven et al., 2015; Stone et al., 2019). This suggests that temperature is not an exclusive requirement for bloom development (Fernández-Alías et al., 2021). At the same time, the scyphozoan jellyfish species do not seem to have the thermal control on their phenology modified in the context of climate change (Fernández-Alías et al., 2023), but an increased period of suitable temperatures could extend the duration of the scyphozoan blooms (Ruiz et al., 2012; Edelist et al., 2020; Leoni et al., 2021b). In any case, both situations raise more questions and challenges about the interannual variability of bloom intensity in relation to thermal oscillations.

After more than 30 years of combined scientific research (monitoring systems, empirical laboratory and field studies, modeling, etc.), we are still unable to answer the main question asked by managers, tourists and other stakeholders: "Will there be jellyfish next season?". There are several socio-economic implications of our inability to answer this demand, but one of the clearest examples is the cannonball jellyfish fishery in Mexico, where the national government promoted the activity and businesses developed in anticipation of a long-term productive industry, only to eventually experience a collapse in catches due to interannual variability or fisheries mismanagement (López-Martínez and Álvarez-Tello, 2013; Girón-Nava et al., 2015; Brotz et al., 2021). Improving the quality of jellyfish bloom predictions using traditional approaches, when not a single bloom has been correctly predicted in more than three decades of research, seems unlikely. Therefore, we have focused this review both on less commonly addressed sources of variability that affect the viability of scyphozoan blooms (*e.g.* predation on larval stages, parasitism, or interspecific competition), and on sources of variability that are commonly referred to as promoters of jellyfish blooms, but which can also induce physiological stress when they are not optimal (*e.g.* temperature, food availability or salinity).

This work builds on the systematic review by Fernández-Alías et al. (2021) in which all scyphozoan genera were individually used as keywords in the Web of Science and Scopus search engines to identify the bloom forming genera and species. The search algorithm was modified in the genera *Cyanea, Chrysaora, Pelagia* to *Genus AND Jellyfish* to eliminate papers from unrelated scientific fields and further modified to *Genus AND Jellyfish AND (Bloom OR "Life cycle")* in the case of *Aurelia* due to its use as a model species. The original search was replicated to include the publications on blooming genera from January 2021 to December 2023. Previously selected papers on blooming species were re-analyzed with the recent publications using the following selection criteria of i) reference to scyphozoan species, ii) analysis of aspects of the jellyfish ecology at any developmental stage, iii) description of possible facilitators or perturbations to the regular development of the life cycle. The review was supplemented by additional searches in Google Scholar under combinations of the term "Jellyfish" with "Predation", "Disease", "Parasitism", "Fisheries", "Mortality" and "Stress" to include thesis and other 'gray literature' items. No filter was applied in terms of number of citations or year of publication. Since the aim of the review was to construct a conceptual model of the factors that control the biological cycle of scyphozoans and to discuss the sources of variability that influence the difficulty of predicting the events of massive proliferations of these organisms, and not to perform meta-analyses, no attempt was made to quantify the retrieved publications, selected or excluded papers.

2 Control of the 'never-ending jellyfish joyride'

The proposed conceptual framework for a jellyfish-dominated ocean depicted a series of interrelated mechanisms that further enhanced this jellyfish dominance over other marine species, based on how their own biological characteristics seemed to overcome any possible control over populations (Richardson et al., 2009). However, reports of long-term monitoring of jellyfish populations usually reveal the existence of years of unexplained absence of jellyfish. In the Mar Menor coastal lagoon (Spain), an ecosystem affected by eutrophication over the last 30 years, habitat modification, global warming, and fishing (Pérez-Ruzafa et al., 2019; Fernández-Alías et al., 2022), populations of *Cotylorhiza tuberculata* (Macri, 1778) and *Rhizostoma pulmo* (Macri, 1778) unexpectedly collapsed after two decades of benefiting from the factors described in the conceptual framework (Fernández-Alías et al., 2022; Fernández-Alías et al., 2023). In the Dutch Wadden Sea (Netherlands), another monitored eutrophic ecosystem, the different scyphozoan jellyfish species showed different patterns of abundance over the years, alternating between years of unexplained absence or sparse abundance of some individual species and bloom years (van Walraven et al., 2015).

Scyphozoan jellyfish species generally have a metagenic life cycle, alternating between benthic and pelagic phases (Hamner and Dawson, 2009). During the same, there are several stages where a numerical expansion of the population can occur: a single medusa can carry thousands to millions of planulae (Kikinger, 1992; Lucas, 1996), the polyp population can double to five times its initial number within a month under the appropriate food-temperature conditions (Lucas et al., 2012; Wang et al., 2015), and each strobila

can release from 1 to 30 ephyrae (Di Camillo et al., 2010; Fuentes et al., 2011; Lucas et al., 2012). Under the most optimal conditions without any kind of mortality, neither natural nor predatory, a single medusa can yield from a minimum of 2×10^3 (≈1 medusa × 1000 planulae/medusa × 2 polyps/planula × 1 ephyra/polyp) to a maximum of 1.5×10^8 medusae (≈1 medusa × 10^6 planulae/medusa × 5 polyps/planula × 30 ephyrae/polyp) within a single year (Figure 2, black arrows). Consequently, the large interannual variation in the abundance of the medusa phase of the scyphozoan jellyfish populations can only be explained by the existence of complex interactions that regulate, either as enhancers (Figure 2, green arrows) or inhibitors (Figure 2, red arrows), the dynamics of the different scyphozoan jellyfish populations during the different stages of the life cycle.

2.1 Planula stage

Scyphozoan planulae can settle on a variety of natural and artificial hard substrates, including shells, concrete, plastic, glass, wood, rope, seagrass, macroalgae, rocks, etc., with different efficiencies depending on the type and orientation of the substrate and the different scyphozoan species (Miyake et al., 2002; Holst and Jarms, 2007; Malej et al., 2012; Marques et al., 2015; Franco, 2016; Gambill et al., 2018; van Walraven et al., 2020). There is an environmental control by factors such as temperature, salinity or light on the settlement and excystment of the planulae, providing an efficiency of the process, with the absence of competition for the substrate or predation, which decreases from a maximum of ~ 60% under the most suitable conditions to a minimum of 0% in a progression towards less suitable conditions (Prieto et al., 2010; Franco, 2016; Gambill et al., 2018; Feng et al., 2021; Gueroun et al., 2021; Holst et al., 2023). Even under the preferred environmental conditions and in the absence of competitors and predators, the settlement needs to occur within the first few days after planula release to prevent a significant decline in its effectiveness (Gambill et al., 2018). However, spatial competition and predation cannot be ignored when attempting to build predictive models of jellyfish blooms, yet both topics remain largely understudied. Boughton et al. (2023) conducted an *in-situ* fouling settlement experiment on PVC panels testing the settlement efficiency of *Aurelia aurita* (Linnaeus, 1758) planulae against potential competitors, showing high competition for the space and a relative increase in planula settlement efficiency after removal of potential competitors. Predation on scyphozoan planulae, which is rarely addressed, can occur at least by ctenophores, ascidians, and bivalves at rates of 10 – 25, 20 and 40 planulae × ind^{-1} × h^{-1}, respectively (Javidpour et al., 2009; Kuplik et al., 2015), as well as by scyphozoan polyps (Gröndahl, 1988a; Gröndahl, 1988b). In this line, Franco (2016) linked the absence of planula settlement on live oyster shells to the filtering capacity of oysters. In contrast, Marques et al. (2015) linked the absence of polyps attached to oyster shells in the Thau lagoon (France) to the oyster farming method rather than to the oyster predation on planulae, while Malej et al. (2012) do provide images of polyps over oyster shells. However, in the latter example it is not certain whether the planulae have settled directly over the shell or whether the presence of polyps is due to a colonization by asexual reproduction and polyp motility (Feng et al., 2017; Zang et al., 2023).

2.2 Polyp stage

After the planula settlement, the polyps emerge in a process called excystment and develop tentacles to acquire their typical morphology in a process that can be negatively affected by inadequate temperature-salinity conditions or by the lack of food (Holst et al., 2023). Newly formed polyps can colonize the substrate through 7 different modes of asexual reproduction (Schiariti et al.,

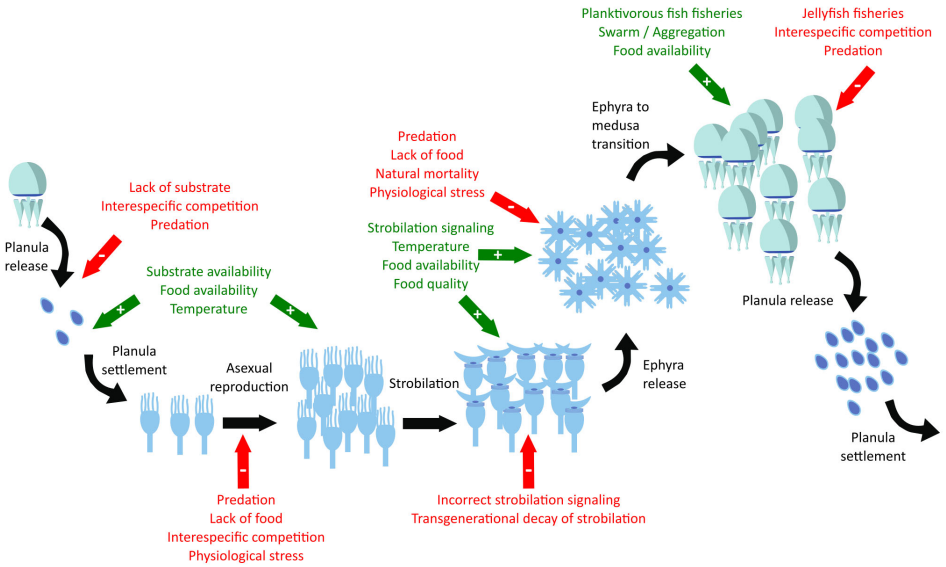

FIGURE 2
Scyphozoan life cycle (black arrows), enhancer factors (green arrows with plus sign), and limiting or inhibiting factors (red arrows with minus sign).

2014; Wang F. et al., 2023). The different scyphozoan jellyfish species can exhibit a mono-mode asexual reproductive strategy (*e.g. Phyllorhiza punctata* von Lendenfeld, 1884; Schiariti et al., 2014), multi-mode asexual reproductive strategy (*Aurelia* spp.; Schiariti et al., 2014; Wang F. et al., 2023), or a preferential and a secondary strategy as it found in *R. pulmo* (Fuentes et al., 2011; Schiariti et al., 2014). Under the adequate food and temperature conditions, each polyp can produce 8 to 20 buds from which new polyps can develop (Purcell et al., 2012), but the overall efficiency in the absence of competitors or predators is typically limited to a two to fivefold increase in the initial number of polyps (Lucas et al., 2012; Wang et al., 2015). In general, species with multi-mode asexual reproductive strategies exhibit higher asexual reproduction rates (Schiariti et al., 2014).

Scyphozoan polyps generally exhibit a wide thermal and salinity tolerance, but the asexual reproduction rates can decline rapidly when the optimal conditions are not met and eventual mass mortality can occur when the upper or lower tolerance limits are exceeded (Purcell et al., 1999; Prieto et al., 2010; Purcell et al., 2012; Treible and Condon, 2019). As a result, the evolution of the different scyphozoan species has led to higher asexual reproduction rates of polyps at temperatures when their planulae are present in the water column (Prieto et al., 2010; Purcell et al., 2012; Schiariti et al., 2014; Treible and Condon, 2019). Scyphozoan polyps can also withstand starvation conditions, but surprisingly, when the food scarcity conditions are coupled with the optimal temperatures for the asexual reproduction, the survival is significantly reduced, likely due to increased metabolic demands (Zang et al., 2023).

In nature, the scyphozoan polyps face interspecific competition for food and space, predation, synergies with other organisms derived from the construction of their hard structures, and physiological stress associated with environmental conditions (Feng et al., 2017; Marques et al., 2019; Feng et al., 2021; Zang et al., 2023). The organisms that efficiently compete for the space and reduce substrate availability for scyphozoan polyps by killing and displacing them, have a slimy or soft surface that cannot be used as a substrate for polyp development (Zang et al., 2023). This first group mainly includes sponges and ascidians, but there are some exceptions, as *Aurelia* sp. has been shown to be able to grow on certain solitary ascidians (Miyake et al., 2002; Feng et al., 2017; Rekstad et al., 2021). A second group of organisms are those with a spiny or multibranched surface. This group includes species that never provide a suitable substrate for settlement and others that may eventually provide a suitable substrate, as happens when the mud tubes of amphipods become stiffer (Miyake et al., 2002). The third group includes bivalves, the calcareous tubes of polychaetes, balanoids, and, in general, organisms that build hard structures and increase the available substrate for polyps to attach to (Miyake et al., 2002; Rekstad et al., 2021; Zang et al., 2023). Scyphozoan polyp predators include crustaceans, nudibranchs, and gastropods with consumption rates greater than 300 polyps $\times$ ind^{-1} $\times$ day^{-1} (Arai, 2005; Takao et al., 2014; Feng et al., 2017; Tang et al., 2021). Intraguild predation among scyphozoan polyps has also been observed in laboratory studies co-culturing multiple species (Tang et al., 2020). The overall balance between polyp asexual reproduction, competition, predation, and physiological stress may benefit the scyphozoan polyps during the initial stages of colonization of a bare substrate (Feng et al., 2021; Boughton et al., 2023), but it is reversed within months, leading to severe reductions in scyphozoan polyp densities or even the disappearance of polyp colonies of certain species (Hernroth and Gröndahl, 1983; Feng et al., 2017; Feng et al., 2021).

2.3 Strobila and post-strobila stages

The strobilation process involves the reabsorption of polyp tentacles and the differentiation of segments that will eventually produce ephyrae at the oral end of the scyphistoma (Schiariti et al., 2008; Fuentes et al., 2011). Triggering of the process occurs following physical or chemical signals (Holst, 2012; Lucas et al., 2012; Helm, 2018). The molecular mechanism of strobilation is not fully understood, but the candidate hormones that induce the process exhibit strong temperature regulation during the polyp stage (Fuchs et al., 2014; Brekhman et al., 2015; Ge et al., 2022) and show structural similarities to certain compounds used in aquaria to chemically trigger the process (Spangenberg, 1965; Helm, 2018). Temperature must act in concert with other factors to induce strobilation: in tropical ecosystems with low thermal oscillations, strobilation can be signaled by salinity shifts (Lucas et al., 2012; Helm, 2018), zooxanthellate bearing species must host their symbionts and be exposed to both light and temperature appropriate conditions (Kikinger, 1992; Prieto et al., 2010; Schiariti et al., 2014), and there is a food requirement for polyps to strobilate (Wang et al., 2015; Zang et al., 2023). In non-zooxanthellate species, where the light and symbionts are not required, the microbiota organisms still play a key role in the strobilation, as the process is inhibited by a downregulation of the genetic pathway in their absence (Jensen et al., 2023).

The seasonal appearance of the medusa phase in most of the scyphozoan species is indicative of a temperature regulated strobilation process (Holst, 2012; Fernández-Alías et al., 2021), but there are reports of ephyra appearing at temperatures unsuitable for their posterior development (Fernández-Alías et al., 2023). Incorrect strobilation signaling can be problematic for the completion of the life cycle as it is a stressful process for the scyphozoan polyps. In most species, the calix diameter of the polyp shrinks after ephyra release (Feng et al., 2017), and the remnant is not always able to recover. In *C. tuberculata*, the polyp population completely disappears shortly after the strobilation (Kikinger, 1992; Prieto et al., 2010), and the polyps of *Cyanea nozakii* Kishinouye, 1891, *Rhopilema esculentum* Kishinouye, 1891, and *Nemopilema nomurai* Kishinouye, 1922 were unable to recover their original size and eventually disappeared in the field experiment by Feng et al. (2017). In contrast, *R. pulmo* has been reported to regrow the tentacles within two weeks after strobilation (Fuentes et al., 2011), and *Rhopilema nomadica* Galil, Spanier and Ferguson, 1990 can undergo multiple strobilation events while reproducing asexually (Lotan et al., 1992). As a result, some scyphozoan polyp cultures can be maintained in an aquarium for years (Lucas et al., 2012), but

their ability to reproduce asexually may decline with successive generations (Chi et al., 2022). However, Holst (2012) observed that *Cyanea capillata* (Linnaeus, 1758) produced more ephyrae per polyp in older polyps, but the latter development to the medusa phase was not recorded and the overall effect on jellyfish population dynamics remains unknown.

2.4 Ephyra stage

The ephyra stage is not typically reported to limit the magnitude of the jellyfish blooms, but there is evidence that ephyra peaks followed by a massive mortality reduce the abundance of the medusa phase and even lead to an absolute absence of the same (Fernández-Alías et al., 2023). This occurs when a strobilation event occurs outside the appropriate temperature range for the development of the ephyrae, as there are upper and lower thresholds for the transition from ephyra to medusa (Astorga et al., 2012; Fernández-Alías et al., 2023).

The transition from ephyra to medusa involves a somatic growth, fusion of the rhopaliar lappets by the extension of the umbrella, the development of a gastric system, oral arms, and tentacles, and can last from 10 to 150 days, depending on the species and the environmental conditions (Holst et al., 2007; Fuentes et al., 2011; Astorga et al., 2012; Fernández-Alías et al., 2020; Gueroun et al., 2020; Fernández-Alías et al., 2023). During this period, ephyrae are exposed to natural mortality and intraguild predation by scyphozoan polyps, ephyrae, and medusae (Carrizo et al., 2016; Avian et al., 2021; Stoltenberg et al., 2021; Wang P. et al., 2023). To maintain the growth rate of the ephyra and increase the likelihood of completing the transition from ephyra to medusa, food requirements must be matched in quantity and quality (Chambel et al., 2016; Miranda et al., 2016; Ballesteros et al., 2022).

Mortality at this stage is rarely addressed, but it is likely to influence the development of the bloom. In the most conspicuous blooms of *C. tuberculata*, where ephyra abundance was also assessed, mortality at this stage was less than 5%, but the average mortality of *C. tuberculata* ephyra is around 70% and greatly affects the intensity of the bloom (Fernández-Alías et al., 2023). In the case of the moon jellyfish, *Aurelia* spp., the minimum recorded mortality at the ephyra stage is over 70%, the average mortality is over 90% and the maximum mortality is over 99% (Ishii et al., 2004; Fernández-Alías et al., 2023). The most likely factors involved in ephyrae mortality are physiological stress or predation (Carrizo et al., 2016; Stoltenberg et al., 2021; Fernández-Alías et al., 2023), but the absence of microbiota results in deformed ephyra after strobilation (Jensen et al., 2023), whose correct development is unlikely.

2.5 Medusa phase

The first observations in the water column of some individuals in their medusa phase can be a sign of an outshore bloom whose individuals have not yet been drifted ashore by winds or tides (Zavodnik, 1987; Keesing et al., 2016), an early bloom warning or an unsuccessful inshore jellyfish bloom (Fernández-Alías et al., 2023). The importance of the medusa phase goes beyond the ecosystem services and disturbances resulting from the bloom that occurs, as they can carry from thousands to millions of planulae (Kikinger, 1992; Lucas, 1996). The underlying biological reason for the occurrence of swarms or aggregations of medusae during the bloom events is not fully understood, but it has been argued that the reproductive success and the protection from predators could be enhanced by these behaviors (Hamner and Dawson, 2009; Fernández-Alías et al., 2021).

In this line, the scyphozoan jellyfish have traditionally been considered as a trophic dead end, but their trophic role has probably been underestimated as their absence in stomach contents can be explained by their extremely high digestion rate (Ates, 1988; Arai et al., 2003; Hays et al., 2018). Recent analyses, including increased data collection of stomach contents, direct observations, stable isotope analyses, DNA metabarcoding, and animal-borne cameras have significantly increased our knowledge of gelatinous zooplankton predation (Hays et al., 2018). The wide variety of organisms that predate on scyphozoan medusae include sea anemones, corals, starfish, brittle stars, sea cucumbers, balanoids, amphipods, decapods, fishes, flying seabirds, penguins, turtles, and other scyphozoan jellyfish (Ates, 1988; Arai, 2005; Titelman et al., 2007; Heaslip et al., 2012; Thiebot et al., 2016; Ates, 2017; McInnes et al., 2017; Thiebot et al., 2017; Hays et al., 2018; Wang P. et al., 2023).

The interest in studying the link between scyphozoan jellyfish and predators is partly driven by the parasites that the scyphozoan medusae harbor as intermediate hosts before infecting commercially exploited fish (Browne, 2014; Kondo et al., 2016; Motta et al., 2023). This developmental stage can harbor parasites with single host life cycles, such as amphipods or anemones, and parasites with multiple host life cycles, such as digeneans and cestodes (Arai, 2005; D'Ambra and Graham, 2009; Diaz Briz et al., 2012; Browne, 2014). The high prevalence of parasites in scyphozoan medusae suggests that a fundamental part of the parasite life cycle may occur in jellyfish (Diaz Briz et al., 2012), providing benefits such as protection, feeding or transport (Sal Moyano et al., 2012; Gonçalves et al., 2022), but the effect of parasites on the scyphozoan life cycle is poorly understood (D'Ambra and Graham, 2009). This infection may be important for life cycle completion, as somatic growth, gonad size, and egg production of scyphozoan medusae may be reduced by parasitism (Chiaverano et al., 2015).

The final factor influencing the medusa phase of the scyphozoan jellyfish life cycle is fishing, which can promote or disrupt the biological strategies of scyphozoan species, depending on the species targeted by the fishery (Lynam et al., 2006; Brotz, 2016). Overfishing of filter-feeding fish has promoted a shift in the system toward jellyfish dominance in some locations (Lynam et al., 2006), but this has not occurred when an alternative stock of filter-feeding fish could replace the original species (Schwartzloze et al., 1999). Similarly, filter-feeding fishes may benefit from the collapse of a predatory fish fishery (Mullon et al., 2005). In these cases, there is no increase in jellyfish abundance (Richardson et al., 2009), but they are indicative of the complexity of the system. This can be further illustrated by the case of salmon fisheries on the Pacific coast

of North America, where the population of the sea nettle *Chrysaora fuscescens* Brandt, 1835 showed a complex pattern of zooplanktonic relationships that affected its abundance as well as the fisheries for the targeted salmon species (Ruzicka et al., 2016).

Scyphozoan jellyfish are also targeted species, and the impact of their fisheries on population dynamics must also be discussed. Indeed, jellyfish fisheries have become increasingly important worldwide, with more than 20 countries reporting their activity and average annual jellyfish landings exceeding 7.5×10^8 kg (Brotz, 2016; Brotz et al., 2017), but the biological parameterization of the species necessary to develop sustainable fishing programs has only been carried out for certain species and locations (Palomares and Pauly, 2008; Brotz, 2016; Fernández-Alías et al., 2020; López-Martínez et al., 2020; Leoni et al., 2021a; Behera et al., 2022). Consequently, the overfishing has been identified as the main cause of the collapse of the jellyfish fisheries of *R. esculentum* in China (Dong et al., 2014) and of *Stomolophus meleagris* Agassiz, 1860 in Mexico (Brotz et al., 2021). However, it is important to consider that jellyfish populations fluctuate naturally, and this is one of the main challenges in establishing long-term, productive jellyfish fisheries. For example, to maintain the economic productivity of the *R. esculentum* fishery in China, a stock enhancement program was developed to maintain and increase the catches in anticipation of a population collapse due to overfishing (Dong et al., 2009). In contrast, the collapse of the *C. tuberculata* population in the Mar Menor coastal lagoon (Spain) occurred after the jellyfish removal program was suspended (Fernández-Alías et al., 2022; Fernández-Alías et al., 2023), suggesting that overfishing is not the only cause of population collapse.

2.6 Non-metagenic life cycle

The scyphozoan species do not require a metagenic life cycle to bloom (Hamner and Dawson, 2009). The most relevant holopelagic jellyfish of the class Scyphozoa capable massive proliferation *Pelagia noctiluca* (Forsskål, 1775) and *Periphylla periphylla* (Péron and Lesueur, 1810). The set of factors affecting their life cycle is likely to be similar to that described previously in this review, but their lack of a benthic stage justifies the inclusion of an additional section to discuss the transitions from planula to ephyra (*P. noctiluca*) and from fertilized egg to medusa (*P. periphylla*).

The mauve stinger, *P. noctiluca*, is one of the most conspicuous scyphozoan species in the western Mediterranean (Canepa et al., 2014). This species lacks a benthic phase, and the planula larva transforms directly into an ephyra (Canepa et al., 2014; Ramondenc et al., 2019; Ballesteros et al., 2021). The medusa stage can survive for more than one year (Lilley et al., 2014), shows different reproduction peaks during the same (Milisenda et al., 2018), and shows a heterogeneous bloom pattern and spatial variability across the Mediterranean Sea (Marambio et al., 2021; Pastor-Prieto et al., 2021, Bellido et al., 2020). The population dynamics seems to follow a regular seasonality (Benedetti-Cecchi et al., 2015) with the spawning period adapting to the most suitable temperature frame for the transition from planula to ephyra (Rosa et al., 2013; Milisenda et al., 2018). This seasonality is likely to be a product of evolutionary selection, as the larval survival rate through the planula to ephyra transition decreases from 50% to approximately 12% when the temperature requirements are not met (Rosa et al., 2013). However, during the medusa spawning period, when the gonads of *P. noctiluca* reach their largest size (Milisenda et al., 2018), certain fish species have been reported to selectively feed on these organs, which are more nutritious than the somatic tissues (Milisenda et al., 2014), but the impact of this selective foraging over the species dynamics requires further exploration. Finally, during the ephyra stage, as is the case for the species with a metagenic life cycle, food requirements must to be matched in quantity and quality for its proper development to the medusa phase (Ballesteros et al., 2022).

P. periphylla is one of the scyphozoan blooming species that deviates the most from the metagenic life cycle and from the 'boom and boost' appearance of the medusae. In this species the medusae appear after direct transformation from the fertilized egg, thus, lacking not only the benthic phase, but also the planula and ephyra stages (Jarms et al., 1999). Moreover, the medusa stage has a low growth rate, and a lifespan of several years (Jarms et al., 1999; Båmstedt, 2023). The number of oocytes carried by a female *P. periphylla* increases with the medusa size and can be as high as 1000 oocytes per female in a 12 cm diameter, 9 year old female (Båmstedt et al., 2020; Båmstedt, 2023). This species has only been found in significant numbers in fjords, where there appears to be no predation or parasitism on the medusae, thus contributing to their longevity (Fosså, 1992). Within the fjords, *P. periphylla* medusae make vertical migrations to the surface during the night for reproductive purposes, allowing the fertilized eggs to sink to depths that prevent their predation by visual predators (Båmstedt et al., 2020), but leaving them vulnerable to the deep-water renewal (Båmstedt, 2023). Despite this strategy, and analogous to the planula settlement or the ephyra to medusa transition, the mortality in the fertilized egg to medusa transition exceeds 90% and can be almost complete in most cases (Båmstedt, 2023).

2.7 Combined effect of the control points over the life cycle

The predictability of jellyfish blooms is extremely limited because the "never-ending jellyfish joyride" is in fact strongly influenced by non-typically measured external conditions (Table 1). The magnitude of the link between planula settlement, polyp development, and medusae population size at any temporal and spatial scale is unexplored (Gibbons et al., 2016), but from our review it can be inferred that the blockage of the life cycle in any of the stages by any of the aforementioned factors can limit the occurrence of future blooms, while, on the other hand, the success of the different developmental stages may increase the number of individuals by orders of magnitude from tens, asexually in the benthic phase, to millions, sexually in the pelagic phase (Figure 2; Table 1). This means that the collapse of a scyphozoan population can be followed by a sudden explosive recovery of the same through the survival of sparse medusae from the previous season or through the reception of a few new individuals that restore

TABLE 1 Effect and magnitude of the different factors modulating the biological processes of the developmental stages during the scyphozoan life cycle.

Developmental stage	Biological process	Factor	Effect	Magnitude	Studied species	References
Planula	Settlement	Maximum yield		60% of the released planulae	*Acromitus hardenbergi, Aurelia* spp., *Catostylus tagi, Chrysaora* spp., *Cotylorhiza tuberculata, Cyanea* spp., *Nemopilema nomurai, Rhizostoma octopus, Rhopilema esculentum*	Holst and Jarms, 2007; Javidpour et al., 2009; Prieto et al., 2010; Kuplik et al., 2015; Franco, 2016; Dong et al., 2018; Gambill et al., 2018; Takao and Uye, 2018; Feng et al., 2021; Gueroun et al., 2021; Miyake et al., 2021; Boughton et al., 2023; Holst et al., 2023
		Temperature (not optimal)	Longer settlement time	Up to 30 days of delayed settlement		
			Decreased settlement success	Up to 100% reduction of efficiency		
		Salinity (not optimal)	Decreased settlement success and mortality	Up to 100% reduction of efficiency and up to 100% mortality		
		Light (absence)	Decreased settlement success in zooxanthelated species	Up to 75% reduction of efficiency		
			Increased settlement success in non-zooxanthelated species	Up to 40% increase of efficiency from high light intensity to low intensity or absence of light		
		Substrate (type)	Better performance on artificial substrate	0 to 60% higher settlement on artificial substrate		
		Substrate (orientation)	Differential preferencies between species	Generally better performance in substrate undersides		
		Predation	Removal of planulae	Removal of 10 to 40 planulae $\times$ ind^{-1} $\times$ h^{-1}		
		Fouling organisms	Reduction of available space	Negative, not quantified		
	Excystment	Maximum yield		45% of the settled planulae	*Catostylus tagi, Cyanea* spp., *Rhopilema esculentum*	Fu et al., 2019; Gueroun et al., 2021; Holst et al., 2023
		Temperature (not optimal)	Decreased excystment success	Up to 100% reduction of efficiency		
		Salinity (not optimal)	Decreased excystment success	Up to 60% reduction of efficiency		
		Salinity (oscillation)	Decreased excystment success	Up to 27% reduction of efficiency		
		Food	No effect	No effect		

(Continued)

TABLE 1 Continued

Developmental stage	Biological process	Factor	Effect	Magnitude	Studied species	References
Polyp	Metamorphose from planulae	Temperature (not optimal)	Abnormal polyp development	Up to 60% reduction in the number of tentacles per polyp	*Catostylus tagi, Cyanea* spp.	Gueroun et al., 2020; Holst et al., 2023
		Salinity (not optimal)	Abnormal polyp development	Up to 20% reduction in the number of tentacles per polyp		
		Food (absence)	Abnormal polyp development	Up to 50% reduction in the number of tentacles per polyp		
	Asexual reproduction	Maximum yield		8-30 polyps derived from the original	*Aurelia* spp., *Cassiopea* sp., *Cephea cephea, Cotylorhiza tuberculata, Chrysaora* spp., *Lychnorhiza lucerna, Mastigias papua, Nemopilema nomurai, Phyllorhiza punctata, Rhizostoma* spp., *Rhopilema esculentum, Sanderia malayensis*	Hernroth and Gröndahl, 1983; Purcell et al., 1999; Holst et al., 2007; Purcell et al., 2007; Di Camillo et al., 2010; Prieto et al., 2010; Lucas et al., 2012; Pascual et al., 2015; Schiariti et al., 2014; Takao et al., 2014; Wang et al., 2015; Treible and Condon, 2019; Rato et al., 2021; Rekstad et al., 2021; Schäfer et al., 2021; Tang et al., 2021; Zang et al., 2023
		Asexual reproduction strategy	Better performance by multi-mode asexual reproduction species	0 to 95% asexual reproduction rate reduction from multi-mode to mono-mode strategy		
		Temperature (not optimal)	Decreased asexual reproduction rate	Up to 90% reduction of the asexual reproduction rate		
			Mortality of the polyps	Up to 100% in 30 days		
		Temperature (optimal)	Higher asexual reproduction rates at higher temperatures	2 to 5 times increase in the asexual reproduction rate		
		Salinity (not optimal)	Decreased asexual reproduction rate	Up to 90% reduction of the asexual reproduction rate		
			Decreased survival rate	Up to 60% decrease in survival rate		
		Food (absence)	Inhibition of asexual reproduction	Up to 100% reduction of the asexual reproduction rate		
		Food (absence) + Temperature (optimal)	Polyp mortality	Up to 100% polyp mortality		
		Light (absence)	No effect	No effect		

(Continued)

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TABLE 1 Continued

Developmental stage	Biological process	Factor	Effect	Magnitude	Studied species	References
		Long-term cultures	Transgenerational loss of asexual reproduction capacity	Up to 30% of asexual reproduction rate decay		
		Fouling organisms	Displacement and mass mortality by slimy surface organisms	Up to 100% of species replacement		
			Colonization of sessile organisms' hard structures	Positive, not quantified		
		Predation	Removal of polyps	Up to 300 polyps × ind^{-1} × day^{-1}		
Strobila	Strobilation	Maximum yield	Monodisc strobilation	1 ephyra/polyp	*Aurelia* spp., *Cassiopea* spp., *Catostylus mosaicus, Cephea cephea, Chrysaora hysoscella, Cotylorhiza tuberculata, Cyanea* spp., *Lychnorhiza lucerna, Mastigias papua, Nausithoe aurea Nemopilema nomurai, Phyllorhiza punctata, Rhizostoma* spp., *Rhopilema* spp., *Stomolopus meleagris*	Kikinger, 1992; Purcell et al., 1999; Stampar et al., 2008; Prieto et al., 2010; Fuentes et al., 2011; Astorga et al., 2012; Holst, 2012; Lucas et al., 2012; Pascual et al., 2015; Feng et al., 2017; Treible and Condon, 2019; Feng et al., 2020; Enrique-Navarro et al., 2021; Schäfer et al., 2021; Jensen et al., 2023; Wang F. et al., 2023
			Polydisc strobilation	Up to 30 ephyrae/polyp		
		Temperature (oscillation)	Trigger strobilation	Up to 80% increase in total strobilating polyps		
		Temperature (not optimal)	Inhibition of strobilation	Up to 100% reduction in the strobilation rate		
			Polyp mortality	Up to 100% polyp mortality		
		Salinity (not optimal)	Inhibition of strobilation	Up to 100% reduction in the strobilation rate		
		Light (absence)	Inhibition of strobilation in some zooxanthelated species	100% reduction in the strobilation rate		
		Zooxanthellae (absence)	Inhibition of strobilation in some zooxanthelated species	100% reduction in the strobilation rate		
		Microbiome (absence)	Inhibition of strobilation	Up to 85% reduction in the strobilation rate		
		Food (absence)	Inhibition of strobilation	100% reduction in the strobilation rate		
			Polyp mortality	Up to 100% polyp mortality		

(Continued)

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TABLE 1 Continued

Developmental stage	Biological process	Factor	Effect	Magnitude	Studied species	References
		pH (future scenario)	Malformed ephyrae	Abnormal rhopalium development		
		Long-term cultures	Increased ephyra production per polyp	Up to double the number of ephyrae per polyp		
	Post-strobilation	Stress	Calyx diameter shrinkage	Up to 75% reduction of calyx diameter	*Aurelia* spp., *Cotylorhiza tuberculata, Cyanea nozakii, Nemopilema nomurai, Rhopilema* spp., *Rhizostoma pulmo*	Kikinger, 1992; Lotan et al., 1992; Prieto et al., 2010; Fuentes et al., 2011; Feng et al., 2017; Chi et al., 2022
			Polyp' residuum mortality	Up to 100% polyp mortality		
			Regrowth of the tentacles and survival	Up to 100% polyp recovery		
Ephyra	Ephyra to medusa transition	Maximum yield		1 medusa per ephyra	*Aurelia* spp., *Cassiopea xamachana, Cephea cephea, Chrysaora* spp., *Cotyorhiza tuberculata, Cyanea nozakii, Lychnorhiza lucerna, Pelagia noctiluca, Phyllorhiza punctata, Rhizostoma pulmo, Stomolophus meleagris*	Ishii et al., 2004; Astorga et al., 2012; Wang and Li, 2015; Wang and Sun, 2015; Carrizo et al., 2016; Chambel et al., 2016; Miranda et al., 2016; Schäfer et al., 2021; Ballesteros et al., 2022; Muffett et al., 2022; Fernández-Alías et al., 2023; Wang P. et al., 2023
		Temperature (optimal)	Reduced time in the ephyra to medusa transition	Not quantified		
		Temperature (not optimal)	Ephyrae mortality	Up to 100% ephyrae mortality		
		Salinity (not optipal)	Ephyrae mortality	Up to threefold increase in mortality risk		
		Food (quality and quantity)	Reduction in growth	Up to 45% reduction in growth under inadequate feeding regime		
			Ephyrae mortality	Up to 100% ephyrae mortality under inadequate feeding regime		
		Light (absence)	Reduced growth and bleaching in zooxanthelated species	Up to 4.5 times reduction in size in growth experiments		
		Predation	Removal of ephyrae	Removal of more than 7 ephyrae × ind-1 × h^{-1}		
Medusa	Growth and sexual reproduction	Maximum yield		1.7×10^4 to 2×10^6 planulae per female	*Acromitus hardenbergi, Aurelia* spp., *Cassiopea* spp., *Catostylus* spp., *Cephea cephea, Chrysaora* spp., *Cotylorhiza tuberculata, Crambione* spp, *Crambionella* spp., *Cyanea* spp., *Dyrmonema* spp., *Linuche unguiculata, Lobonema smithi, Lobonemoides* spp., *Lychnorhiza*	Kremer et al., 1990; Kikinger, 1992; Lucas, 1996; Kawahara et al., 2006; Bayha et al., 2012; Heaslip et al., 2012; Chiaverano et al., 2015; Brotz, 2016; Båmstedt et al., 2020; Fernández-Alías et al., 2020; Ciriaco et al., 2021;
		Size of the individual	Increased gametes/planulae production with size	Positive		

(Continued)

TABLE 1 Continued

Developmental stage	Biological process	Factor	Effect	Magnitude	Studied species	References
		Parasitism	Decreased medusa diameter	Up to 20% reduction in size	*lucerna, Nemopilema nomurai, Periphylla periphylla, Phyllorhiza punctata, Rhizostoma* spp., *Rhopilema* spp., *Stomolophus meleagris*	Båmstedt, 2023; Mammone et al., 2023; Wang P. et al., 2023
			Lower egg production	Up to 50% reduction in egg production		
			Higher egg size	Up to 30% increase in egg sizes		
		Predation	Removal of medusae	Up to 330kg of medusae × ind^{-1} × day^{-1}		
		Fisheries	Removal of medusae	7.5×10^{8} kg of medusae × $year^{-1}$		

Studied species and references are indicated for each biological process. The rows were shaded differently for each biological process to ease the reading.

the population. Examples of the same are the recovery of the population of *Mastigias* sp. Agassiz, 1862 in the Jellyfish Lake (Palau) (Martin et al., 2006) or the recovery of the population of *C. tuberculata* in the Mar Menor (Spain) (Fernández-Alías and Pérez-Ruzafa, 2023). In the case of *Mastigias* sp., the collapse of the population was attributed to a warming of the waters beyond its tolerance limit, and the recovery of the same to a decrease in water temperature, both physical events driven by El Niño/Southern Oscillation (ENSO) (Dawson et al., 2001; Martin et al., 2006). For *C. tuberculata*, the control of the population is part of a complex top-down and bottom-up equilibrium in which phytoplankton could prevent the light from reaching the substrate, thus inhibiting the strobilation, while *C. tuberculata* predates on the phytoplankton and the symbiont zooxanthellae compete with the same for nutrient uptake (Pérez-Ruzafa et al., 2002; Fernández-Alías et al., 2020; Fernández-Alías et al., 2022; Fernández-Alías and Pérez-Ruzafa, 2023; Fernández-Alías et al., 2023).

3 Main challenges and future research directions

The small size and fragility of the larval stages (planula, polyp and ephyra) of scyphozoan species has limited the number of field studies on them, as it is difficult to find them and monitor their interactions with biotic and abiotic factors (Feng et al., 2017; Marques et al., 2019; Fernández-Alías et al., 2020; van Walraven et al., 2020; Leoni et al., 2021a; Boughton et al., 2023; Fernández-Alías et al., 2023; Zang et al., 2023). However, far from being discouraging, it should be noted that since the proposal of the conceptual framework for a general increase of jellyfish in the ocean (Arai, 2001; Purcell, 2005; Purcell et al., 2007; Richardson et al., 2009; Purcell, 2012), our knowledge of the factors that contribute to modulate the intensity of proliferations has greatly increased (Table 1).

Nevertheless, we are still far from developing truly useful predictive modeling tools, given the limited number of species for which each individual factor has been studied (Table 1) and the asymmetric response of different scyphozoan species to biotic and abiotic factors (Purcell et al., 1999; Schiariti et al., 2014; Feng et al., 2017; Fernández-Alías et al., 2021; Fernández-Alías et al., 2023). This likely limits the reliability of multispecies analyses across broad spatial and temporal scales (Brotz et al., 2012; Condon et al., 2013), but reinforces the need to build models that are site- and species-specific (Fernández-Alías et al., 2021). In this line, we propose a future research path that addresses the main knowledge gaps and sources of variability in jellyfish abundance to improve our understanding of the complex interactions (Figure 3).

3.1 Planula stage

The planula stage is affected by physiological stress, interspecific competition for the substrate, and predation. However, even if suboptimal environmental conditions for planula settlement reduce the success of this biological process (Table 1), in nature planulae are typically released under optimal settlement conditions (Prieto et al., 2010; Rosa et al., 2013; Franco, 2016; Boughton et al., 2023). Therefore, we believe that planula settlement is more likely to be constrained by substrate availability and predation. We propose a potential research pathway to increase our knowledge of planula settlement efficiency in nature: testing the effects of substrate competition with both other potential settlers and previous colonizers, and calculating the effect of predation on planulae over the initial polyp population density.

Planulae are known to settle efficiently on bare substrate (Prieto et al., 2010; Franco, 2016; Boughton et al., 2023; Holst et al., 2023), but the competition for hard substrate in the ocean is one of the clearest examples of competition in nature (Dial and Roughgarden, 1998;

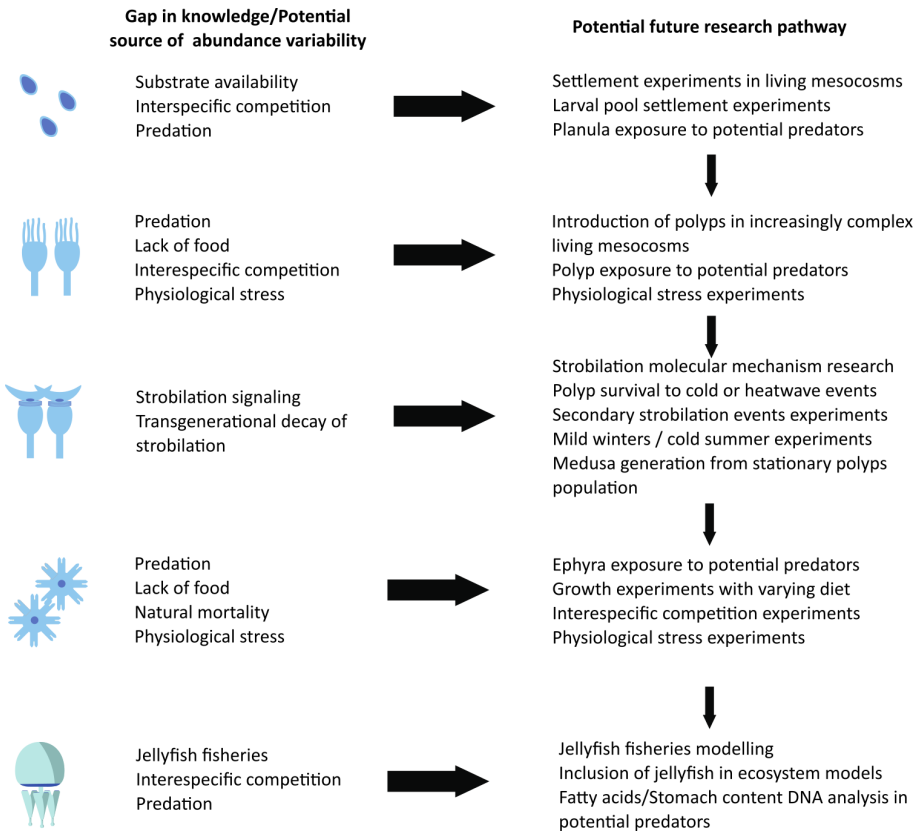

FIGURE 3
Main potential sources of abundance variability and gaps in knowledge along the potential research pathway to improve our forecast on scyphozoan jellyfish blooms.

Connolly and Roughgarden, 1999). This substrate is typically dominated by species with an adult benthic phase, but the experimental designs of planula settlement have mostly been conducted on non-living substrates. The only examples we are aware of are a settlement experiment of *C. tuberculata*'s planulae on living oyster's shells with 0% settlement success (Franco, 2016), and a second in which *C. nozakii*'s planulae were uncapable of settling on plates heavily colonized with biofouling organisms (Feng et al., 2021). Therefore, we suggest conducting planula settlement experiments in living mesocosms with bare and colonized substrate.

Marine species with a benthic adult phase have pulses of reproductive activity when the larvae are released into the water column before resettling to complete the life cycle (*e.g.* Gittings et al., 1992; Cárdenas and Aranda, 2000), and planulae compete with the larval pool present in the water column for the space in which to settle (Boughton et al., 2023). However, the observation of this competition is based on a single scyphozoan species and ecosystem (Boughton et al., 2023), and a quantification of the magnitude of the competition is lacking (Table 1). This highlights the need for settlement experiments with a larval pool of potential colonizers rather than just the scyphozoan planulae.

Finally, even though there is some evidence for the presence of planulae's predators (Javidpour et al., 2009; Kuplik et al., 2015), the effect of planula removal by naturally present predators on population dynamics is unknown, indicating the need for further research on planula exposure to potential predators.

3.2 Polyp stage

The polyp stage faces a similar set of factors as the planula stage (Table 1), but contrary to what happened to the planulae, the perennial presence of polyps in most scyphozoan life cycle strategies (Fernández-Alías et al., 2021) implies that the role of physiological stress is higher in this stage. In fact, the further away the polyp population is from its optimal conditions, the lower the asexual reproduction rate and the higher the polyp mortality rate (Prieto et al., 2010; Wang F. et al., 2023). Therefore, when constructing polyp density models, it is important to consider where the thresholds of tolerance are and how long the benthic population is exposed to these inadequate conditions. Our information on these thresholds is limited to a few species, and yet it is sufficient to determine that they are species specific (Purcell et al., 1999; Schiariti et al., 2014). Thus, it is a prerequisite to know the thresholds, the decline in asexual reproduction, and the survival of the modeled species under inadequate conditions.

Most studies of polyp population dynamics have been conducted in the absence of competitors, synergistic organisms, or predators (Prieto et al., 2010; Purcell et al., 2012; Schiariti et al., 2014; Treible and Condon, 2019). These interactions should not be neglected, as their overall balance may be detrimental to the scyphozoan polyp populations (Feng et al., 2017; Zang et al., 2023). To fully understand polyp dynamics, it is necessary to increase the biological complexity of the mesocosms in which the physiological stress experiments are conducted.

3.3 Strobila and post-strobila stages

Strobilation is a stressful process for polyp populations (Feng et al., 2017), and their posterior recovery is not guaranteed in some species, while others have better chances (Prieto et al., 2010; Fuentes et al., 2011; Feng et al., 2017). In this context, it remains unclear why certain conditions, which could be cold or heat waves, trigger the strobilation process, when their return to normal water temperatures could affect the correct development of ephyrae into medusae (Fernández-Alías et al., 2023). It has also been shown that the strobilation process and the ephyra production are affected by the minimum sea temperature reached during the winter season, the length of the winter season, the water warming speed and the food regime (Feng et al., 2015a; Feng et al., 2015b; Loveridge et al., 2021; Zang et al., 2022), factors that should be further studied to increase our bloom predicting tools.

A better understanding of the process could be achieved with a complete description of the molecular mechanism of strobilation (Helm et al., 2018), but for now our knowledge of the molecular pathway is limited to certain aspects and to the genus *Aurelia* (Fuchs et al., 2014; Brekhman et al., 2015; Khalturin et al., 2019; Jensen et al., 2023). In fact, we are not aware of the presence of the gene CL390, the most overexpressed gene in the strobilation process (Fuchs et al., 2014; Brekhman et al., 2015), in any other scyphozoan species outside this genus. In the nucleotide database (GenBank) of the National Center for Biotechnology Information (https://www.ncbi.nlm.nih.gov/, accessed on 30 November 2023) there are only 4 DNA sequences of the gene translated into this protein, all of them belonging to *Aurelia*, and launching a Basic Local Alignment Search Tool (BLAST) with the most permissive parameters does not provide any additional sequence from a scyphozoan species (Fernández-Alías, A., unpublished result). Of the four available sequences, only two are supported by a publication, the one sequenced in Fuchs et al. (2014) and the one from Brekhman et al. (2015). Moreover, their transcribed proteins have only 68% identity (Brekhman et al., 2015), and their expression is induced by opposite temperature changes, a decrease in the case of the Fuchs et al. (2014) gene and an increase in the case of the Brekhman et al. (2015) gene. Therefore, there is a need for more transcriptomic analysis throughout the life cycle of the different scyphozoan species.

Finally, polyp populations have been reported to decrease their asexual reproduction rate within successive generations, but this may be associated with a higher ephyra production per polyp (Chi et al., 2022; Holst et al., 2023), and the overall balance of long-lived polyp populations in ephyra production remains unclear. In addition, medusae developed from long-lived polyp cultures in the aquarium may show abnormal pulsation or even absence of pulsation (Fernández-Alías, pers. obs.), suggesting a need for refreshment of benthic populations.

3.4 Ephyra stage

It takes between 10 and 150 days for the ephyrae to reach the medusa stage, with an average success rate of less than 30% (Ishii et al., 2004; Kawahara et al., 2006; Fuentes et al., 2011; Astorga et al., 2012; Fernández-Alías et al., 2020; Gueroun et al., 2020; Fernández-Alías et al., 2023). Predation and physiological stress have been identified as the two most important factors affecting mortality at the ephyra stage (Table 1), but evidence is limited. The extremely fast digestion rate of the medusa phase has made it difficult to detect them as prey by stomach content analysis (Arai et al., 2003), and given their smaller size, the lack of detection of the ephyra phase in predator stomachs should be more acute. In fact, all the collected evidence on predation of ephyrae is based on their direct exposure to predators in aquarium experiments (Table 1), and the list of potential predators is likely to be much more extensive than those observed so far. The composition of the planktonic community available for the ephyrae to prey on is likely to influence proper development to the medusa stage (Chambel et al., 2016; Miranda et al., 2016; Ballesteros et al., 2022), suggesting the need to monitor the plankton assemblages along the ephyrae and medusae and conduct experiments to determine the most appropriate diet for the ephyrae. Finally, the disappearance of ephyrae when temperature conditions were inadequate has been observed in long-term studies (Fernández-Alías et al., 2023), but they did not discriminate whether temperature was the primary cause of mortality or whether it was starvation or the long-term exposure to potential predators without reaching the medusa phase. Thus, physiological stress experiments need to be conducted to determine the resilience of the ephyrae to inadequate conditions for their development.

3.5 Medusa phase

Once a bloom of a species occurs, interest usually shifts to the socioeconomic impacts of the massive proliferation and how to mitigate them (Bosch-Belmar et al., 2020), and less attention is paid to the implications of its development for subsequent seasons. In fact, attention to future blooms seems to have gained interest only since the development of jellyfish fisheries threatened by interannual variability in medusae abundance (Brotz et al., 2017), and yet not many efforts have been made to calculate the biological parameters required to implement sustainable fishing programs (Palomares and Pauly, 2008; Brotz, 2016; Fernández-Alías et al., 2020; López-Martínez et al., 2020; Leoni et al., 2021a; Behera et al., 2022). Traditionally considered a trophic "dead end" (Hays et al., 2018), medusae are not typically included in ecosystem management models (Pauly et al., 2008), and larval stages are

even less likely to be included in these models, despite their potential to influence adult abundance (Table 1). The inclusion of jellyfish in ecological models is particularly important in small, sheltered ecosystems, since the smaller the ecosystem, the greater the importance of jellyfish as keystone species (Pauly et al., 2008), to the point where they can act as top pelagic predators and as a buffer against dystrophic crises in eutrophicated coastal lagoons (Pérez-Ruzafa et al., 2002; Fernández-Alías et al., 2022; Fernández-Alías et al., 2023). In this line, it is also important to consider that the trophic role of scyphozoan jellyfish changes between species, within species between locations, and throughout their ontogeny (Holst et al., 2007; Marques et al., 2020; Wang et al., 2020; Leoni et al., 2022). For the correct implementation of these models, we need to put more effort in the parameterization of jellyfish growth and in the determination of trophic links with upper and lower levels.

4 Conclusions

The scyphozoan life cycle has the potential to numerically increase the number of individuals in the order of several million during a single generation, but the contour conditions can block the life cycle and cause a collapse of the population. The complex interactions between the different developmental stages of the life cycle and the set of biotic and abiotic factors are the main causes of the interannual variability in the abundance of the medusa phase, the most conspicuous stage of the life cycle. During the last decade we have increased our knowledge of the controlling factors that modulate the densities of the different developmental stages, but we are still far from being able to provide reliable predictions of the scyphozoan blooms. Therefore, it is important to distinguish between what it is known and what remains a gap in knowledge to effectively direct the future research on this topic.

Temperature seems to be the most important factor involved in the correct development of the life cycle, triggering processes and favoring the transition between phases when it is optimal, and causing mass mortality or abnormal development when it is not. The second important factor is the availability of food, the quality and quantity of which modulate the asexual reproduction, the strobilation process and the somatic growth. In general, the factors regulating the transition between the different stages of the life cycle would be what allows the species to anticipate adequate conditions for the development and growth of the individuals. In this context, food availability, productivity, and temperature act in concert with salinity, being it a key factor in many tropical and sheltered habitats, prone to host scyphozoan blooms, where salinity fluctuates due to storms, flash floods, and evapotranspiration, affecting the life cycle and the species distribution. In the same way, salinity may play a key role in the Mediterranean Sea under temperature rising scenarios. Despite their importance, these factors are reported to act asymmetrically between the different scyphozoan species, and here appears one of the most important limitations in our ability to predict massive proliferations: the knowledge we have generated is species-specific and cannot be extrapolated to the whole class. Moreover, for most of the species the magnitude of the effect of these factors in some (or in all) of the biological processes that take place during the life cycle is unknown.

A second gap in our knowledge is the interspecific interactions between the scyphozoan species and the other faunistic groups. As a scientific community, we have reported the existence of numerous relationships between scyphozoan jellyfish and the other groups, including predator-prey interactions, both in the benthic and the pelagic stages, competition for the substrate in the planula settlement and polyp dynamics, symbiosis, commensalism, and parasitism. However, the description of the relationships is still in its infancy, not yet quantified and most likely we still underestimate the number of predators and competitors for the different stages.

To improve our forecasting ability, our research should focus on determining the parameters needed to implement ecosystem-based models. This includes determining the environmental tolerance limit for each species and stage, parameterizing how the growth, asexual reproduction, strobilation and mortality rates vary under inadequate conditions, and determining the interspecific and trophic relationships by progressively increasing the complexity of the design of the mesocosms in which the experiments are conducted.

Author contributions

AF-A: Conceptualization, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. CM: Funding acquisition, Project administration, Writing – review & editing. APR: Conceptualization, Funding acquisition, Project administration, Supervision, Visualization, Writing – review & editing.

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Conflict of interest

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

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Top predator status and trends: ecological implications, monitoring and mitigation strategies to promote ecosystem-based management

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The conservation and management of marine ecosystems hinge on a comprehensive understanding of the status and trends of top predators. This review delves into the ecological significance of marine top predators, examining their roles in maintaining ecosystem stability and functioning through an integrated analysis of current scientific literature. We first assess the efficacy of various monitoring methods, ranging from traditional field observations to cutting-edge technologies like satellite tracking and environmental DNA (eDNA) analysis and evaluating their strengths and limitations in terms of accuracy, spatial coverage, and cost-effectiveness, providing resource managers with essential insights for informed decision-making. Then, by synthesizing data from diverse marine ecosystems, this study offers a comprehensive overview of the trends affecting top predator populations worldwide. We explore the multifaceted impacts of human activities, climate change, and habitat degradation on the abundance and distribution of these key

species. In doing so, we shed light on the broader implications of declining top predator populations, such as trophic cascades and altered community structures. Following a thorough assessment of successful strategies for reversing the decline of top predators, a compilation of recommendations is presented, encompassing effective governance interventions. A crucial aspect of effective ecosystem-based management is the implementation of robust monitoring strategies. Mitigation measures are imperative to reverse the adverse impacts on marine top predators. We present a comprehensive array of mitigation options based on successful case studies. These include the establishment of marine protected areas, the enforcement of fisheries regulations, and the promotion of sustainable fishing practices. We deepen the synergies between these strategies and their potential to mitigate human-induced stressors on top predator populations to safeguard their pivotal role in maintaining marine ecosystem structure and function. By examining marine top predators' ecological significance, analyzing population trends, discussing monitoring techniques, and outlining effective mitigation strategies, we provide a comprehensive resource for researchers, policymakers, and stakeholders engaged in fostering ecosystem-based management approaches. We conclude that integrating these insights into current management frameworks will be essential to safeguard both top predators and the broader marine environment for future generations.

KEYWORDS

top predators, monitoring, ecosystem-based management, ecosystem modelling approach, population trend estimation

1 Introduction

1.1 Marine top predators in a changing environment

In the Anthropocene Era, marine predators occupying high trophic levels - including some marine mammal, elasmobranch, large teleost, and seabird species - have been reported to be rapidly declining worldwide and are generally assessed as threatened or in poor population conservation status (Ferretti et al., 2008; Phillips et al., 2016; Dulvy et al., 2017; Rodríguez et al., 2019; Burgess and Becker, 2022). In addition to the issue of increasingw extinction risk, top predator populations' fluctuations have been linked to cascading effects in food webs, behavioral modifications in prey communities, and overall losses of ecosystem functions and services (Myers et al., 2007; Heithaus et al., 2008; Baum and Worm, 2009; Estes et al., 2016).

The main drivers of top predators declines include historical hunting, overfishing, fishery-related bycatch, habitat degradation and loss exacerbated by climate change, prey depletion due to overfishing, invasive species, and other interacting local and global stressors (Pauly et al., 1998; Pauly, 2000; Jackson et al., 2001; Myers and Worm, 2003; Lotze et al., 2006; Ryan et al., 2009; Dias et al., 2019; Ripple et al., 2019; Giménez et al., 2022; Juan-Jordá et al., 2022). In recent years, the escalating climate crisis and the depletion of marine food resources have pushed forward Marine Renewable Energy solutions (e.g., offshore wind farms, offshore hydrogen production, technologies exploiting wave and tidal energy, floating solar photovoltaic energy, etc.) (Borthwick, 2016) and seafood production through mariculture (Campbell et al., 2021). These are important Blue Economy sectors and are generally considered as environmentally friendly. However, they introduce novel and poorly understood stressors on marine ecosystems. If not properly managed or regulated, these emergent '*uses of the sea*' could contribute to cumulative pressures with significant repercussions on top predator populations and their prey (Bailey et al., 2014).

High trophic-level predator declines have alarmed the scientific community because they compromise the sustainability of whole social-ecological systems. Top predators are instrumental in nutrient cycling, carbon sequestration, habitat engineering, and counterbalancing biological invasions. Their value is also linked to socio-economical aspects, e.g., fishery sustainability, tourism, and bioinspiration (Atwood et al., 2015; Doughty et al., 2016; Haas et al., 2017; Hammerschlag et al., 2019). In addition, marine top predators can be used as sentinels of marine ecosystem status (Hazen et al., 2019; Coll et al., 2019b), and changes in their abundance can act as an early warning of decreasing marine health and trigger species and ecosystem conservation interventions. In this context, our ability to track population trends in marine top predators is key for monitoring the Good Environmental Status (GES) under the European Union Marine Strategy Framework Directive (MSFD;

Directive 2008/56/EC) and other similar frameworks (e.g., UN Regional Sea Conventions (RSCs; OSPAR for the north-east Atlantic, HELCOM for the Baltic Sea, Barcelona Convention for the Mediterranean Sea, and Bucharest Convention for the Black Sea), and for informing management actions. For example, 23% of the Indicators of the OSPAR 2023 Quality Status Report on the Northeast Atlantic targeted top predators. See sections 5.1 for a detailed example under the MSFD.

Given all this, conventional sectoral management and piecemeal governance, focusing on a single species or economic sector (e.g., fisheries), is generally seen as an ineffective approach to halting biodiversity loss and securing sustainable use of marine resources. Holistic approaches are necessary to understand ecosystem processes (Pikitch et al., 2004; Curtin and Prellezo, 2010; Long et al., 2015) and enable the conservation of top predators by implementing an ecosystem-based approach. Policy and management strategies need to be informed by a fair understanding of: (i) top predators' role in ecosystem functioning and services; (ii) the socio-ecological implications of changes in their populations, in particular of processes associated with changes in their abundance and distribution, e.g., due to climate change (driver-pressure-state-impacts) to assess plausible socio-economic scenarios; (iii) conflicts caused by ocean human uses; (iv) management options and tradeoffs costs and effectiveness. This translates into an overall assessment of the costs and benefits of conservation efforts.

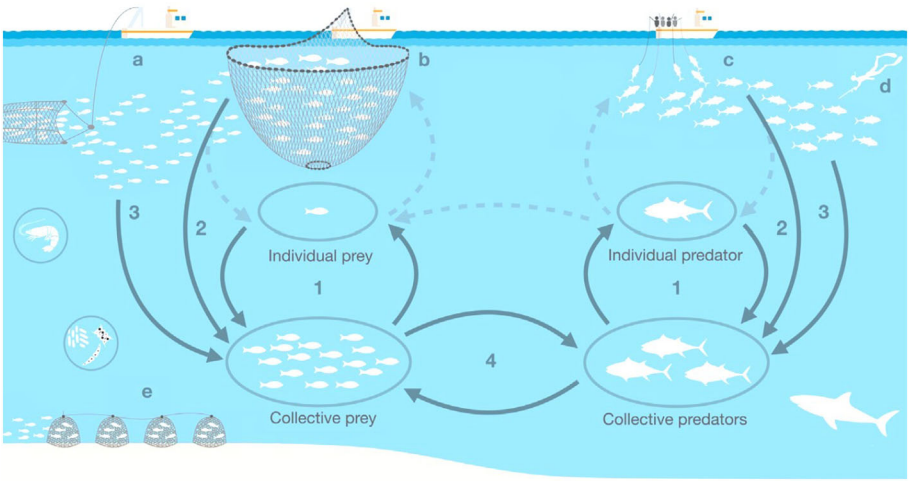
Notwithstanding the importance of the holistic approach, dedicated management approaches may be still required for marine top-predator populations and species known to be in very 'unfavorable conservation status'. The full and/or partial recovery of some top predators, such as for example several species of whales subject to commercial whaling, and of swordfish and tunas subject to large pelagic driftnetting (see examples in Box 1 and section 7) in the 1970-80s, were possible thanks to drastic sectorial measures banning those activities and implementing quotas (UNGA, 1990a, b; UNGA 1992; European Council, 1992; European Council, 1997; European Union, 2019).

From a public perspective, there is a relatively limited number of flagship marine top predators. Among them, for example, the charismatic polar bear (*Ursus maritimus*), the feared killer whales (*Orcinus orca*), and the great white sharks (*Carcharodon carcharias*). In this review, we consider 'top predators' in a broad sense. These are species that predominantly feed at or near the top of the food web in their ecosystem (upper trophic level consumers) and are relatively free from predation once they reach adult size. Hence, in this review, top predators are not completely free of predation risk, and they may not always occupy the top predator position throughout their life history or across all habitats within their spatial distributions (Sergio et al., 2014).

With a focus on the global policy context, this review critically considers: (i) the existing knowledge on the status and trends of top predators; (ii) the best practices to improve their monitoring,

BOX 1 - The recovery of the Atlantic bluefin tuna

A recent example of recovery, following management measures and favorable environmental conditions, is that of the Atlantic bluefin tuna (*Thunnus thynnus*) eastern population, a species migrating between the Mediterranean and the eastern Atlantic. In 2007, this bluefin tuna population was considered depleted due to a 60% decline in spawning biomass compared to 1970s levels, a population restructuring toward younger individuals, and predictions of stock collapse (Andrews et al., 2022). In the last two decades, the ICCAT has limited catches by imposing strict quotas (ICCAT, 2017), and strong surveillance of the bluefin tuna fishery has been implemented (Bjørndal, 2021). Such management measures, in combination with several years of favorable environmental conditions for spawning, have led to the recovery of the species to 1970s levels (ICCAT, 2020). However, the recovery of this predator may contribute to conflicts with fisheries targeting small pelagic fish (the main prey of bluefin tuna), which are currently overfished and subject to adverse climate conditions (Coll et al., 2019b; Sbragaglia et al., 2021).



Parallel pathways affecting fisheries-induced changes of shoaling behavior (This figure was published in Sbragaglia et al., 2021, Copyright Elsevier 2021) - Key: Factors affecting directly prey and predator shoaling behaviour: (1) ecological and behavioural traits, demographic and evolutionary processes; (2) fisheries targeting larger shoals. Factors indirectly affecting prey and predator shoaling behaviour: (3) fisheries influencing population density and fish group dynamics. Fishing techniques: (a) pelagic trawls; (b) purse seiners; (c) longliners; (d) recreational fishers; (e) traps/pots fishers.

including the potential of novel methods (e.g., eDNA, metabarcoding, biologgers, and remote sensing); (iii) data needs and modeling capacity for assessing the status and trends of top predators; (iv) management options to mitigate their decline in line with the marine biodiversity conservation policy framework.

After reviewing best practices in reversing top predator declines, we provide a set of recommendations on possible effective governance interventions, which would help prevent further declines and rebuild top predator populations.

1.2 Marine ecosystem and international policy framework

For top predators characterized by a large home range or performing migrations, international cooperation is fundamental in identifying and disentangling the underlying causes of changes in distribution and abundance and developing management measures to halt population declines (e.g., ACCOBAMS, 2021; Geelhoed et al., 2022). In 1995 the UN Convention on Biological Diversity (CBD) identified the 'Ecosystem Approach' as the main framework for biodiversity protection and sustainable use, from which most Ecosystem-based Management (EBM) terminology derives. This policy also relies on legal principles (e.g., articles 61-67) embedded in the UN Convention on the Law of the Sea (O'Hagan, 2020). The general objective of EBM is sustainable resource exploitation for the benefit of present and future generations (Long et al., 2017). The implementation of the CBD Ecosystem Approach was linked to various strategies, including the 12 Malawi Principles '*to take effective and urgent action to halt the loss of biodiversity*', the Strategic Plan for Biodiversity 2011–2020, the Aichi Biodiversity Targets and the latest post-2020 global biodiversity framework, which as an ultimate goal in 2050 has that '*biodiversity is valued, conserved, restored and wisely used, maintaining ecosystem services, sustaining a healthy planet and delivering benefits essential for all people*'. EBM recognizes the full array of interactions within an ecosystem, incorporating ecological, economic, social, and cultural perspectives and supporting an adaptive approach tailored to the scale of ecosystems (Katsanevakis et al., 2011). Due to dynamic ecosystems and a chronic lack of comprehensive knowledge of their functioning, the EBM needs to be adaptive (O'Hagan, 2020). In line with these global policies and related initiatives, halting the loss of biodiversity has been one of the key missions of several Regional Seas Conventions (e.g., the Barcelona Convention, OSPAR, HELCOM, etc.), regional Agreements under the Bonn Convention (e.g., Wadden Sea seals Agreement, Agreement on the Conservation of Albatrosses and Petrels, Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area, etc.) and regional supranational political and economic inter-governmental entities (e.g., the European Union). Regional commitments and policy tools (e.g., EU MSFD, Barcelona Convention EcAp (Barcelona Convention 2008, 2012, 2013, 2016), EU Maritime Spatial Planning Directive (Directive 2014/89/EU), Barcelona Convention Protocol on Integrated Coastal Zone Management in the Mediterranean (2008), EU Common Fisheries Policy, etc.) have, at least on paper, linked to the concept and ultimate goal of EBM, with contrasting results and some serious inconsistencies (e.g., Berg et al., 2015; O'Hagan, 2020). Such inconsistencies arise from the need for regional legislative and policy frameworks to transition from a sectoral management to more integrated approaches (O'Hagan, 2020). This transition requires (a) a shift in perspective, necessitating both the redesign of frameworks to accommodate additional/new expertise and to expand their geographical scope in terms of shared responsibility, as national jurisdictions are insufficient for ensuring success, and (b) a consistent and clear codification of terminology into legal and policy instruments (e.g., to incorporate the notion of 'healthy ecosystem', 'habitats', 'conservation status', 'pressure', 'state', 'impact', etc.) (Berg et al., 2015; O'Hagan, 2020). The latter is still far from being resolved, and the often ambiguous language in policies allows countries to implement them in rather different ways.

Examples of species and population recovery or stable decline in the Atlantic and Mediterranean Sea (Boxes 1, 2) demonstrate that management measures (or the lack of them) clearly affect the chance to deliver on the CBD's ultimate goal (i.e., '*living in harmony with nature*'; CBD, 2021). However, these frameworks often employ different monitoring and assessment approaches (e.g., due to the issue of scales, both geographic and temporal, to which legal requirements apply; O'Hagan, 2020), thus applying a holistic framework, such as the 'Ecosystem Approach', is a daunting task.

1.3 Effects of top predators on the whole marine ecosystem

The decline of marine top predators (e.g., Box 2) can have diverse and far-reaching ecological consequences. The disruption of food webs is the most studied consequence, as top predators play a crucial role in regulating prey populations (e.g., Ferretti et al., 2010). However, field experiments examining the effects of top predator declines on lower trophic levels have produced varying results, depending on the environment and habitat type (e.g., Heithaus et al., 2008). Declines of marine top predators have been associated with overgrazing, causing a cascade of ecological effects resulting in the loss of ecosystem functions and services (Atwood and Hammill, 2018; Bevilacqua et al., 2021). Such effects can drive regime shifts in coastal systems, leading to biodiversity decline (Guidetti, 2006). Fluctuations in marine top predator abundance can also impact the ecosystem structure; for example, predation loss can boost scavenger populations. Besides an ecosystem top-down control (Aarts et al., 2019), marine top predators contribute to various ecosystem services, such as nutrient cycling, nutrient deposition around their terrestrial sites (for pinnipeds and seabirds), soil formation in polar environments (Şekercioğlu et al., 2004), carbon sequestration, and cultural and recreational services (Roman and McCarthy, 2010).

There are several key examples of ecological consequences of marine top predator decline or loss. In a global analysis, Baum and Worm (2009) reported that declines in large predatory fish, such as sharks and tuna, were associated with changes in prey abundance and diversity and shifts in ecosystem structure and function. The

BOX 2 - The Mediterranean Sea case

The Mediterranean Sea is a hotspot of both biodiversity (Coll et al., 2010) and human uses and pressures (Coll et al., 2013; Micheli et al., 2013). It has suffered from overexploitation (Tsikliras et al., 2015), destructive fishing (Claudet and Fraschetti, 2010), marine pollution (Danovaro, 2003), including emerging pollutants such as marine litter (Anastasopoulou and Fortibuoni, 2019; Angiolillo and Fortibuoni, 2020; Fossi et al., 2020), global change (Chatzimentor et al., 2023), and invasive species (Tsirintanis et al., 2022). Various EU and regional environmental and conservation policies (e.g., MSFD, Habitats and Birds Directives, EU Biodiversity Strategy, Common Fisheries Policy, Barcelona Convention) aimed to safeguard Mediterranean Biodiversity and the sustainability of marine resources, with varying outcomes.

The Mediterranean monk seal

The conservation of the endemic Mediterranean monk seal, Monachus monachus, is an example of successful conservation efforts in the last decades. Although the species was assessed in 2008 as Critically Endangered with decreasing trend (Aguilar and Lowry, 2010), its global status was recently downgraded first to Endangered (2019) then to Vulnerable (2023), due to an increasing trend in abundance (Karamanlidis et al., 2019, 2023).

Monk seals were historically overexploited for subsistence needs and also killed by fishers due to causing damage to fishing gear and because seals were perceived as competitors for fish. habitat deterioration, coastal development, increased touristic activities, and accidental entanglement in fishing gear also contributed to their dramatic decline (Karamanlidis et al., 2015). By the mid-20th century, the species was eradicated from most of its former range. Since then, it has been protected throughout its range, and conservation measures over the past 30 years have led to an increasing trend in all known subpopulations (Karamanlidis et al., 2015). In all countries with significant monk seal populations, action plans for the conservation of the species have been established, including the protection of essential habitats via MPAs, mitigating interactions with fisheries, improved monitoring, education and public awareness, and rescue and rehabilitation of wounded, sick, and orphaned seals (Karamanlidis et al., 2015). The recent use of eDNA and citizen-science initiatives have offered complementary information on species presence and distribution (Valsecchi et al., 2023).

The case of Audouin's Gull in the Ebro Delta region

The Audouin's Gull (*Ichthyaetus audouinii*, formerly *Larus audouinii*) in the Ebro Delta region (Western Mediterranean) is an example of both successful management and challenges linked to managing predatory species. The breeding colony in the Ebro Delta showed a rapid growth between the early 1980s and 1990s (Oro and Martinez-Villalta, 1992). This growth can be attributed, in part, to the protection of their breeding area. However, the gulls' ability to exploit highly abundant and predictable food resources associated with human activities, such as fishing discards, also contributed to this trend (Oro et al., 2013). In fact, Audouin's gulls from the Ebro Delta have completely adapted their behavior to capitalize on these A'nthropogenic food resources' (Ouled-Cheikh et al., 2020, 2022). More recently, this colony has faced new challenges because of the arrival of foxes, prompting a substantial number of individuals to disperse to smaller and less accessible colonies (Payo-Payo et al., 2018).

Elasmobranchs

The Mediterranean Sea is a hotspot of extinction risk for sharks and rays (Dulvy et al., 2014). No improvement was observed between the regional International Union for the Conservation of Nature (IUCN) Red List assessments of 2006 and 2016 (Cavanagh and Gibson, 2007; Dulvy et al., 2016).

Indeed, compared to the previous assessment, threatened species increased from 42.3% (2006) to 53.4% (2016), probably due to the significant increase of species included in the CR Category. Pelagic sharks are particularly vulnerable to fishing gear, and the abundance of many species has declined by more than 90%, putting some Mediterranean species at high risk of extinction (Ferretti et al., 2008).

Semi-quantitative analyses of data from FAO, ICCAT, and MEDLEM databases - yielding more than 770 records gathered between 1860 and 2016 from different sources - revealed a significant decline in landings (in both tons and numbers) of some pelagic sharks and rays starting in the early 2000s (Moro et al., 2020). This trend mainly concerns basking sharks (*Cetorhinus maximus*), blue sharks (*Prionace glauca*), porbeagles (*Lamna nasus*), shortfin makos (*Isurus oxyrinchus*), common threshers (*Alopias vulpinus*), spinetail devil rays (*Mobula mobular*) and white sharks, whose negative trend began in the 1970s. Depending on the Mediterranean region, there were between 52% and 96% declines in catches and a contraction of distributions (Moro et al., 2020). The decline in reported catches may be due to a severe population decrease from overexploitation or more responsible fishing practices. Indeed, better enforcement of fishing regulations and banning large driftnets (UNGA, 1990a, b; UNGA 1992) in Mediterranean must have positively affected many marine organisms, including elasmobranchs, over the last decade. This may explain, for example, the increased frequency of sightings of spinetail devil rays (Mancusi et al., 2020), suggesting population recovery. For this reason, this species was considered in an IUCN Green Status assessment (Grace et al., 2022).

The critically endangered Balearic shearwater

The Balearic shearwater (*Puffinus mauretanicus*) is one of the most endangered seabird species in Europe - classified as Critically Endangered in the IUCN Red List (BirdLife International, 2021). It has a small breeding range and a relatively small population. This species is undergoing an extremely rapid decline, largely related to low adult (and immature) survival rates (BirdLife International, 2021), which is unusually low for a Procellariiform (Oro et al., 2004; Genovart et al., 2016). This is a long-lived species, and therefore the main threats to this species identified are those causing adult mortality.

The greatest threat is fishing bycatch, affecting adults and immatures throughout the species' range. It is the main driver of the species' decline, with almost 50% of the mortality caused by this factor (Genovart et al., 2016). Population models predict over 90% decline in three generations with an average extinction time of about 60 years (Genovart et al., 2016). The analyses were based on data from an important colony free of predators, meaning that the average survival rate of the whole population could be even lower (BirdLife International, 2021). Therefore, conservation measures related to reducing mortality in fishing gear are essential for the conservation of the species.

decline in shark abundance at coral reefs caused increases in mesopredator densities and changes in their behavior (Sherman et al., 2020). Similarly, Estes et al. (2009) showed that the decline of sea otters in the Aleutian Islands led to altered behavior and increased abundance of sea urchin, resulting in declines in kelp forests and other ecosystem changes. Along the California coast, the decline of sea otters and sea stars in kelp forests led to changes in prey abundance and diversity, including of sea urchins, crabs, and other invertebrates, which consequently affected the entire ecosystem structure and function (Duffy-Anderson et al., 2019).

The complete removal of top predators from an ecosystem can lead to significant changes in the biomass size spectrum, which can have profound implications for ecosystem function and stability. McCauley et al. (2010) and Atwood et al. 2015 demonstrated that the removal of large predatory fishes, such as groupers and snappers and large sharks, from coral reefs caused a shift towards smaller organism sizes in the biomass size spectra, with an increase in the abundance of small fish and invertebrates and a decrease in the abundance of large predatory fish, leading to deterioration of coral health. The impact of top predator removal on the biomass size spectra may vary depending on the type of ecosystem and the specific predators involved.

2 Monitoring approaches to detect trends of marine top predators

Various techniques are used to monitor abundance trends of marine top predators. These can be divided into 'direct monitoring methods' deploying visual and remote sensing tools, and 'indirect monitoring methods' using biogeochemical markers, eDNA, biologging, and emerging digital tools. The scope of these

approaches depends on the ecological features of the investigated top predators.

2.1 Direct sampling methods to assess trends of top predator distribution and abundance

2.1.1 Scientific trawling surveys

Trawling is one of the most common sampling methods applied to monitor fish, including elasmobranchs, both in fishery-dependent and scientific surveys. Various pelagic and bottom trawls are used to assess species' presence and estimate their relative abundance (catch per unit effort, CPUE) (Franco et al., 2022). Additional biological variables (e.g., body size, age structure, sex and maturity stage, and stomach content) can often be derived from the catch.

Examples of broad-scale and long-term bottom trawl monitoring programs applying random stratified sampling designs are the International Bottom Trawl Surveys (since 1965) coordinated by the International Council for the Exploration of the Seas (ICES, 2017; ICES, 2020) in the Baltic, North Seas, and adjacent North Atlantic waters and the Mediterranean International Trawl Survey (since 1994) (MEDITS: Spedicato et al., 2019). Data from these monitoring programs have been used to estimate demersal predators' abundance and distribution (e.g., ICES stock assessments) and to identify the environmental drivers of the population dynamics for some fish species (e.g., Follesa et al., 2019).

2.1.2 Fishery-dependent data

Onboard fishery observations are used to monitor commercially valuable top predators or non-target bycaught species, such as seabirds or marine mammals (e.g., Arcos and Oro, 2002; Louzao et al., 2011a; Field et al., 2013; Louzao et al., 2020). Landing data can also provide valuable information - including species, numbers, weight, and size - albeit with certain limitations. Such data offer broad spatial and temporal coverage of the abundance, distribution, and biological characteristics of fish populations, which can be used to develop conservation management strategies (e.g., Walsh et al., 2009). Onboard observers can help address some of the limitations of fishery-dependent surveys, such as biases resulting from management constraints or intentional misreporting of catches. However, logistic limitations (e.g., non-random sampling) are linked to the intrinsic fisheries nature. At present, only a small portion of fishing activities are monitored (Pennino et al., 2016); however, Remote Electronic Monitoring (REM) via video cameras is a powerful and promising monitoring tool that will improve understanding of the actual impact on top predators (Course et al., 2020).

2.1.3 Visual and acoustic surveys

The abundance and distribution of top predators, such as seabirds, marine mammals, and elasmobranchs at sea can be monitored through systematic aerial and vessel surveys (e.g., Fortuna et al., 2014; Giménez et al., 2018; Louzao et al., 2019; Waggit et al., 2019) and land-based visual surveys (e.g., Arroyo et al., 2016; den Heyer et al., 2021; Gutiérrez-Muñoz et al., 2021; IJsseldijk et al., 2021). These sampling methods can produce robust absolute or relative abundance estimates (e.g., Hammond et al., 2013; Authier et al., 2018; Saavedra et al., 2018; García-Barón et al., 2019; ACCOBAMS, 2021; Hammond et al., 2021). Visual surveys may require the correction of biases associated with observers, availability of species at the surface, weather conditions, and estimation of distances in boat-based surveys (Buckland et al., 2004; Borchers et al., 2006). Under specific conditions, data collected from platforms of opportunity (e.g., from ferries: Robbins et al., 2020; cargo ships, fishing vessels: Louzao et al., 2020; or whale watching: Pérez-Jorge et al., 2016) may be used to detect relative trends and complement the knowledge, e.g., on species presence. However, the lack of a systematic data collection approach can drive biases and low predictive power (e.g., Glad et al., 2019).

Many pinniped and seabird species breed or molt in colonies where they return annually, providing a unique opportunity to record changes in the population by surveying them via land-based or aerial surveys (Russell et al., 2019; ICES, 2022). In synchronous breeders, such counts often represent either a constant and known proportion of the entire population (e.g., during seal molt; Brasseur et al., 2018) or a key subset of the population (e.g., pups or breeding pairs of seabirds). This is not the case for asynchronous breeders (e.g., grey seal *Halichoerus grypus* pups; Russell et al., 2019), for which colony counts often represent a slightly variable proportion of a population subset. Even though these seasonal agglomerations do not represent their distribution at sea, these counts can provide population indexes for trend assessment and demographic parameters.

Acoustic monitoring can also offer a non-invasive and cost-effective method of evaluating densities and distributions of marine predators that are difficult to observe directly in their natural habitats, such as deep-diving cetaceans, bony fish and elasmobranchs, or rare species. This technique is based on the use of hydrophones or underwater microphones to passively record vocalizations made by marine predators (e.g., Jaramillo-Legorreta et al., 2017; Amundin et al., 2022; Westell et al., 2022) or active sonars or echosounders detecting species based on their echoes (e.g., Bertrand and Josse, 2000).

2.1.4 Marking and photo-identification techniques

Top predators, such as whales, dolphins, seals, and some species of sharks that bear natural markings (e.g., dorsal fin nicks, coloration patterns) can be individually recognized through photo-identification (Hammond, 1986; Brooks et al., 2010; Pérez-Jorge et al., 2016). Seabirds and pinnipeds can be artificially marked through tags or brands (Ollason and Dunnet, 1978; Tavecchia et al., 2008; Walker et al., 2012),. Depending on the type of artificial mark, individuals may need recapture for identification (e.g., metal rings in birds) or can be "recaptured" visually. Such data can be used to estimate abundance through Mark-Recapture models (see section 3.1.2).

2.2 Indirect sampling methods to assess trends of top predator distribution and abundance

2.2.1 Biogeochemical markers to inform ecosystem modeling

Intrinsic bio-geochemical markers, such as stable isotopes, fatty acids, trace elements, and pollutant levels are commonly used in ecology to understand changes in the spatial and trophic ecology of marine top predators (Louzao et al., 2011b; Ramos and González-Solís, 2012; Kytinou et al., 2020). They can also inform on the processes behind some of the declines that marine top predators face (Jepson et al., 2016).

Over the last decades, the use of stable isotope analysis, especially those based on $^{13}C/^{12}C$ ($\delta^{13}C$), $^{15}N/^{14}N$ ($\delta^{15}N$), and $^{34}S/^{32}S$ ($\delta^{34}S$) ratio determinations in species tissues, has revolutionized the way we look at wild species' trophic ecology, particularly in marine top predators (Bond and Jones, 2009; Newsome et al., 2010). These approaches provide insight into habitat use, feeding ecology, intra- and inter-specific food resource competition, migration, physiology, and nutritive condition, among others (e.g., Giménez et al., 2013, 2017; García-Vernet et al., 2021; Gaspar et al., 2022). Stable isotope ratios can also provide quantitative assessments of the multiple dimensions of the 'ecological niche' (Hutchinson, 1957). The term 'isotopic niche' was first coined by Newsome et al. (2007) and has been extensively used for addressing complex ecological questions related to intra- and inter-specific trophic interactions (e.g., Borrell et al., 2021). Recently, compound-specific stable isotopes in amino acids (CSIA-AA) have emerged as a complementary method to overcome some of the drawbacks of bulk stable isotope analysis and enhance the ability to discriminate trophic resources (Whiteman et al., 2019; Bode et al., 2022).

2.2.2 Biologging and telemetry

Animal-borne electronic devices (Ropert-Coudert and Wilson, 2005) allow the remote collection of a vast array of high-resolution quantitative data on individual distribution, movement, behavior, trophic and social interactions, and internal state (McConnell et al., 1992; Weimerskirch et al., 2012; Watanabe and Takahashi, 2013; Banks et al., 2014; Andrzejaczek et al., 2022; Papastamatiou et al., 2022; Sulikowski and Hammerschlag, 2023; Watanabe and Papastamatiou, 2023). These tools can also be used to estimate at-sea species distributions (e.g., Aarts et al., 2008; Louzao et al., 2011c; Carter et al., 2022). The data can be stored (in archival devices) or sent remotely (through ARGOS, VHF/UHF, or GSM). The most common types of data collected are position (through geolocation, ARGOS, or GPS), acoustic, diving, and speed data. Ancillary environmental data (e.g., temperature) can also be collected (Charrassin et al., 2008). The multi-parametric sensors in these devices allow the physical characterization of the environment, effectively turning animals into 'biological samplers' (McMahon et al., 2021; Holland et al., 2022). These data can also help estimate mortality rates (Heupel and Simpfendorfer, 2002) and define populations (Lewis et al., 2009). Although they do not allow the estimation of abundance indexes, they are essential for improving abundance estimates obtained through other methods, for example by providing species information on time spent at the surface (i.e., availability bias in Distance Sampling) in relation to specific physiographic and behavioral conditions (e.g., Louzao et al., 2011c; Hagihara et al., 2016).

2.2.3 Environmental DNA

The environmental DNA (eDNA, i.e., the genetic material released to the environment by organisms) is an emergent, powerful approach to marine top predator monitoring (Foote et al., 2012; Albonetti et al., 2023; Jenrette et al., 2023). DNA traces of top predators can be retrieved from the environment by filtering water to confirm species' presence in areas where they were not visually detected (Postaire et al., 2020). The metabarcoding allows the simultaneous identification of several taxa using short, conserved DNA fragments (primers), amplifying the DNA of the taxa of interest (e.g., Bakker et al., 2017). The species-specific assays target single (or a few) species and can be used to detect the presence of top predators (e.g., Budd et al., 2021). Both approaches can potentially contribute to megafauna monitoring (Suarez-Bregua et al., 2022), particularly for the most elusive or rare species (e.g., Juhel et al., 2021; Faure et al., 2023), such as deep-diving odontocetes or sharks. Recent studies have successfully used DNA metabarcoding to describe top predators' diets using stomach contents or fecal samples (de Sousa et al., 2019).

2.2.4 Remote sensing and other digital tools

Remote sensing technologies also provide a non-invasive means for evaluating top predators' presence, distribution, and behavior. For instance, satellite-based monitoring can help determine the presence and distribution of marine mammals, elasmobranchs, and seabirds in vast areas (e.g., McConnell et al., 1992; Fretwell et al., 2014; Labrousse et al., 2022). Unmanned vehicles, such as drones, autonomous underwater vehicles (AUVs), and remotely operated vehicles (ROVs) equipped with cameras, acoustic sensors, and other instruments, can also be used to collect data on the size, distribution, and behavior of marine predators (e.g., Giacomo et al., 2021). This information can also be obtained from baited fixed cameras deployed in inaccessible areas where top predators aggregate or individuals are attracted (e.g., Currey-Randall et al., 2020).

Monitoring of top predators can benefit from ongoing social digitalization and emerging disciplines such as culturomics and iEcology (Jarić et al., 2020). From one side, hyper-connectivity through social media and digital platforms can boost citizen/community science programs by increasing engagement and participation. On the other hand, passive mining of the digital activity of users can complement traditional methods in tracking the occurrence of top predators (Morais et al., 2021; Sbragaglia et al., 2024). The main advantages of emerging digital monitoring are reduced data collection costs and almost real-time data (Lennox et al., 2022). Disadvantages are reduced data quality and reliability (e.g., data tend to be biased by the lack of research design that affects, for example, temporal and spatial coverage) and limited

usability (e.g., such data may be valuable for 'presence' only studies on top-predators only if the issue of 'lack of reporting species absence' is considered and temporal and spatial observation coverage is large); these limits imply major investments on data quality and data mining (Aceves-Bueno et al., 2017).

3 Modeling approaches to detect trends of marine top predators

The monitoring approaches previously discussed provide data on the abundance and distribution trends of marine top predators that need to be analyzed. Both data-driven models and models based on first-principle assumptions and biological mechanisms can directly use monitoring data. In this section, we review both dimensions and categorize modeling techniques according to their main targets (species, community, and ecosystem).

3.1 Population and demographic parameters and models

3.1.1 Distance sampling

The most common methodology to estimate the abundance and distribution of top predator species at sea is Distance Sampling (Buckland et al., 2004). This statistical method calculates distances to the animals (e.g., seabirds and marine mammals) from predefined line-transects or fixed positions. The method estimates the detection probability function based on the sampled distances between the observer and the animals/groups (Buckland et al., 2004). This methodology has been successfully used to estimate the large-scale abundance of cetaceans, elasmobranchs, and sea turtles and detect trends (e.g., Hammond et al., 2013; Fortuna et al., 2014; Authier et al., 2018; Hammond et al., 2021).

3.1.2 Mark-recapture methods

Recaptures of previously marked individuals allow monitoring the absolute marine top predator abundance throughout mark-recapture estimators (Barbraud and Weimerskirch, 2003; Cooch and White, 2008; Hammond, 2010), which can also be used to detect changes on demographic parameters (e.g., birth, survival/mortality, emigration/immigration rates, growth rates; Genovart et al., 2016; Lunn et al., 2016; Verborgh et al., 2019).

3.1.3 Stock/population assessments

Population models are frequently used in stock assessments to inform Regional Fisheries Management Organizations, such as the International Commission for the Conservation of Atlantic Tunas (ICCAT), the International Council for the Exploration of the Sea (ICES), and the General Fisheries Commission for the Mediterranean (GFCM). The age-structured stochastic modeling approach, used to assess Atlantic bluefin tuna dynamics and to predict the future development of fish populations (over 10-20 years) under different fishing mortality and population biology scenarios (e.g., growth rates, maturity schedules, reproduction rate; MacKenzie et al., 2009, 2021), informed the recovery plan for this species. Population models integrate empirically derived estimates of the uncertainty of input variables to estimate probabilistic outputs of population variables (e.g., biomasses) and information on biological and fishing mortality rates from assessments.

The International Whaling Commission (IWC) conducts assessments of cetacean populations rather than of species, which is the IUCN approach. This is because local populations within a species may face very different conditions and threats, and some may be thriving, whereas others may be at risk of geographical extinction. The IWC assessments, mostly done for baleen whale populations, are based on a Bayesian logistic population dynamics model (Punt and Donovan, 2007), which incorporates information on current and pre-exploitation absolute abundance estimates, a species-specific productivity parameter, time-series of human-induced mortality (catch and bycatch), and factors to account for environmental variability. The Bayesian approach allows the downweighting of noisy input data (IWC, 1999).

The IUCN species assessments are most commonly semi-quantitative, allowing inferred trends to be based on expert knowledge and semi-quantitative data. However, there is an option for "quantitative analysis" (i.e., criterion E), which includes the Population Viability Analysis (PVA). A PVA is a model investigating how several known factors interact and determine the risk of extinction for a population, given a set of conditions, including a certain timeframe. Criterion E is seldom used for marine top predators as it requires background knowledge of ecological, genetic, and demographic parameters (including spatial distributions of suitable habitat, patterns of occupancy, and habitat relationships) that are usually unavailable. Nevertheless, for certain marine predator populations, PVAs are possible (e.g., Balearic shearwaters, *Puffinus mauretanicus*; Oro et al., 2004; California sea lions, *Zalophus californianus*; Hernández-Camacho et al., 2015). The IUCN Green Status of Species (Box 3) is a complementary tool to the Red List, which assesses the recovery and conservation success of species. A species is considered "fully restored" if it meets three conditions throughout its range (including historical areas): it is present, is not threatened with extinction, and performs its ecological functions.

3.2 Species distribution models

Species distribution models (SDMs) can be used to predict the spatial presence and distribution of marine species based on their relationship with environmental variables (Guisan and Zimmermann, 2000). They can fit to presence/absence, density, or presence-only data (e.g., generalized linear or additive regression models, classification and regression trees, autoregression models).

BOX 3 - The IUCN Green Status tool: putting the Red Listing into a historical perspective

The IUCN Red List of Endangered Species is a globally recognized benchmark for assessing the threat of extinction that certain animal, fungus, and plant species face. The IUCN Green Status of Species is a relatively recent and complementary tool (available since 2020) that assesses the recovery of species populations and measures their conservation success. A species qualifies as "fully recovered" if, in all parts of its range (including those occupied historically), it satisfies three conditions: it is present (i), is not threatened with extinction (ii), and performs its ecological functions (Akçakaya et al., 2018).

Of the seven most commonly feared top predators listed in the Introduction, only for the white shark (*Carcharodon carcharias*) the IUCN has produced a global and regional (i.e., Mediterranean Sea and Europe) Red List assessment ('Vulnerable' and 'Critically Endangered', respectively) and a Green Status is "Moderately Depleted". At present [on 15/06/2023], the IUCN Green Status has been given to 37 animal species. Of these, only 10 are linked to the marine environment, and only one has been assessed as 'Fully Recovered', the banded wobbegong in Australia. It is worth noting that being classified as 'Least Concern' does not mean being 'Fully Recovered', with the Eurasian otter being an extreme case of a LC species still considered 'Largely Depleted'. This highlights the importance of the historical context.

Taxon	Species	Trend	Red Listing	Green Status
Elasmobranchs	White shark, *Carcharodon carcharias*	*Decreasing*	VU	MD
	Whale shark, *Rhincodon typus*	*Decreasing*	EN	LD
	Bonnethead shark, *Sphyrna tiburo*	*Decreasing*	EN	LD
	Banded wobbegong, *Orectolobus hale*	Stable	LC	FR
Mammalia	Eurasian otter, *Lutra lutra*	*Decreasing*	LC	LD
Reptilia	Roatán spiny-tailed iguana, *Ctenosaura oedirhina*	*Decreasing*	EN	MD
Aves	Chinstrap penguin, *Pygoscelis antarcticus*	*Decreasing*	LC	MD
	African penguin, *Spheniscus demersus*	*Decreasing*	EN	LD
	Blue crane, *Anthropoides paradiseus*	*Decreasing*	VU	MD
Merostomata	American horseshoe crab, *Limulus polyphemus*	*Decreasing*	VU	MD

Key: Endangered (EN), Least Concern (LC), Vulnerable (VU), Fully Recovered (FR), Largely Depleted (LD), Moderately Depleted (MD).

For the other six most commonly feared top predators mentioned in section 1.1, only Red List assessments are available. The sand tiger shark is assessed as Critically Endangered at global and regional levels with a decreasing trend. The Polar bear is assessed as Vulnerable (Wiig et al., 2015), with an unknown global trend and a decreasing trend in Europe (Wiig et al., 2007). The same applies to the bull shark with a global decreasing trend. Sperm whales, which suffered overexploitation by the whaling industry until the late 1980s and extremely high mortality due to bycatch in large driftnets until the early 2000s, are currently assessed as Vulnerable at the global scale, but Endangered in the Mediterranean Sea, with a decreasing trend. Leopard seals are classified globally as Least Concern. The Killer whale is assessed as Data Deficient. The lack of Green Status for these and other top predator species limits the ability of managers to fully understand the extent and the meaning of their declines and the level of concern around their regional and global conservation status. Green Status assessments should be systematized and realized in synergy with Red List Assessments.

This modeling approach can be seen as an operational application of the ecological niche (Hirzel and Le Lay, 2008). SDMs are also used to predict species distribution under varying climate change scenarios (e.g., Russell et al., 2015; Moullec et al., 2022). Ensemble SDMs have been used to predict changes in marine species distribution (Lotze et al., 2019; Tittensor et al., 2021; Erauskin-Extramiana et al., 2023). SDMs accounting for the potential distribution prediction uncertainty and for relationships with key environmental variables on a regional or global scale can be used to inform mechanistic ecosystem models (Coll et al., 2019a).

SDMs have been widely used to predict distributions and identify geographical regions suitable for different cetacean species (e.g., Fortuna et al., 2018; Giménez et al., 2018; Chavez-Rosales et al., 2019; García-Barón et al., 2019; Ramírez-León et al., 2021), seabirds (e.g., Louzao et al., 2006; Oppel et al., 2012; Frederiksen et al., 2013; Astarloa et al., 2021), elasmobranchs (e.g., Pennino et al., 2013; Lauria et al., 2015; Follesa et al., 2019; González-Andrés et al., 2021), pinnipeds (Aarts et al., 2008) and combined taxonomic groups (e.g., Louzao et al., 2019; García-Barón et al., 2020).

3.3 Ecosystem modeling: from energy flows to multispecies and food-web interactions

3.3.1 Stable Isotope mixing models and trophic position

Stable isotope analyses have emerged as a suitable alternative to conventional approaches to reconstruct the individuals' and populations' assimilated diet and trophic position through mass-balance mixing models (e.g., Navarro et al., 2009; Gaspar et al., 2022). Bayesian statistics allow adding priors to modeling diet mixtures. They also allow adding fixed and random effects as covariates explaining variability in mixture proportions and calculating relative model support through information criteria (Stock et al., 2018; Lloret-Lloret et al., 2020).

Trophic Position (TP) is commonly used to describe the trophic structure and relationships at the community level and to study the effects of human and environmental changes on marine food webs. In trophic studies, when $\delta^{15}N$ baseline and predator values are known, the use of this isotope is common practice to calculate the

TP. Additionally, the use of compound-specific stable isotopes in amino acids (CSIA-AA) has recently enabled modeling TP using only values from the predator, as some amino acids are considered source (i.e., baseline) and others trophic (Bode et al., 2022).

3.3.2 Bioenergetic models

Bioenergetics modeling provides a mechanistic basis for projecting climate change effects on marine living resources. It has been applied widely to fish, marine mammals, and other taxa (Rosen and Trites, 2000; Winship et al., 2002; Fortune et al., 2013; Rechsteiner et al., 2013; Louzao et al., 2014; Jeanniard-du-Dot et al., 2017; Booth et al., 2023). These approaches are often species-specific, and integrating data related to individual and short-term processes into population dynamics can be challenging. Additionally, major challenges arise from climate change projections centered on predictions of organism and population responses to novel environmental conditions, which may strain current modeling capabilities (Moullec et al., 2022; Erauskin-Extramiana et al., 2023).

3.3.3 Multispecies models

Several statistical and mechanistic approaches exist to simultaneously model multiple species. For example, Joint Species Distribution Models (JSDM) integrate species interactions into metacommunity and macroecology (Tikhonov et al., 2020). JSDM allows for integrating data on species densities, environmental covariates, species traits, phylogenetic relationships, and spatio-temporal information. This approach enables the analysis of species occurrence patterns, which can be decomposed into environmental responses and residual correlations not explained by predictors (Hui, 2016), potentially indicating biotic interactions. In a recent JSDM application in the Bay of Biscay, Astarloa et al. (2019) demonstrated that the co-occurrence patterns of top predators (marine mammals and seabirds) and prey (pelagic fish and crustaceans) were driven by a combination of environmental and biotic factors. Many multispecies mechanistic models exist (Plagányi, 2007), including models of intermediate complexity (Plagányi et al., 2012). Additionally, empirical relationships of biomass and abundance estimates obtained from observations and population models have been used to establish links between predator requirements and prey. For example, one study links seabird colony-years per breeding site to the abundance of principal prey for each species, determining the proportion of prey abundance needed to ensure seabird success (Cury et al., 2011).

3.3.4 Marine ecosystem models (EwE, SNS, Mizer)

Ecological processes and human activities can be explicitly incorporated into process-based marine ecosystem modeling (Fulton, 2010; Peck et al., 2018; Tittensor et al., 2018; Moullec et al., 2022), as in Ecopath with Ecosim and Ecospace models (EwE hereafter; Christensen and Walters, 2004). These tools allow for building food-web models by describing the ecosystem as energy flows between functional groups, each representing a species, a subgroup of a species (e.g., juveniles and adults), or a group of species with functional and ecological similarities. Ecospace is the spatial-temporal dynamic module of EwE, allowing temporal and spatial 2D dynamics representation of trophic web components.

EwE has been widely applied to analyze the spatial impacts of fisheries, management scenarios (e.g., marine protected areas, MPAs), and climate change on marine species and ecosystems. This is achieved by linking Ecospace with low trophic level models (Fulton, 2011) or external spatial-temporal data (Steenbeek et al., 2013) and developing spatial optimization routines (Christensen et al., 2009). An addition to the spatial-temporal modeling capabilities of EwE is the Habitat Foraging Capacity model (Christensen et al., 2014). This model allows for the spatial derivation of foraging species' capacity from cumulative effects of multiple physical, oceanographic, environmental, and topographic conditions in conjunction with the food web and fisheries dynamics. This integration bridges the gap between envelope environmental and food-web models (Coll et al., 2019a). EwE has been used to assess the role and dynamics of predators in marine ecosystems, such as sea otters (Espiro et al., 2011), endemic skates (Coll et al., 2013), tunas (Cox et al., 2002), and Steller sea lions (Guénette et al., 2006). It is increasingly used to assess the effect of cumulative impacts in the ocean (de Mutsert et al., 2023), including underwater noise (Serpetti et al., 2021), and to study global scale dynamics through hybrid modeling approaches (Coll et al., 2020).

4 Historical perspective and ecological implications

Understanding the ecological status of top predator populations is essential to identify the key measures required for their effective conservation. These species are ecosystem sentinels that respond to ecological fluctuations of ecosystems and generate essential information about the ecological implications of other organisms (Hazen et al., 2019). The long-term historical exploitation of large predators has influenced their contemporary abundance. Thus, neglecting historical data may lead to excessively optimistic assessments of their conservation status, lower recovery targets, and larger exploitation quotas than if the historical perspective is considered (McClenachan et al., 2012). Shifting baselines (Pauly, 1995) can result from the intergenerational loss of knowledge regarding species abundance, directly affecting how species and ecosystems are perceived and managed. Historical data allow scientists and managers to understand species and population dynamics better and make informed decisions promoting the long-term sustainability of marine populations.

Notwithstanding the lack of reliable data from the pre-industrial fishing age (ca. 1960 and back), global oceans are estimated to have lost 90% of the biomass of large predatory fish species since the start of industrialized fisheries, with major stock biomass declines of up to 80% within 15 years of industrialized exploitation (Myers and Worm, 2003). Paleczny et al. (2015) conducted a global meta-analysis and reported that seabird populations declined by an average of 69% from 1950 to 2010. Certain groups, such as albatrosses and petrels, experienced even more pronounced declines. McCauley et al. (2015) reported a

decline in marine mammal and seabird populations worldwide by 45% and 28%, respectively, over the past 40 years.

Incorporating historical data into assessments of marine populations frequently reveals more severe declines that may go unnoticed when relying solely on short-term observations. A meta-analysis of instantaneous rates of change for blue sharks (*Prionace glauca*) in the Mediterranean indicated population declines of 97%. This suggests a baseline population size 2.5 times higher than that derived from earlier estimates based on comparisons of CPUEs between 1978 and 1999. This conclusion was based on a comprehensive data series beginning in 1950, including commercial landings, scientific surveys, and sighting records (Ferretti et al., 2008).

A large-bodied fish whose population collapsed before standardized monitoring began during the 1950s is the critically endangered common skate (*Dipturus batis*). Bom et al. (2022) placed the recent increase in population numbers in the North Sea in a 120-year perspective by examining various recent and historical data of standardized capture counts. The species had a relatively high abundance between 1901 and 1920, followed by a steady decline from 1920 onwards, nearly leading to extinction around 1970 in the North Sea. The authors found that the current abundance of the species is still well below historical baselines and shows a slight recovery only at the far north edge of its geographical range.

A long-term perspective is crucial to avoid overly optimistic assessments, even for recovering populations. The standardized sampling of marine populations began in the 1970s or later in most regions, after many species had already experienced significant declines or collapse. This can lead to overstating recent recovery levels of top predator populations (Bom et al., 2022). For instance, the southern right whale (*Eubalena australis*) has experienced centuries of exploitation. The pre-exploitation abundance in the southwestern Atlantic Ocean was estimated at roughly 58,000 individuals, and it dropped to its lowest levels in the 1830s, with fewer than 2,000 individuals remaining. The current median population estimate is about 4,700 whales, indicating a certain recovery but much lower numbers than the pre-exploitation period (Romero et al., 2022).

Setting realistic goals for conservation efforts requires comprehensive knowledge of abundance over an ecologically meaningful "long time" period. An emblematic example is the large Gulf grouper (*Mycteroperca jordani*) in the Gulf of California (Saénz-Arroyo et al., 2005). Based on increased catch from data systematically collected since 1986, an annual catch increase of up to 5% was recommended in 2000. However, integrating historical evidence, observations from naturalists, and systematic documentation on fishers' perception of the abundance of this species, revealed that the Gulf grouper had undergone an alarming decline since the peak of the Gulf grouper fishery before the 1970s. It is worth noting that this decline occurred well before formal fishery statistics were established.

Long-term time series may provide data supporting a more robust understanding of the potential future trajectories of change in population distribution and abundance, for example, in response to climate change. We currently have limited knowledge of the climate change-induced processes that shift the distribution of top predators, particularly in amplitude and lagged processes (Lan et al., 2021). Louzao et al. (2013) showed a progressive habitat shift, between 1958 and 2001, for the Wandering Albatross (*Diomedea exulans*) of recurrent, occasional, and unfavorable foraging habitats, driven by the propagation of sea surface height from SE South Africa towards Antarctica. Using relatively long-term time series data (1988-2018) from two fjords in West Spitsbergen (Svalbard), Descamps and Ramírez (2021) investigated the relationship between sea ice extent and population size of two of the most prevalent Arctic seabirds, the Brünnich's guillemot (*Uria lomvia*) and black-legged kittiwake (*Rissa tridactyla*). The authors concluded that the ongoing decline in Arctic Sea ice plays a role in Arctic seabird population trajectories, even if its disappearance on the breeding grounds is likely not the main driver of change in seabird populations.

Historical data have a high potential for application in "data-poor" stock assessments, where reference points and recovery targets are often established using a variety of data types, limited in quality, quantity, and coverage. One example of a marine top predator stock assessment based on historical data is the case of the Northwest Atlantic population of the white shark (Curtis et al., 2014). In the early 20th century, white sharks were commonly caught as bycatch in commercial fisheries targeting other species, such as tunas and swordfish. The authors used historical data from various sources, including newspaper articles, fishery records, and interviews with fishers and other experts to understand the past trends and current status of the white shark population. This information, combined with recent data from tagging studies and aerial surveys, indicated that the Northwest Atlantic population of white sharks had declined by approximately 73% (median estimate) between the mid-1970s and throughout the 1980s. The white shark relative abundance stabilized during the 1990s then increased during the 2000s until the end of the study (i.e., 2010). The increase was linked to the implementation of specific fishery management measures, including species protection.

More prominently, historical data are key in extinction risk assessments such as those coordinated by the IUCN Red List, which estimates population changes over '*10 years or three generations of a species, whichever is the longer*'. Given the inherent generation length of top predators, these assessments are frequently hindered by a lack of data, particularly for marine mammals, elasmobranchs, large teleosts, and seabirds, which in many cases are long-living species. Ascension Island has the largest colony of sooty terns (*Onychoprion fuscatus*) in the Atlantic Ocean, and censuses between 1990 and 2013 have shown that its population size is static. However, historical data showed that the breeding population contained over 2 million individuals in the 1870s and remained at this level for at least 70 years. The population declined from > 2 million in 1942 to 350,000 birds by 1990. The population trend spanning a period equivalent to three generations of the species (63 years; 1942–2005) showed an approximate 84% decline (Hughes et al., 2017). Using IUCN criteria, sooty terns on Ascension could be considered 'Critically Endangered'; hence Hughes et al. (2017) concluded that re-evaluating its conservation status is necessary at the local level and possibly globally.

Seals have been severely exploited for centuries, primarily for oil rather than fur, which became a later cause for their demise. In Western Europe, for example, grey seals (*Halichoerus grypus*) were numerous based on archaeological findings (Reijnders et al., 1995) but completely disappeared from the continental coasts before the Middle Ages. After protection in the United Kingdom at the beginning of the 20th century, grey seal populations gradually recovered and re-colonized most of their former distribution (Brasseur et al., 2015). Estimates of former population sizes of severely hunted species can be back calculated from well-documented hunting records. For example, annual catch data were used to estimate the potential size of the harbor seal population in 1900 (Reijnders, 1992). However, bounties and regular hunting in previous centuries had already decreased the population by 1900 (de Vooys et al., 2012). This is an example of shifting baselines and highlights the need to put things into perspective also when reconstructing the sizes of top predator populations from historical data.

4.1 The human factor in marine top predators decline

Humans are playing a main role on marine top predators' decline. This ranges from being the cause of direct mortalities - either purposefully (i.e., fishing and hunting) or accidentally (i.e. fishery bycatch and collisions with ships) - to causing the widespread and, at times subtle, habitat degradation (e.g., food web disruption, habitat loss and fragmentation, seafloor damage, coastal zone modification, chemical and acoustic pollution, climate crisis, etc.).

The depletion of populations due to overfishing or overhunting has been identified or suspected as a major cause of the decline for many marine top predators (Pauly et al., 1998; Stevens et al., 2000; Myers and Worm, 2003; Lotze and Worm, 2009). A recent review of marine extinctions (Nikolaou and Katsanevakis, 2023) reported 8 cases of top predators' global extinctions (4 seabirds, 3 marine mammals, and 1 teleost fish) and 89 cases of local extinctions; the main driver of extinction of top predators was human-induced direct mortality (i.e., overexploitation and bycatch).

Bottom-up processes related to the overexploitation of lower trophic levels cause a reduction in food for higher-trophic level animals such as seabirds and marine mammals, potentially resulting in losses in reproduction or reductions in their population size (Myers et al., 2007; Terborgh and Estes, 2013).

The harmful consequences of the exposure of individuals to certain pollutants are also recognized as a primary driver of the decline of top predators. Most pollutants tend to accumulate (bioaccumulation) in marine organisms and are eventually transferred along the food web (biomagnification) with significant consequences for top predators (Kelly et al., 2009). Top predators are, therefore, under pressure from pollution and can also serve as sentinel species for monitoring the environmental health of the marine environment they inhabit (Garcia-Garin et al., 2021; Garcia-Garin et al., 2022).

In addition, given that climate change is expected to have a major impact on marine top predator species' distributions and abundances, marine conservation and management efforts will need to consider these ongoing changes and factor them in their decision-making (e.g., Braun et al., 2023).

5 Examples of assessments linked to policy frameworks

This review does not have a specific focus on the EU Habitats Directive, as this has been absorbed into the conservation and management approaches of the more recent MSFD and MSP directives. However, both sections 5.1 and 5.2 refer to several aspects and tools deriving from the Habitats Directive (e.g., links to HD monitoring and assessment framework in Commission Decision 2017/848; Natura 2000 network, etc.).

5.1 Assessment examples

The EU MSFD and UN Regional Sea Conventions aim to improve the governance of the marine regions surrounding the European continent and reinforce the protection of the marine environment through cooperation among all riparian countries. The MSFD aimed to achieve or maintain GES for European seas by 2020. Top predators are considered in the MSFD assessments under three descriptors: D1 'Biodiversity', D3 'Fishing', and D4 'Food webs'. Under D1, MSs consider 139 species of birds, 40 species of marine mammals, and 321 species of fish. The latter includes elasmobranchs and commercial species that may be assessed under D3 and D4 (EC, 2018; JRC, 2018).

A recent review of the MSFD reports (for the reporting cycle 2012/13-2018) of a sample of nine Member States (Croatia, Estonia, Finland, France, Germany, Malta, Netherlands, Romania, and Spain; Franco et al., 2021) has shown that, amongst the bird species most commonly assessed under the MSFD D1, there are terns (little tern *Sternula albifrons*, common tern *Sterna hirundo*, and Sandwich tern *Sterna sandvicensis*) in the Baltic, Atlantic, Mediterranean, and Macaronesia, cormorants (European shag *Phalacrocorax aristotelis* and great cormorant *P. carbo*) in the Atlantic, Baltic, and Mediterranean, and Scopoli's shearwater (*Calonectris diomedea*) in the Mediterranean Sea. The assessments focused, in particular, on their breeding colonies. Small-toothed cetaceans, such as the common bottlenose dolphin (*Tursiops truncatus*) and harbor porpoises (*Phocoena phocoena*), and grey seals are amongst the most frequently reported sea mammals, depending on the regions, with the bottlenose dolphin and grey seal being most often reported as in 'Good status'. In contrast, harbor porpoise is often classified as 'Not-good status' (Franco et al., 2021). As for predator fish, commercial species including gadoids (e.g., *Gadus morhua, Micromesistius poutassou*), seabass (*Dicentrarchus labrax*), bluefin tuna and turbot (*Scophthalmus maximus*), as well as elasmobranchs such as rays (e.g., *Raja clavata*) and dogfishes (e.g., *Scyliorhinus canicula, Squalus acanthias*), are the most commonly reported fish under D1, D3 or D4.

The status of individual species ('Element status' in MSFD reports) is the integration of the status assessment of a set of criteria based on established indicators. Examples of the D1 criteria and associated

indicators used by Member States to assess the state of seabirds and mammals are given in Table 1, with a reference to the homologous indicator used by or adopted from RSCs. The EU European Information System WISE-Marine provides a useful comparative table on the European and Regional Indicators used in the GES assessment by various RSCs. Table 1 shows only the 'state' criteria, not 'pressure'; hence fishery-related mortality (D1C1) was excluded.

Most of the indicators used for MSFD D1 assessments align with those used in assessments by RSCs. The MSFD Art 5(2) and the more recent Commission Decision (EU) 2017/848 explicitly require Member States to ensure that the implementation of the different articles is coherent and coordinated across the region or subregion. From a geographical perspective, the lowest level of harmonization (in terms of indicator re-use) occurs in the Barcelona Convention region, whereas the highest level of re-use was observed for the Netherlands, followed by France and Germany (Franco et al., 2021). The highest level of harmonization between MSFD and RSCs appears to occur for marine mammals (compared to marine reptiles, birds, and benthic habitats), as suggested by the re-use of assessments, from the monitoring data to the indicators used (Franco et al., 2021). This is likely the result of the RSCs having established methods for marine Great cormorant, mammal data collection as well as other international agreements, such as ACCOBAMS (the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea, and contiguous Atlantic area) and ASCOBANS (the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas), which have promoted common standards and established data flows. Harmonizing the Barcelona Convention's Ecosystem Approach (Barcelona Convention 2008, 2012, 2013, 2016) with the MSFD is ongoing; major improvements and a quasi-complete alignment are expected in the next triennium.

Franco et al. (2021) showed that population abundance (D1C2) for birds and population abundance (D1C2) and distributional range and pattern (D1C4) for mammals were the criteria most successfully assessed by Member States, i.e., sufficient data and established indicators for these allowed the status to be classified as 'good' or 'not good' in most cases.

Although Franco et al. (2021) did not consider it in their evaluation, the criterion D1C1 is fundamental to assessing the biodiversity GES. D1C1 quantifies the '*mortality rate per species from incidental bycatch*' and prescribes that fishery-induced mortality is kept '*below levels which threaten the species, such that its long-term viability is ensured*' (Commission Decision (EU) 2017/848). In terms of policies, this criterion is linked to the concept of EBM and various targets of the EU Common Fisheries Policy on reducing bycatch and discards. The species concerned are potentially all '*non-commercially-exploited species (incidental bycatches)*'. Despite the recent EC Communication on the EU Action Plan on '*Protecting and restoring marine ecosystems for sustainable and resilient fisheries*' (EC, 2023), which calls for concrete actions on D1C1 by EU Member States by the end of 2023, nothing is ready to be adopted. In particular, no major improvements are seen regarding officially adopting threshold algorithms to estimate the '*maximum allowable mortality rate from incidental catches*', nor a fully operational monitoring system is in place for the EU fleet to gather

TABLE 1 MSFD D1 criteria and indicators for seabirds and marine mammals (see Commission Decision (EU) 2017/848), with reference to OSPAR and HELCOM analogous indicators, as reported by a sample of nine Member States in 2018 MSFD reports (source: Franco et al., 2021).

MSFD Criterion	Indicator for Seabirds	Indicator for Marine Mammals
D1C2 - Population abundance	Abundance (breeding, number of pairs) (32%)	Abundance (number of individuals) (57%)
	Abundance of waterbirds in the breeding season (number of pairs/ ratio) (10%)	Relative abundance of cetaceans within community (short term trend) (MM_Abond, % of mean annual difference in the relative abundance of a species, over the assessment cycle) (7%)
	Abundance of waterbirds in the breeding season (HELCOM indicator) (16%)	Relative abundance of *P. phocoena* within community (short term) (M4b_OSPAR, %) (3%)
	Relative abundance of breeding pairs within community (long term) (OSPAR B1, %) (43%)	Relative abundance within community (short term) & Relative abundance within community (long term) (M3_OSPAR, %) (7%)
	Abundance (number of individuals) (6%)	Relative abundance within community (short term) (M4a_OSPAR, %) (7%)
	No indicator estimated in 10% of MSFD bird assessments reported for D1C2	No indicator estimated in 20% of MSFD mammal assessments reported for D1C2
D1C3 - Population demographic characteristics	–	Age distribution (indicator taken directly from HD assessment) (15%)
		Age distribution (year) (31%)
		Size length (cm) (4%)
		Sex distribution (e.g., % females/ males) (16%)
		Survival rate (SUR) (8%)
		Mortality rate (4%)
		Extreme mortality events of harbor porpoises (MM_EME, number of extreme strandings) (12%)
		Fecundity rate (12%)
		Annual gestation rate AGR (calves/ year) (4%)
		Reproductive status of seals (proportion of females pregnant %) (4%)
		Breeding interval BI (year) (4%)
		No indicator estimated in 31% of MSFD mammal assessments reported for D1C3

(Continued)

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TABLE 1 Continued

MSFD Criterion	Indicator for Seabirds	Indicator for Marine Mammals
D1C4 - Population distributional range and pattern	Distribution range (DIST-R, breeding, km^2) (8%)	Distribution spatial (DIST-S, taken from HD assessment, km^2) (32%)
	Distribution spatial (DIST-S, taken from HD assessment, km^2) (4%)	Distribution range (DIST-R, e.g., distribution of haul-out sites, breeding sites, and foraging areas, km^2) (18%)
	Relative abundance within community (short term, %) (4%)	Distribution and abundance of coastal populations of bottlenose dolphins (M4a_OSPAR, %) (7%)
	Spatial distribution of birds observed at sea (number of individuals per km^2) (12%)	Distribution of Baltic seals (4%)
	No indicator estimated in 72% of MSFD bird assessments reported for D1C4	Distribution of cetaceans (MM_Distri, % difference in the proportion of area occupied by the species over the assessment cycle) (11%)
		Distribution of seals (M3_OSPAR, %) (7%)
		Distributional pattern (DIST-P, e.g., continuous/fragmented) (29%)
		No indicator estimated in 18% of MSFD mammal assessments reported for D1C4
D1C5 - Habitat for the species	–	HAB-CON: Grey seal habitat for the species (Habitats Directive parameter) (23%)
		HAB-CON (unspecified) (23%)
		Extent (7%)
		PCB concentration in tissues (CONC-B-OT) (3%)
		No indicator estimated in 50% of MSFD mammal assessments reported for D1C5

Percentages refer to the proportion of the MSFD assessments reported for each criterion which used the specific indicator.

appropriate data on bycatch rates (ICES, 2021). Moreover, both EU and national fishery management frameworks are not adequately prepared to: (i) use such thresholds to assess their sustainability, ensuring the long-term viability of concerned species; and (ii) minimize the effect of recorded bycatch rates to enable the full recovery of concerned species and populations. The ultimate deadline to realize and implement such frameworks for all species is 2030.

5.2 Area-based tools to implement an ecosystem approach

The current trajectories of changes in top predators and the complexity of monitoring and understanding the factors affecting their long-term viability call for a holistic approach to their conservation and management. A key management tool to conserve their habitats is MPAs. MPAs have proven to be effective in conserving and restoring ecosystems and marine species (Leenhardt et al., 2015; Giakoumi et al., 2017; Pérez-Roda et al., 2017), and protecting important marine habitats for top predators (Gormley et al., 2012). However, MPAs are often too small or inappropriately designed to be effective for the conservation of wide-ranging top predators, also considering the level of pressure and degradation of the unprotected surrounding ecosystems (Fortuna et al., 2018). To fully harness MPAs strengths, their designation should be incorporated into Maritime Spatial Planning (MSP). MSP is an adaptive EBM tool aiming to define the spatial allocation of human activities at sea. MSP addresses emerging challenges resulting from increasing human activities and their impacts on threatened marine ecosystems, aiming to manage oceans sustainably (Gissi et al., 2019). Guidelines to assist in the definition of appropriate time and space requirements to better meet fisheries management objectives within an MSP context have been also proposed (Dunn et al., 2011). MSP should be adopted also for the designation of Other Effective area-based Conservation Measures (OECMs) representing a novel conservation approach distinct from MPAs, contributing to conservation goals as a byproduct of other management objectives on specific human activities (Laffoley et al., 2017). However, human-wildlife interactions are still scarcely explicitly addressed in planning and rarely in MSP, and should be further implemented given the evidence of positive results (Shabtay et al., 2020; García-Barón et al., 2021).

Recently, structured public consultation involving stakeholders has demonstrated that MSP can address shark attack risk while considering multiple sea uses and conservation objectives. This highlighted the importance of integrating shark risk as a driver in the MSP process and developing a transparent, sustainable, and evidence-based public policy for managing shark risk within a broader social-ecological spectrum of stakes (Shabtay et al., 2020).

It must be stressed that the designation of EU MPA networks (Natura 2000) within MSP has often lacked systematic conservation planning principles, such as connectivity, adequacy, representativeness, and efficiency, and its focus has been more on structural characteristics of habitats and iconic species and populations in unfavorable conservation status rather than on ecosystem functioning and whole biodiversity (Katsanevakis et al., 2020). Robust and systematic approaches are necessary to recover predators and prey with threatened status. In this context, systematic conservation planning tools such as Marxan, the open-source R Prioritzr or Zonation are useful for finding a solid planning scenario that balances conservation and socio-economic perspectives (Afán et al., 2018; Giménez et al., 2020; García-Barón et al., 2021). Other spatial analyses based on GIS have been developed to incorporate the complexity of spatial management (Queirós et al., 2016), including the identification of specific areas for the protection of species at risk (Louzao et al., 2006, 2012; Coll et al., 2015). Mechanistic models (such as Ecospace) can assess the effects of management on marine ecosystems, including top predators, while considering the impacts of climate change and

human activities in the ocean (Fulton et al., 2015; Gomei et al., 2021). Better systematic conservation planning accounting for functional connectivity and climate change impacts is recommended to improve the status of this key biodiversity component (Katsanevakis et al., 2020).

6 A systematic global review on success stories: factors for success

A systematic global review was conducted to identify success stories in managing threats to top predator populations, applying the PRISMA-EcoEvo approach (*Preferred Reporting Items for Systematic Reviews and Meta-Analysis extension for Ecology and Evolutionary Biology*; Moher et al., 2009; O'Dea et al., 2021). Details on the methods used and additional results are shown in Supplementary Materials. The aim was to identify (a) the concerned threats, (b) the types of conservation actions applied, (c) how their performance was assessed, (d) the factors contributing to their success or failure, and (e) the stakeholders involved in these success stories.

Studies included in the review met two criteria: (1) one or more populations of a marine top predator were assessed, and (2) one or more successful conservation actions were described (i.e., actions that led to a population increase/recovery or status improvement or were successful in mitigating specific threats in pilot trials). In total, 481 success stories were identified, and 181 studies were included in the review (Supplementary Figure 1; Supplementary Material). The extracted data from the reviewed papers were classified into five categories: (1) bibliographic information; (2) species-specific and study-specific information; (3) information on conservation actions; (4) participation of stakeholder groups; and (5) threat(s) mitigated through the conservation action(s). Complementary data were extracted from the IUCN Red List (IUCN, 2023) (i.e., the IUCN status and trend of the assessed species and populations).

Most success stories referred to seabirds (53%), followed by marine mammals (24%), elasmobranchs (12%), and large teleosts (11%) (Figure 1A). Over 50% of these success stories occurred in temperate regions of South America, Southern Africa, and the Northern Atlantic (Figures 1B, 2). The country with the most reported success stories was South Africa (18%), followed by Australia (14%), the US (13%), and Brazil (11%) (Supplementary Figure 6). However, the global distribution of success stories varied by taxon (Supplementary Figures 2–5).

Management measures were predominantly local (Figure 1C); 48% of the cases were actually implemented, whereas 52% were only pilot cases. A temporal pattern in the prevalence of actual implementation of conservation measures *versus* pilot cases was detected, with the latter increasing drastically in the 2000s and 2010s (Supplementary Figure 7). The harbor porpoise was the most commonly targeted species, followed by the black-browed albatross (*Thalassarche melanophris*) and the white-chinned petrel (*Procellaria aequinoctialis*) (Figure 1D).

More than half of the target species in these studies were classified as 'Least Concern' by the IUCN, whereas only 5% were 'Critically Endangered' and 17% 'Endangered'; remarkably, only three cases of 'Data Deficient' species were reported (Figure 3A). Most population trends for which a trend was available were classified as declining (Figure 3B).

The most commonly reported management measure was bycatch reduction (57%), followed by the establishment of MPAs (15%) and invasive species management (6%) (Figure 4A). The frequency of the types of management measures in success stories significantly differed by taxonomic group (chi-square test; $p < 0.0001$) (Figure 5). For seabirds and marine mammals, bycatch reduction measures were by far the most commonly reported, whereas, for elasmobranchs and large Osteichthyes, the establishment of MPAs was the most common measure. In the 1980s and early 1990s, the establishment of MPAs was the main reported management measure, but in the following decades bycatch reduction measures have been dominant (Supplementary Figure 8).

In terms of conservation objectives, the most common was the reduction of bycatch mortality rates (57%), followed by population size recovery/increase (31%). Other objectives, with a frequency below 5%, included: (i) increased post-release survival, (ii) reduction of intended killing or hunting, and (iii) increase of breeding population size (Figure 4B).

Various indicators were used to assess population status and the effectiveness of management, bycatch rates being the most common one (29%), followed by abundance (20%), frequency of interactions with fishing gear (other than bycatch) (16%), and survival rate (6%) (Figure 4C). The most common threat reported was bycatch (59%), followed by overexploitation (14%), hunting/whaling (6%), and invasive species (7%) (Figure 4D).

Success stories of pilot bycatch mitigation measures were four times higher than those of institutional implementation. Cox et al. (2007) acknowledged the significant progress in reducing the bycatch of marine mammals, sea turtles, and seabirds through fishing gear modifications, but underlined the challenge of transferring the efficacy of pilot mitigation measures to operational fisheries. They highlighted the collaboration among scientists, resource managers, and fishing industries, complemented by a mixture of outreach, robust enforcement, pre- and post-implementation monitoring, and economic incentives as key factors for the success of bycatch reduction measures in fisheries. Examples of implemented bycatch mitigation measures, guided by evidence-based research, include the adoption of seabird and dolphin bycatch reduction measures by all major tuna Regional Fishery Management Organizations, which are responsible for the management of over 90% of tuna fishing in the global oceans (Jiménez et al., 2020), and by the Australian Fisheries Management Authority (Koopman et al., 2018) and U.S. NOAA Fisheries.

The stakeholders involved in success stories were mostly central authorities and governmental agencies, followed by research institutions, fishing industry representatives, local NGOs, and multilateral governance instruments (Supplementary Figure 9). Miller et al. (2018) highlighted the benefits of multi-stakeholder project processes involving national and international actors. These collaborations allow for the pooling of knowledge and resources from diverse stakeholders to address complex sustainability challenges. As regularly reported in success stories, collaboration

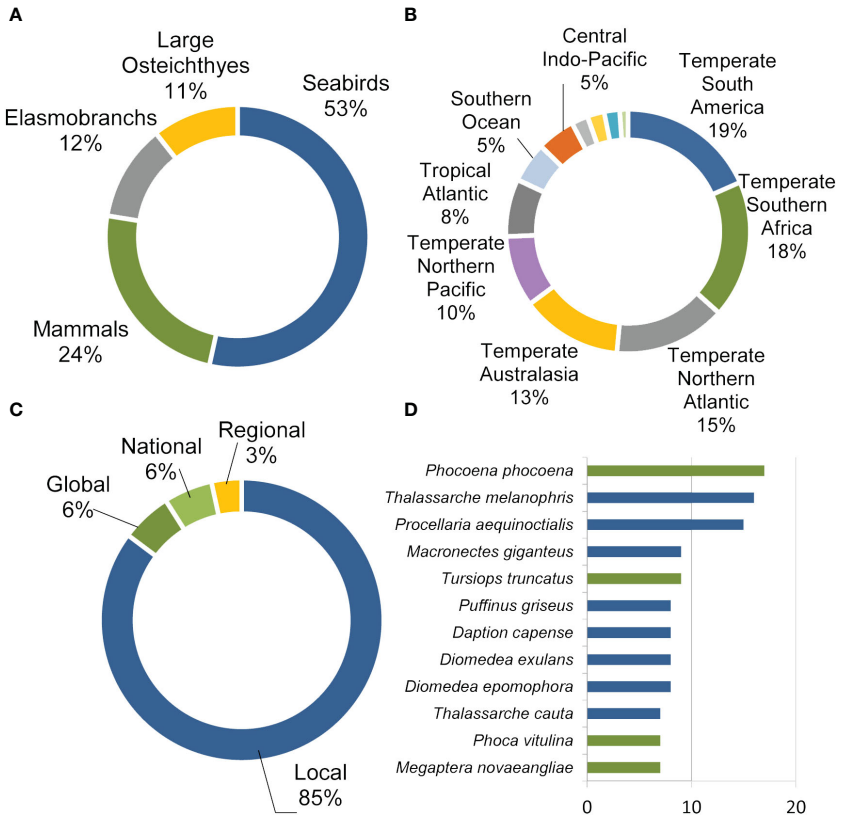

FIGURE 1
(A) Share of the four taxonomic groups in the success stories retrieved through the systematic review. **(B)** Distribution of success stories in marine realms (sensu Spalding et al., 2007). **(C)** The scale of management measures implemented in success stories. **(D)** Most commonly targeted species by management measures in the reviewed success stories (green: mammals, blue: seabirds).

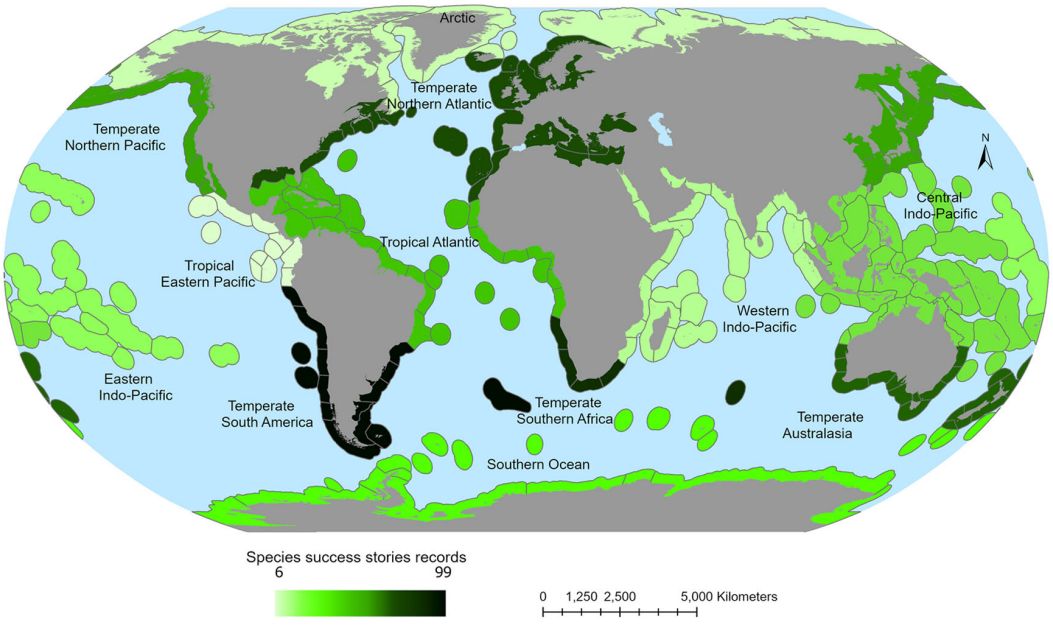

FIGURE 2
Spatial distribution of success stories in the twelve marine realms, sensu Spalding et al. (2007).

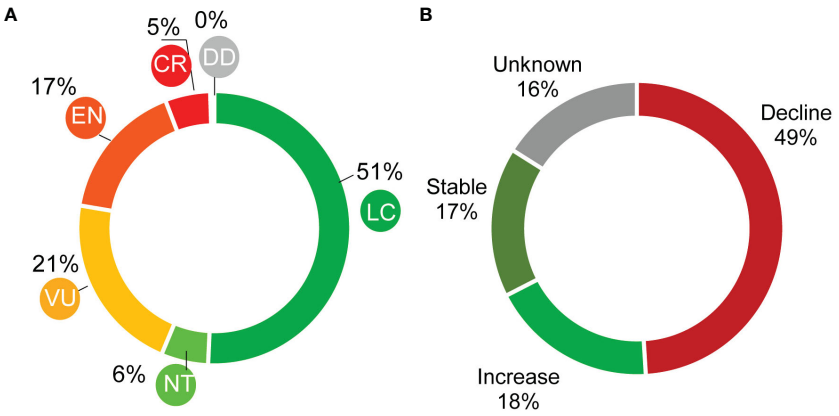

FIGURE 3
(A) The IUCN Red List categories of the species reported in success stories (CR: Critically Endangered, EN: Endangered, VU: Vulnerable, LC: Least Concern, DD: Data Deficient). **(B)** The regional population trends of the species reported in success stories according to the IUCN Red Lists assessments.

among stakeholders, local communities, and scientists are crucial factors for the success of conservation actions. For example, Lambert (2002) presented the case of the grey seal in Britain as a success story resulting from collaboration among multilateral organizations (i.e., IUCN and the European Parliament), governmental agencies, local community associations, nature conservation bodies, and NGOs. Local ecological knowledge and feedback from concerned stakeholders can provide useful insights on the status of top predator populations and options of pressures' mitigation (e.g., Sáenz-Arroyo et al., 2005; Coll et al., 2014) and improve the chances of translating experimental measures into effective mitigation in commercial fisheries, e.g., for bycatch reduction (Cox et al., 2007). Education was highlighted in many success stories as playing a vital role in conservation efforts,

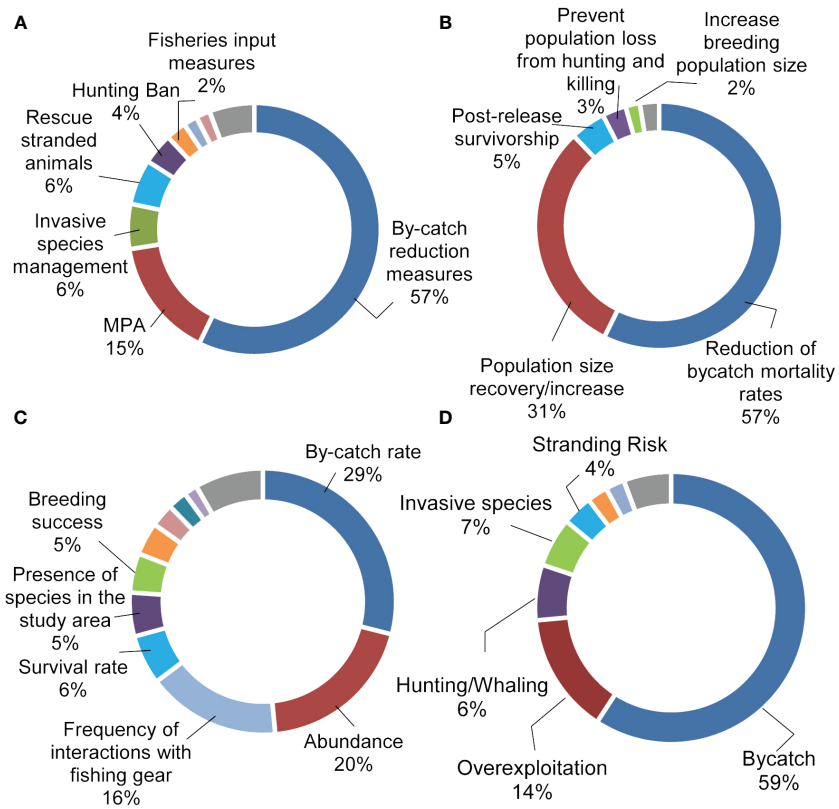

FIGURE 4
Summary of success stories including **(A)** share of the management measures, **(B)** conservation actions targets, **(C)** indicators of project success, and **(D)** threat mitigated.

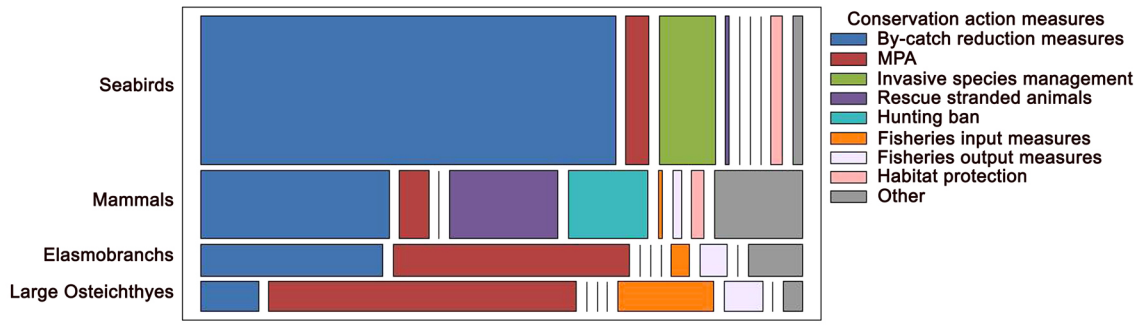

FIGURE 5
Type of management measures reported in success stories by taxonomic group (Key: the bar size is proportional to the number of success stories).

ensuring that stakeholders, including local communities and industry sectors, are aware of the importance of sustainable practices (Huang, 2011).

In success stories, the effective establishment and function of MPAs were attributed to a combination of social factors, effective self-enforcement by local stakeholders, good compliance, and widespread support from local communities (Guidetti et al., 2008; Aburto-Oropeza et al., 2011; Jaiteh et al., 2016; Speed et al., 2019). Furthermore, continuous monitoring of an area allows for the adaptation of management measures over time. In the case of the Madeira Natural Park and the Desertas Islands, the success of the Mediterranean monk seal (*Monachus monachus*) conservation project (see also Box 2) was attributed to active patrols and environmental educational programs (Pires and Neves, 2001). Hamilton et al. (2011) highlighted the success of community-based MPAs, which achieved positive outcomes despite their small size due to well-designed plans and effective enforcement.

Securing benefits for local economies (e.g., through ecotourism) contributed to success. For example, shark diving is a rapidly growing industry that benefits not only the diving industry directly but also other economic aspects of a community (Huveneers et al., 2017). Cisneros-Montemayor et al. (2013) determined that the global shark diving industry generates $314 million per year, supporting 10,000 jobs. Also, whale sharks (*Rhincodon typus*) in the Philippines serve as a great example of sustainable integrated coastal governance: destructive fishing has decreased, and shark abundance has increased due to the implementation of alternative livelihood management actions based on whale shark tourism (Lowe et al., 2019). On the other hand, Mustika et al. (2020) argued that fishers in Indonesia, a biodiversity hotspot facing significant fishing pressure, do not directly benefit from shark and ray tourism. Consequently, overfishing remains a top threat to shark populations in the region.

The time required for recovery varies among species depending on their life-history characteristics and can extend beyond a century for some long-lived top predators (Lotze et al., 2011; Duarte et al., 2020). The duration of the implemented measures (excluding pilots) in the reviewed success cases was 22yr on average (median: 15yr), confirming that adequate time is needed before a significant positive result can be ascertained. Therefore, despite the substantial increase in MPAs coverage (a ten-fold increase since 2000) and the implementation of other management measures in recent years, tangible conservation outcomes for top predators are yet to be observed.

7 The way forward - recommendations

Despite all claims by global and regional policy and management organizations, the dichotomous approach to the conservation (as synonyms of management ensuring a long-term sustainable use/conservation) of the marine environment has played a key role in adoption of measures effectively halting the decline of some top predators or biodiversity in general. On the one hand the complex and not fully understood relationships between the myriad of marine ecosystem elements and on the other the systematic governmental or supra-governmental approach that is strictly sectoral, have undermined the actual application of the EBM. To move a step further towards devising efficient solutions for the conservation of top predators and biodiversity as a whole, we need to embrace more holistic and adaptive approaches to decision-making (Elliott and O'Higgins, 2020). The full understanding of socio-ecological and economical elements is difficult too given the complex interconnections between human activities and ecosystems. The Drivers-Pressures-State-Impact-Response model of intervention (DPSIR model family) is typically best suited to look at some of these links and complexities. However, elements of the ecosystem (e.g., top predators) may represent an important natural capital asset, contributing to both the structure and functioning of the marine ecosystem and delivering of societal goods and benefits (in the human domain). Hence, Elliott and O'Higgins (2020) proposed the DAPSI(W)R(M), a more holistic DPSIR-derived framework including benefits offered by nature. Further analyses of the application of this extended framework, including positive impacts on human welfare, resulted in a more comprehensive integrated model (Figure 6A), which links natural and social sciences with governance and management (Elliott, 2023), accounts for cumulative impacts across natural and social systems under a risk management framework (Stelzenmüller et al., 2018; 2020), and includes conservation as a key management measure ensuring that humans can live '*in harmony with nature*' (see (R(M))

in Figure 6A). Figure 6B Lists all elements of the DAPSI(W)R(M) matrix that are deemed relevant to marine top predators, according to our analysis on marine mammals, marine birds, elasmobranchs and bony fish. Details on specific Responses (measures) can be found in the reviewed papers.

Biodiversity loss in marine ecosystems has far-reaching consequences that extend beyond the context of these top-down or bottom-up effects (McCauley et al., 2015). Defaunation can disrupt cross-system connectivity (McCauley et al., 2012a, 2012b) and undermine ecosystem stability (Britten et al., 2014). Moreover, the depletion of genetic diversity in top predator populations can reduce resilience and adaptive potential in changing environmental conditions (Heithaus et al., 2013).

The recovery of marine animal populations can be a slow and complex process (Jackson et al., 2001; Worm et al., 2006; Lotze et al., 2011). Rebuilding and restoring efforts can be successful (e.g., Bowen and Iverson, 2020) but may require sustained conservation measures and robust ecosystem-based management approaches accounting for all key ecological interactions (Pandolfi et al., 2011). Recognizing the historical role of top predators in ecosystems is a crucial initial step toward their recovery, as their past abundance and baseline may exceed estimates based on recent survey data.

In general, EBM efforts should incorporate all essential ingredients for successful implementation: accounting for ecological connections, making the best use of scientific knowledge, implementing adaptive and integrated management (and monitoring) at appropriate spatial and temporal scales, involving all relevant stakeholders, accounting for the dynamic nature of ecosystems, recognizing socio-ecological links by reflecting societal choices, and acknowledging the overall uncertainty linked to the large inherent variability of any ecosystem (Long et al., 2015).

In the following subsections we offer key recommendations to guide science-based effective conservation actions, which are summarized in Table 2.

7.1 Lessons learned from success and unsuccessful stories

The systematic review of success stories highlighted that the conservation of marine top predators requires, more than for other species or habitats, a combination of robust knowledge, education and outreach, specific and adaptive management measures, high-level stakeholder involvement (including enforcement agencies). Bycatch reduction measures and the establishment of well-managed MPAs were the most commonly reported successful actions, depending on the characteristics of the taxa. Social factors, community involvement, and securing economic benefits to local communities were critical drivers for success.

For many top predators, the primary causes of their decline are well-understood, and in many cases, effective management measures have been implemented and led to reversed trends (e.g., marine mammals that have been generally protected from hunts since mid-1980s-early 1990s; see also Boxes 1, 2). The 481 success stories identified by our review underscore the existence of a valuable knowledge base that can assist marine managers and decision-makers in taking action to reverse the decline of top predators under a holistic EBM approach aiming at the recovery of the entire marine ecosystem.

Success requires political will to implement the necessary management measures (e.g., whaling moratorium or rigorous setting of exploitation quotas). However, challenges remain when the interests at stake are much larger and linked to societal demands (e.g., fishery-related impacts on top predators and more recent intensified use of the marine system for energy, transport, and food), and the transferring of tested mitigation measures to operational fisheries addressing bycatch and overfishing remains unresolved. Our analysis shows that bycatch is by far the highest priority issue; when mitigation measures (technological, operational, and socioeconomic ones) are implemented, they become the most successful tool to reverse the decline of top predators. Compared to other direct mortalities (e.g., collisions with ships), bycatch is easier to be monitored/quantified and mitigated. Yet, implementing bycatch mitigation and monitoring policies is moving at too slow a pace, both at global and regional levels. Bycatch is an issue for which relevant authorities already have many off-the-shelf solutions. Even though the issue will likely require adaptive management because mitigation measures often work well in the short- but not the long-term, this challenge does not justify inaction. In line with the DAPSI(W)R(M) framework, a governance solution could be to equally direct funding opportunities to develop innovative methods and technologies and test other operational and effective socio-economic management tools, as these two fields are complementary.

The relatively low number of studies on the implementation of conservation measures compared to funded pilot research studies since the 2000s may indicate an increasing preference for investment on environmental research rather than on management (including large-scale implementation of technical measures) (see Figure S7). The inability to translate mitigation options identified in pilot studies into large-scale management may directly result from such unbalance or on the fact that solutions based on local tests (i.e., geographically and temporally limited) are not easily exportable or they do not work overtime. The failure to scale up may be also a consequence of the lack of codesign with appropriate stakeholders and/or limited ability to communicate benefits. In this regard, a useful open-source tool evaluating the applicability of existing mitigation and management measures and fact-checking their usefulness is the 'Conservation Evidence' initiative. This is a free reliable information source, built by the Department of Zoology of the University of Cambridge (UK), which is intended to inform decisions on conservation and restoration of biodiversity, by providing a comprehensive synthesis of known conservation measures for major taxonomic groups and an evaluation on their actual effectiveness.

There are different types of stakeholders, and their contribution is highly variable. In success stories, central authorities and governmental agencies were directly involved, highlighting the importance of roles and legitimacy. Conservation needs everyone's contribution but can seldom be achieved without the involvement of competent authorities.

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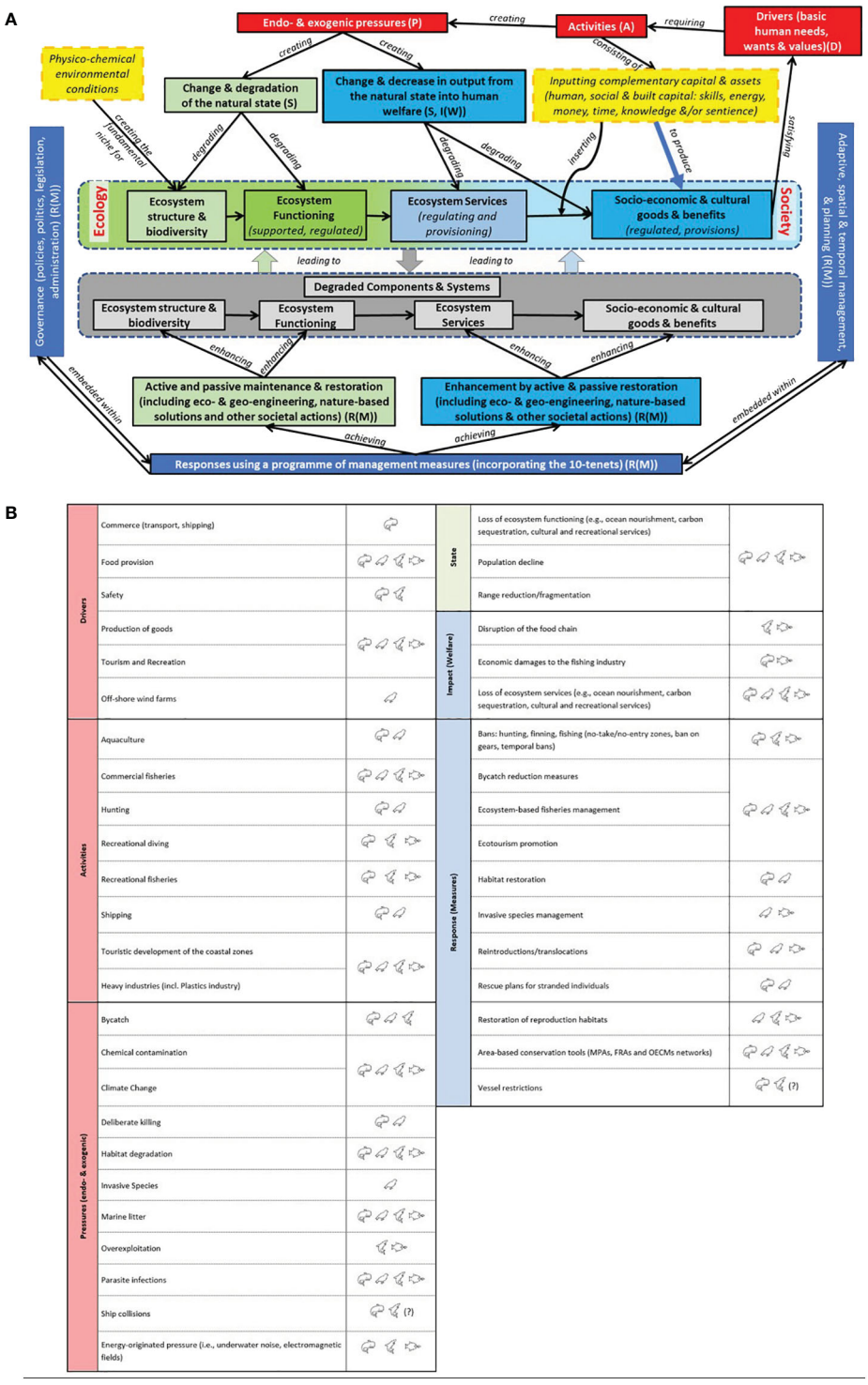

FIGURE 6
(A) The socio-ecological system unifying the DAPSI(W)R(M) framework, the means of degrading the natural system and recovery management measures, and the ecological structure and functioning of ecosystem services and societal goods and benefits continuum (from Elliott, 2023); **(B)** elements of the DAPSI(W)R(M) matrix relevant to marine top predators, according to this review (the right column shows reviewed taxa: marine mammals, marine birds, elasmobranchs, fish).

The overall trends from studies indicate that gaining the whole context is fundamental and that it is essential that we understand "what" and "when" we are measuring from the standpoint of population dynamics. The example of the combined use of the IUCN Green status and the IUCN Red listing categories (Box 1) helps us look at the whole context slightly differently. It provides a more realistic way to weigh and interpret the increases and declines of top predators. For example, very depleted populations may

TABLE 2 Summary of recommendations to guide science-based implementation of effective conservation actions.

Theme	Priority:	Directed to:	Expected outcome & benefits:
Research	Reconstruction of baseline data on ecological, genetic, and demographic variables of top predators	• Scientific community • National/ international monitoring bodies	⇒ Reference points are established, and recovery targets are set to direct appropriate conservation measures.
	Invest in large-scale (spatially and temporally), multi-taxa monitoring programs to fill knowledge gaps on top predators' distribution, abundance and habitats	• Multilateral institutions (e.g., EU, IUCN, UNEP) • Funding agencies & NGOs • National and regional authorities	⇒ Move species out of the Data Deficient category (often DD species are not less endangered than those classified as such), avoiding disaster caused by the lack of knowledge
	Invest in systematic collection of baseline data on human-induced mortality and other direct threats to top predators	• National/ international monitoring bodies	⇒ Improved quality of science-based management
	Development of innovative methods and technologies for monitoring top predators and (at least) related drivers of human-induced mortality	• Scientific community • Stakeholders (fisheries)	⇒ Operational and effective management tools leading to the reduction of top predator decline and a more robust representation of top-down impacts on food webs
	Testing and development of technical tools to reduce top predators' mortality (e.g. bycatch reduction devices)	• Scientific community • Stakeholders (fisheries)	⇒ Co-development and test of successful technologies to reduce top predators' mortality, as a basis for further scaling up of the approach
	Incorporating local ecological knowledge	• Scientific community	⇒ Better historical reconstruction of baseline population status
Theme	***Priority:***	***Directed to:***	***Expected outcome & benefits:***
Policy & Management	Mitigate bycatch of protected species and species of conservation concern	• Multilateral organizations (e.g., EU, CBD, Regional Advisory Councils, RFMOs) • National and regional authorities	⇒ Reduction of human-induced mortality leads to recovery of top-predator population and species ⇒ Meet RFMOs and single stakeholders declared sustainability objectives

(Continued)

TABLE 2 Continued

Theme	Priority:	Directed to:	Expected outcome & benefits:
		• Fishery stakeholders	
	Implement systematic conservation planning and adaptive approaches within an MSP context	• Multilateral organizations (e.g., EU, CBD) • National and regional authorities	⇒ The prioritization of sites for reaching the '30-by-30' target leads to effective and cost-efficient networks of MPAs, capturing the entire biodiversity, including top predators
	Establish well-managed MPAs and OECMs aiming to restore top predator populations	• Multilateral organizations (e.g., EU, CBD) • National and regional authorities	⇒ The effectiveness of MPAs and OECMs is improved, and top predators are effectively protected
	Scaling up successful pilot projects for reducing bycatch and mitigating other threats	• Multilateral organizations (e.g., EU, IUCN, UNEP) • Competent national and regional authorities	⇒ Top predator mortality decreases based on more effective management measures
	Large-scale use/ testing of 'off-the shelf' bycatch mitigation tools	• National and regional authorities • Fishery stakeholders	⇒ Top predator mortality decreases based on more effective management measures, including mitigation tools
Theme	***Priority:***	***Directed to:***	***Expected outcome & benefits:***
Participatory process	Codesign management measures with affected stakeholders	• National and regional authorities • Marine industries	⇒ Decreased opposition to management measures, improved effectiveness of management measures, achievement of higher population growth rates
	Incorporating local ecological knowledge	• Scientific community & local population/ stakeholders	⇒ Improved broad commitment to conservation of top predators and management approaches
	Invest in multi-disciplinary monitoring programs allowing the inclusion of all	• EU funding agencies • National and	⇒ Scale-up data collection and improve our knowledge and understanding on top

(Continued)

TABLE 2 Continued

Theme	Priority:	Directed to:	Expected outcome & benefits:
	necessary stakeholders, but preserving the concept of science-based management	regional authorities	predator ecology ⇒ Increase stakeholder acceptance of conservation measures
	Increase public awareness and ocean literacy	• General public	⇒ Increased public support and political pressure for measures to restore top predator populations - more success stories

increase relatively rapidly if the environmental conditions allow and there are no biological constraints, leading to an excessively positive interpretation. In contrast, populations near or at carrying capacity may decrease or fluctuate in abundance for purely natural reasons. Abundance should always be a high-priority indicator, and a combination of genetic modeling and historical data may help roughly estimate pre-exploitation levels of top predators (e.g., Romero et al., 2022). If no information is available on the historical trajectories of a population, it is essential to consider increases in the light of implemented conservation measures (e.g., the ban of driftnets for large pelagic fish) (UNGA, 1990a, b; UNGA 1992) and the potential ecological benefit on the concerned species.

7.2 State-of-the-art research tools for the best scientific advice

Reinforcing effective monitoring of marine top predators and combining traditional and novel monitoring and modeling strategies is crucial for understanding the dynamics and ecological significance of these species within their marine ecosystems and to identify cause-effect links between human pressures and biodiversity. Long-term monitoring is imperative for these usually long-lived species. While traditional methods play a vital role in this pursuit, incorporating Local Ecological Knowledge (Sáenz-Arroyo et al., 2005; Maynou et al., 2011; Coll et al., 2014), and other novel approaches can greatly enhance our knowledge (Louzao et al., 2009; Ramos et al., 2009; Giménez et al., 2017). Technological advancements have paved the way for innovative tools, such as cheaper and smaller biologging devices (e.g., GPS tags, accelerometers, video cameras), which can be attached to animals to collect high-resolution data on their behavior and habitat use. This invaluable information encompasses diving patterns, prey preferences, and environmental interactions, enabling researchers to gain insights into predator-prey dynamics and the effects of environmental changes (Ramírez et al., 2020; Giménez et al., 2021a). Moreover, the integration of genetic techniques, such as eDNA analysis (e.g., Baker et al., 2018; Ferrari et al., 2018; Mariani et al., 2021; Suarez-Bregua et al., 2022; Valsecchi et al., 2023), or the consideration of publicly available information sourced from digital media (e.g., Sbragaglia et al., 2024), can offer useful complementary information on elusive species. By harnessing the power of both traditional and novel approaches, scientists can bolster monitoring efforts and uncover critical insights into the lives of marine top predators, ultimately aiding in the conservation and management of these species.

One of the biggest caveats when studying the effect of anthropogenic impacts on top predators is quantitative long-term data on human activities. Precise knowledge of human activities at meaningful temporal and geographical scales is often unavailable. This jeopardizes our ability to detect the impacts on top predators and inform management and conservation when needed. To reconcile the biodiversity perspective with the human-related pressures, the implementation of systematic conservation planning (Pressey and Bottrill, 2009) for marine spatial prioritization has been consistently recommended by marine scientists (Katsanevakis et al., 2020). This offers a transparent, comprehensive framework for guiding conservation efforts such as the location, configuration, and management of MPAs to achieve operational targets for ecological components while minimizing the socio-economic costs of use restrictions (Mazor et al., 2014; Yates et al., 2015; Afán et al., 2018; Giménez et al., 2021b). A comprehensive approach is required to support the conservation and resilience of top predators, as these species rely on the whole ecosystem at very large spatial and temporal scales. Despite the worldwide promotion of ecosystem-based approaches, many regions lack specific measures targeting top predators, such as the mandatory utilization of suitable bycatch reduction devices. European Union Member States must adopt programs of measures to attain a GES under the MSFD. These programs should include management actions aimed at safeguarding top predators.

Author contributions

CF: Conceptualization, Supervision, Visualization, Writing – original draft, Writing – review & editing, Project administration. TF: Conceptualization, Writing – original draft, Writing – review & editing. JB-P: Conceptualization, Writing – original draft, Writing – review & editing. MC: Conceptualization, Writing – original draft, Writing – review & editing. AF: Conceptualization, Writing – original draft, Writing – review & editing. JG: Conceptualization, Writing – original draft, Writing – review & editing. YS: Writing – original draft, Data curation, Visualization. MP: Writing – original draft, Writing – review & editing. CC: Writing – original draft. SB: Writing – original draft, Writing – review & editing. EF-C: Writing – original draft, Writing – review & editing. SF: Writing – original draft, Writing – review & editing. OG-G: Writing – original draft, Writing – review & editing. AV: Writing – original draft, Writing – review & editing. ML: Writing – original draft, Writing – review & editing. AP: Writing – original draft. SR: Conceptualization, Writing – original draft, Writing – review & editing. FR: Writing – original draft. JR: Writing – original draft. DR: Writing – review & editing. FS: Writing – original draft, Writing – review & editing. VS: Writing – original draft. SK: Conceptualization, Project administration, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

Author AF was employed by The International Estuarine & Coastal specialists Ltd.

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.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1282091/full#supplementary-material

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The effects of artificial light at night (ALAN) on the circadian biology of marine animals

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The effects of anthropogenic sources of light on the circadian biology of marine animals are largely unexplored at the molecular and cellular level. Given that light is a major driver of circadian rhythms at the behavioral, physiological, cellular, and even molecular levels, it is important to consider the effects that anthropogenic light, especially at night, has on aquatic species. With the expanding data generated from circadian clock research, it is surprising that these techniques have not been applied more frequently to better understand how artificial light affects animal circadian rhythms. Circadian research has been limited to behavioral and physiological observations in wild marine animals rather than a cellular and molecular understanding due to the logistical constraints. While there are some benefits to using artificial light at night (ALAN), there have also been many studies reporting physiological and behavioral consequences in response to exposure to ALAN. Here, the benefits and consequences of using ALAN in the marine environment are reviewed. Furthermore, perspectives on research limitations and future research directions are discussed. Taken together, this is an important area in which more information is required to translate our understanding of circadian biology into better practices to promote the health and welfare of marine animals.

KEYWORDS

circadian biology, marine animals, artificial light, light pollution, animal welfare

Introduction

Environmental stimuli such as photoperiod (light/dark cycles), temperature, and tidal changes govern many behavioral and physiological processes in animals. Because light is a major driver of circadian rhythms, the use of artificial light, especially at night, should be considered in efforts to conserve species in both natural populations and those under managed human care. Disruption of natural lighting through the exposure of artificial light at night (ALAN) or the incorrect use of ALAN in managed care settings can disrupt these pathways. In most animals, the circadian clock is the internal molecular timekeeping mechanism. The hallmark of the circadian clock mechanism is a transcriptional/translational feedback loop

where one revolution of this feedback loop takes approximately 24 hours to complete under normal environmental conditions. (Dubruille and Emery, 2008; Takahashi, 2017; Stanton et al., 2022). This mechanism is integrated with numerous other physiological pathways including metabolism, sleep regulation, reproduction, development, cell turnover, and immune regulation (Morris et al., 2020; Stanton et al., 2022). Outputs of these pathways can also fine-tune the circadian clock mechanism through post-translational modifications, which are well characterized in vertebrate model organisms (Morris et al., 2020).

The circadian clock is entrained by internal and external environmental stimuli referred to as 'zeitgebers' (Figure 1). Many specific behaviors and biological/physiological processes are evolutionarily adapted to the rhythms of natural photoperiods (Tidau et al., 2021). Tidal cycles, as well as photoperiod, function as zeitgebers that entrain biological clocks of marine species and synchronize large scale responses (Tidau et al., 2021). While peripheral circadian clocks can be entrained by localized zeitgebers, such as feeding, the master circadian regulator is entrained by light (Morris et al., 2020; Stanton et al., 2022). Animals perceive light information through their eyes or through photoreceptors in the absence of eyes (Stanton et al., 2022). Cryptochromes (CRYs) function as primitive photoreceptors activated in response to blue light (Schlacher et al., 2007; Mendes et al., 2017; Cheng et al., 2022; Stanton et al., 2022). Sessile organisms such as corals respond to different wavelengths of light, whereas, mobile aquatic species use phototaxis (movement toward or away from a light stimulus). The phototactic nature of fish results in light-directed swimming and aggregation with varying preferences for different wavelengths of light (Marchesan et al., 2005). Furthermore, different wavelengths of light result in different behavioral and physiological effects. For example, red light has been shown to stimulate feeding behavior and metabolism in Nile tilapia (*Oreochromis niloticus*) (Volpato et al., 2013).

Melatonin is another regulator of an animal's circadian biology that is superseded by the molecular circadian clock (Falcón et al., 2009; Tan et al., 2010). Melatonin production has been identified in aquatic invertebrates including cnidarians, dinoflagellates, mollusks, annelids, flatworms, nematodes, and crustaceans (Hardeland and Poeggeler, 2003; Muñoz et al., 2011; Roopin and Levy, 2012; Sainath et al., 2013; Peres et al., 2014; Tosches et al., 2014; Tran et al., 2020; Zhu et al., 2022). ALAN suppresses melatonin synthesis and has been linked to a reduction in fitness (Jones et al., 2015; Grubisic et al., 2019). The ability to monitor melatonin synthesis is another method that may be used to assess the impact of ALAN on marine animals.

Here, the effects of using ALAN are discussed. Considerations such as the timing of light/dark periods and wavelength of light are both important factors when adapting these practices to minimize impacts on an animal's circadian clock mechanism. Accordingly, a perspective on current gaps in knowledge and research opportunities to inform best care and conservation practices for managed marine animals is provided.

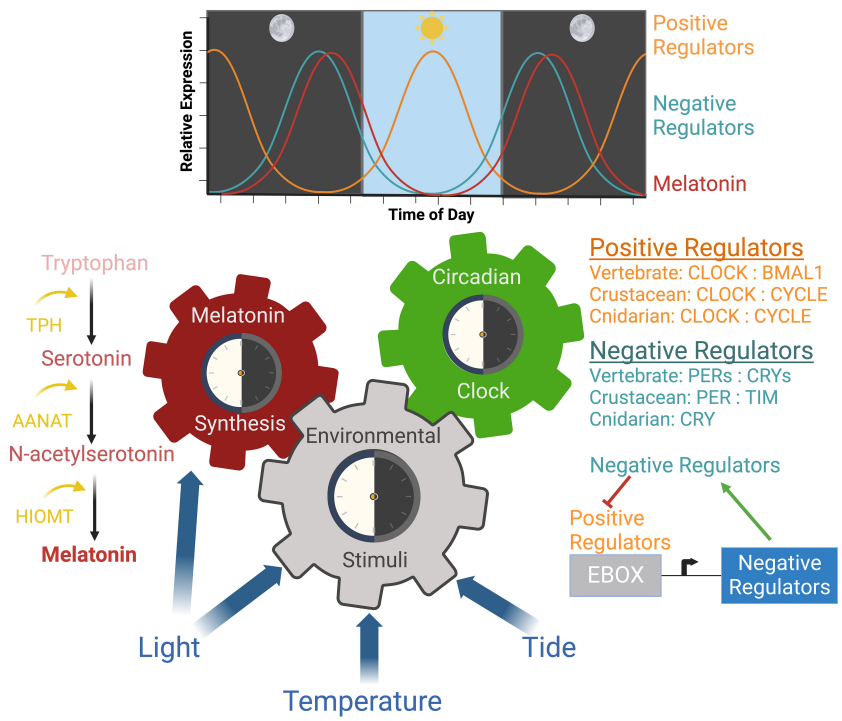

FIGURE 1
Mechanisms and rhythms of circadian regulation. Molecular and hormonal circadian mechanisms occur in response to environmental stimuli. The molecular clock is a transcription/translational feedback loop where the expression of positive regulators are highest during the day and expression of negative regulators are highest at night. Light is the master regulator of this mechanism. Light also regulates melatonin synthesis, which occurs during the night leading to high melatonin accumulation before dawn. Melatonin decreases as it is circulated and utilized. Both mechanisms regulate physiological and cellular processes in a circadian manner in marine animals. Created with BioRender.com.

The effects of ALAN on marine animals in coastal environments

The use of artificial light at night (ALAN) near coastal environments brings few documented benefits, which are generally restricted to enhancing fish yield through aquaculture. This is exemplified by the continuous ALAN illumination in ocean pens that is common practice for species of salmonids (McConnell et al., 2010). This continuous illumination attracts a multitude of invertebrate species that aggregate in the illuminated area, increasing the available food resources for fish in the pens (Delupis and Rotondo, 1988; Jékely et al., 2008; McConnell et al., 2010; McLeod and Costello, 2017; Siddik and Satheesh, 2021). However, the resounding effects that ALAN has on the circadian biology of these farmed fish is largely understudied and it is reasonable to hypothesize that there will be long-term effects on behavior and physiology due to chronic circadian clock disruption.

In coastal communities, specifically marine intertidal areas, the use of ALAN is noted to have substantial negative effects on the aquatic species inhabiting these nearshore locations. These species receive relatively constant exposure to varying levels of ALAN due to significant coastal development and urbanization. Constant exposure to ALAN may disrupt normal circadian clock function by interfering with an individual's ability to function appropriately during natural cycles of light and dark (Kopperud and Grace, 2017). This has downstream effects on different behavioral and physiological processes, many of which are innately tied to circadian or circatidal rhythms (Brüning et al., 2015). Such alterations can be observed in variations in activity patterns or disruptions in the expression of circadian clock genes. Examples include loss of circadian rhythm of activity in the isopod (*Tylos spinulosus*), arrhythmic expression of circadian clock genes in the Pacific oyster (*Crassostrea gigas*), higher activity levels in rockfish (*Girella laevifrons*) that may be attributed to a loss of internal circadian and circatidal rhythms over time, and direct effects on the rhythmic production of melatonin in European perch (*Perca fluviatilis*) with many fish lacking circadian melatonin rhythms as compared to control fish (Brüning et al., 2015; Duarte et al., 2019; Pulgar et al., 2019; Botté et al., 2023).

The use of ALAN in the oceanic environment

Pelagic species may be exposed to ALAN through different venues including lighting from bridges, oil platforms, or vessels such as commercial fishing vessels or cruise ships (Hölker et al., 2010; Davies et al., 2014; Szekeres et al., 2017). Interruptions to the natural biological clocks may have significant detrimental effects on individual marine organisms and biodiversity as a whole (Figure 2).

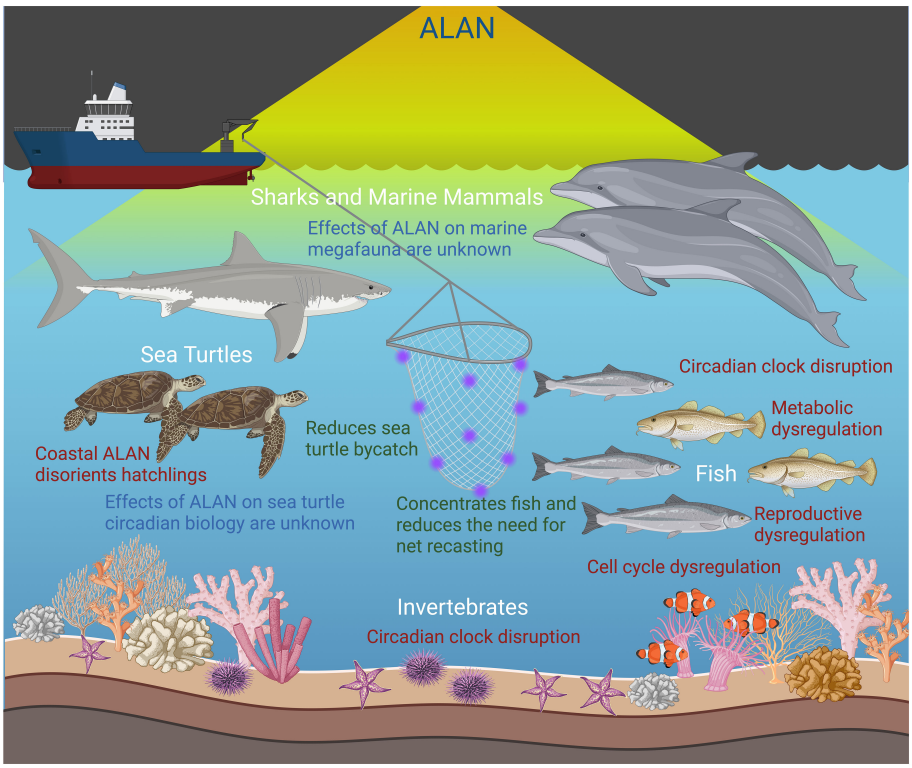

FIGURE 2
Effects of artificial light at night (ALAN) exposure in the aquatic environment. ALAN is beneficial in enhancing fishing practices and reducing bycatch. However, ALAN exposure disrupts the circadian clock in fish and some invertebrates leading to alterations in important processes such as metabolism, cell division, and reproduction. The effects of ALAN on the circadian biology of marine megafauna are currently unknown. Created with BioRender.com.

Data is severely lacking in regards to the effects of ALAN on the circadian rhythms of pelagic species, which is likely due to the logistical constraints of research in the pelagic environment. Regardless, some information does exist demonstrating the advantages and disadvantages of ALAN exposure, particularly in commercial fisheries and coral research, respectively.

ALAN has been utilized on commercial fishing vessels to enhance fish yields as well as reduce bycatch of unwanted species (Arakawa et al., 1998; Marchesan et al., 2005; Nguyen and Winger, 2019). This reduces the need for continuous net redeployment to meet fish quotas and reduces fuel consumption (Nguyen and Winger, 2019). Ultraviolet, blue, and green light-emitting diode (LED) lights on nets and lines have been shown to reduce the amount of bycatch of fish and sea turtles; however, the mechanism by which this occurs is unknown (Wang et al., 2013; Hannah et al., 2015; Virgili et al., 2018). Therefore, use of ALAN in commercial fisheries has proven to be a beneficial conservation tool. The potential effects from commercial fishery use of ALAN on the circadian clock of marine organisms may be short-lived as the clock can resynchronize with the subjective day and animals may not encounter a fishing vessel every night.

Outside of commercial fisheries, simulated ALAN exposure experiments have demonstrated the negative effects of ALAN on different offshore species. The majority of this research has focused on corals, which are highly photosensitive and have well-developed circadian behaviors (Rosenberg et al., 2019), and are thus intensely vulnerable to the effects of ALAN (Fobert et al., 2023). In coral species collected from oceanic environments, ALAN exposure reduced reproductive fitness by delaying gametogenesis and inhibiting synchronization of gamete release (Ayalon et al., 2021). Furthermore, it has also been demonstrated that spawning occurs closer to a full moon in corals exposed to ALAN, suggesting that speeding up the spawning time can lead to decreased fertilization and survival of gametes (Davies et al., 2023). Additionally, metabolic fitness was reduced as a result of a lower rate of photosynthesis, a lower electron transport rate, and the disruption of coral-dinoflagellate symbiosis (Ayalon et al., 2019; Levy et al., 2020; Tamir et al., 2020). In *Acropora eurystoma*, constant exposure to ALAN resulted in arrhythmic expression of known clock genes and alteration of cellular pathways (Rosenberg et al., 2019).

ALAN exposure has also been shown to negatively impact the physiology and overall fitness of reef fishes with significant effects on metabolism, embryo quality, growth, and survival (Fobert et al., 2023). In certain reef fishes, such as clownfish (*Amphiprion ocellaris*) and sergeant majors (*Abudefduf saxatilis*), the timing of embryo hatching is linked to specific intensities of light within the natural photoperiod. Constant illumination by ALAN eliminates photoperiod cues necessary for hatching, thus inhibiting successful hatching in these species (Robertson et al., 1990; Fobert et al., 2019; Fobert et al., 2023). These negative effects demonstrate the potential disruption of the circadian rhythms of various oceanic organisms in response to ALAN exposure, representing yet another conservation concern for overall biodiversity in illuminated areas.

Lessons learned from the laboratory

The circadian clock mechanism and the effects of ALAN on circadian biology have been well-studied in laboratory settings. Exposure to ALAN can result in widespread disruption of the circadian clock mechanism, changes in behavior, irregular sleep and activity patterns, reproductive dysfunction, immune regulation issues, and metabolic dysfunction (Morris et al., 2020; Fobert et al., 2021; Hillyer et al., 2021). Although limited in number, these studies have been instrumental in beginning to elucidate the effects of ALAN on circadian biology, physiology, and behavior of aquatic species.

Circadian clock genes have been identified in several marine invertebrate species including the marine annelid *Platynereis dumerilii*, the Pacific oyster (*Crassostrea gigas*), and a few Xenacoelomorphan and platyhelminth marine worms (Zantke et al., 2013; Stanton, 2015; Stanton et al., 2022; Botté et al., 2023). Laboratory experiments have demonstrated the negative effects of ALAN exposure on these species. For example, changes in activity patterns have been observed after switching *P. dumerilii* from a diurnal photoperiod to continuous light (Zantke et al., 2013). Similarly, the Pacific oyster demonstrates a comparable pattern of disruption in circadian clock gene expression and increase in valve activity when cultured under ALAN conditions (Botté et al., 2023).

Laboratory studies examining the circadian biology of fish have also provided useful insights on the effects of ALAN in *ex situ* populations. This has allowed extensive studies of fish light reception and circadian clock entrainment including: studies of eyes, photoreceptors, pineal gland, brain receptivity to light and their downstream effects on behavior, physiological, and cellular processes (Whitmore et al., 2000; Doyle and Menaker, 2007; Tamai et al., 2012; Foulkes et al., 2016). In the zebrafish (*Danio rerio*), ALAN exposure resulted in arrhythmic melatonin synthesis and an increase in inflammatory cytokines (Khan et al., 2018). In Japanese medaka (*Oryzias latipes)*, zebrafish, and clownfish, ALAN exposure inhibited displays of dominance resulting in fish becoming subordinate and leading to a decline in reproductive success where males under constant light produced half the number of offspring that males maintained under diel lighting conditions produced (Tamai et al., 2004; Fobert et al., 2019; Frøland Steindal and Whitmore, 2019; Fobert et al., 2021; Closs et al., 2023). ALAN exposure also increased the interval between spawning events, resulting in smaller eggs and a reduction in clutch size (Tamai et al., 2004; Fobert et al., 2019; Frøland Steindal and Whitmore, 2019; Fobert et al., 2021).

These examples demonstrate that behavioral and physiological responses are regulated in a circadian manner by the circadian clock mechanism and disruptions to these natural rhythms have significant downstream effects. This emphasizes the need for additional research to understand the effects of ALAN and the development of mitigation strategies to minimize these effects on the aquatic ecosystem. Furthermore, these findings can be used for the improvement of artificial conditions to recapitulate the natural environment for animals under managed care.

Perspectives on the use of ALAN

While there are some benefits to using ALAN, the stark reality is that there is insufficient data to understand how detrimental the use of ALAN can be to species in the aquatic environment. There has been limited research on the effects of ALAN on the potential disruption of the circadian biology of marine animals. The duration of using intermittent ALAN, in the case of commercial fisheries, likely will not have as pronounced an effect on the circadian clock mechanism. With this, daylight will likely re-entrain circadian rhythms and the animal may not encounter a commercial fishing vessel again for some time. Therefore, this represents a situation in which the potential negative effects of ALAN would be minimal. However, the disruption of the circadian clock is likely in animals maintained in aquaculture pens as they would not be able to escape constant ALAN exposure. This is one area of opportunity for additional research to better understand the effects of circadian disruption and increase overall welfare in these animals.

Data from aquatic invertebrates, fish, and marine reptiles have begun to illuminate the consequences of ALAN in managed settings. While laboratory studies have been important in understanding circadian biology and how perturbations alter aspects of their circadian clock, physiology, and behavior, there are additional challenges. Given that the laboratory setting is highly controlled, it is possible that the results of a laboratory experiment are an artifact of the controlled conditions and are not able to be recapitulated in a natural setting. Comparative studies are needed to better understand the effects of ALAN-associated circadian disruption on behavior and physiology.

Apart from sea turtles, there is a lack of studies examining the effects of ALAN on marine megafauna, including marine mammals and elasmobranchs. Effects of ALAN exposure on the circadian clock mechanism and melatonin biosynthesis in marine megafauna represents another area where research efforts should be directed. It is likely that there is variation in circadian regulation among marine megafauna. For instance, vertebrate melatonin produced by the pineal gland appears to be a synapomorphy amongst most vertebrates (Falcón et al., 2009; Tan et al., 2010). The pineal gland has been identified in several aquatic species including fish, sharks, and pinnipeds (Little and Bryden, 1990; Boyd, 1991; Frøland Steindal and Whitmore, 2019; Carroll and Harvey-Carroll, 2023). However, it appears to be vestigial or lost along with the associated melatonin synthesis and receptor genes that have been either inactivated through a mutation or lost in the cetacean and sirenian lineages (Ralph et al., 1985; Huelsmann et al., 2019; Lopes-Marques et al., 2019). Taken together, variation in melatonin regulation should be expected and is likely lineage specific.

Understanding circadian disruption in response to adverse exposure to ALAN is also important for animals under managed care. Facilities often cater to the needs of guests by extending hours beyond the subjective day and leaving work lights on as part of emergency lighting systems (Rose et al., 2017). It is currently unknown if these lights are detrimental and if altering the wavelength could improve aquatic animal welfare. The adjustment of lighting regimens based on research for a given species or groups of species should be considered. The development of LED-based aquarium lighting systems has been beneficial in aquarium settings and has solved problems with light penetrating the water column in deep aquarium environments (Soni and Devendra, 2005; Cheng et al., 2019). Studies are needed to understand the basic circadian biology and the effects of circadian perturbations on behavior and physiology in managed animals. It is possible that disruption of the circadian clock mechanism can impact marine animal health and delay healing in sick and injured megafauna in managed care.

Future directions

While our knowledge of circadian biology and its integration with different physiological systems has expanded over the last twenty years, there remains a significant knowledge gap in regards to aquatic species. This reflects a critical need to gain a foundational understanding of the natural circadian biology of different aquatic species, in particular, marine megafauna, in order to sufficiently understand the potential negative effects of ALAN exposure on different aquatic species. Given that many cell types have an endogenous circadian clock, utilizing samples that are minimally invasive, such as skin/oral mucosa, hair follicles, and blood, may be viable options for assessing changes to an animal's circadian rhythm. Due to the logistical constraints of sampling and/or re-sampling free-ranging animals, adaptations for the laboratory setting, such as cell cultures and CRISPR technologies, can prove to be powerful tools (Gabriel et al., 2021).

Animal activity and sleep patterns have also been measured to understand how patterns of activity change with different perturbations in light exposure. (Alves-Simoes et al., 2016; Wang et al., 2020). This type of data is not easily obtainable in many aquatic species; however, data logger technology implanted into animals has significantly advanced research efforts to record data such as body temperature, heart rate, activity, telemetry, and even depth patterns. This technology has been successfully used in some aquatic species including fish, sharks, pinnipeds, and cetaceans (Lin et al., 2013; Krause et al., 2016; Chaise et al., 2017; Elisio et al., 2019; Piot et al., 2023; Morgenroth et al., 2024). This technology could be translated for use in animals both in wild and managed settings to observe changes in circadian biology in response to ALAN exposure, feeding, water temperature, and/or water quality. These techniques can also be utilized to test the efficacy of different mitigation strategies for improving animal health and welfare.

While these approaches will have multiple applications, a central focus on understanding how light regulates the circadian biology of aquatic species is needed. Knowledge of the effects abnormal lighting conditions, including the use of ALAN, have on an animal's circadian biology is paramount to developing improved mitigation practices. Implementation of novel techniques will allow researchers to gather a vast amount of data that can be directly applied to the development of mitigation strategies to minimize the adverse effects on an animal's circadian biology. This provides an avenue for applying research that will not only benefit species in managed care, but also those in natural settings.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

DS: Conceptualization, Writing – original draft, Writing – review & editing. JC: Funding acquisition, Writing – review & editing.

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Conflict of interest

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

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Habitat changes of a small endemic euryhaline fish species in the northern margin of the South China Sea under the background of global warming

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Hainan medaka (*Oryzias curvinotus*) is a small euryhaline fish species native to the northern margin of the South China Sea. Our long-term field observations indicate a concerning decline in its wild resources. Climate change, an uncontrollable factor, has altered the species' distribution pattern. In this study, we simulated the shifts in the species range of *O. curvinotus* during the Last Glacial Maximum (LGM), current, and the next one hundred year, and analyzed its habitat attributes. The results demonstrate that bio2 (mean diurnal range of temperature) is a crucial factor in shaping the species range of *O. curvinotus*. The simulation results reveal that the current habitats are located in the coastal areas of northern Vietnam, the northeastern Hainan Province, the coastal areas of Guangdong Province and Guangxi Zhuang Autonomous Region, and a few areas in Taiwan Province of China, covering a total area of 17.82×10^4 km^2. Highly suitable habitats are mainly concentrated in the coastal areas of Hai Phong, Nam Dinh, and Thanh Hoa in northern Vietnam, the central part of Leizhou Peninsula, and the west coast of the Pearl River Estuary. For the tropical species Hainan medaka, the impact of the LGM was relatively minor, and there were extensive suitable habitats during historical times, including three refugia. Currently, only Refugium 2 near Guanghai Town, Taishan County, Jiangmen City, Guangdong Province in China remains, while the other two refugia have submerged below sea level. Future climate warming under different carbon emission levels is projected to cause a short-term expansion, followed by a relief in expansion. By 2100, the potential habitat area of *O. curvinotus* is slightly larger than the current scenario. It is noteworthy that under future climate warming scenarios, the highly suitable habitats will not migrate northward but will expand near the 21°N latitude. Overall, Hainan medaka is not expected to be threatened in the future. Our study provides long-term dynamic distribution data, which provides a theoretical basis for the long-term development and conservation management of Hainan medaka.

KEYWORDS

***Oryzias curvinotus*, climate change, habitats, tropical species, distribution**

Introduction

Evidence that the climate is changing is indisputable (Berrang-Ford et al., 2011), and this phenomenon poses a potential threat to the planet's biodiversity (Kappelle et al., 1999). Over the past 100 years, the Earth's climate has visibly warmed, precipitation regimes have changed, and biologists have been concerned about the impact of these shifts on species distribution (Araújo and Rahbek, 2006). Under the background of global climate change, the study of species distribution range has become the premise of biodiversity conservation strategy, especially for those endemic species with narrow distribution range. For example, the endangered endemic annonaceae species in East Africa may lose some of their original suitable habitats due to future warming (Mkala et al., 2023). In addition, climate change will drive some species to higher altitudes or latitudes (Hickling et al., 2005; Chen et al., 2011; Liao et al., 2023). Over the past few decades, more than 1,700 species have been confirmed to migrate poleward at a rate of 6.1 km/decade (Parmesan and Yohe, 2003), and the rate of migration has doubled or tripled in recent years to a staggering 16.9 km/decade (Chen et al., 2011). Of the species studied, the current focus is mainly on plants and various insect groups, etc., while relatively little is known about vertebrates, especially these tropical endemic fish.

Hainan medaka (*Oryzias curvinotus*) is a small euryhaline fish that is confined to the coastal waters of the South China Sea, including mangroves, brackish water confluxes in estuaries, and even freshwater streams extending inland (Dong et al., 2021). It is small in size, usually growing up to 2 inches long. Similar to freshwater Japanese medaka (*Oryzias latipes*), Hainan medaka is an excellent euryhaline model fish resource to be developed. As a euryhaline fish, *O. curvinotus* exhibits unique adaptive traits that are crucial not only for its own survival but also serve as indicators of ecological balance and environmental health in the South China Sea region. Changes in the habitat of this species directly reflect subtle variations in environmental factors such as salinity and water temperature in the region, which may further impact the stability and biodiversity of ecosystems including mangrove forests, coral reefs, and seagrass beds. However, recent fieldwork indicates that the habitat of Hainan medaka appears to be under threat, and the population resources are not optimistic. Climate change, a long-term and irreversible factor, needs to be considered in addition to the immediate effects of human activities (Yao et al., 2022). In particular, the fate of Hainan medaka, which is located in a biological hotspot (Oriental region), is a key ecological issue in the context of global climate change. By conducting thorough investigations into the habitat shifts and adaptive mechanisms of *O. curvinotus*, a more precise understanding of the ecological health of the South China Sea can be gained, thereby providing scientific evidence for the formulation of effective environmental protection and management strategies.

Effectively predicting the species range and their impacts under climate change, as well as understanding their habitat attributes, is crucial for developing appropriate strategies for species conservation (Alabdulhafith et al., 2022). Species distribution models (SDMs), also known as climate envelope-models, habitat models, and (environmental or ecological) niche-models, largely address the urgent need for ecologists to understand the habitat attributes of species and their distribution range shifts. Maximum entropy model (MaxEnt) is the most widely recognized and used SDMs, due to its high prediction accuracy, automatic assessment of important environmental variables, fast operation, and small sample size requirements (Phillips et al., 2006; Ma and Sun, 2018; Li et al., 2019; Xiao et al., 2022; Liao et al., 2023). MaxEnt is therefore widely used to predict the potential distribution of plants, birds, insects, nematodes, corals, bryophytes, and fungi (Sérgio et al., 2007; Phillips and Dudík, 2008; Tognelli et al., 2009; Williams et al., 2009; Young et al., 2009; Alabdulhafith et al., 2022), providing valuable information in biogeography, invasion biology, conservation biology, and ecology.

In this study, we integrated our previous field data with reported occurrence sites and climate data to analyze the historical period (the Last Glacial Maximum, LGM, dating back approximately between 25,000 and 19,000 years ago), current scenarios, and future potential habitats under different warming levels for the euryhaline fish endemic to the coast of the northern South China Sea. The objectives of this study were to (1) comprehend the habitat properties of *O. curvinotus*, (2) investigate its distribution and refuge locations during historical periods, and (3) assess potential habitats in the present context while considering how future climate change may impact its distribution.

Materials and methods

Field survey and occurrence data collection

We conducted field survey work on *O. curvinotus* from 2015 to 2018, and successfully recorded a total of 19 recording sites (Table 1), including mangrove tidal channels, estuary with a wide salinity range and some freshwater streams. In addition to our survey data, we have collected occurrence data of *O. curvinotus* through the Global Biodiversity Information Facility (GBIF database, https://www.gbif.org/, accessed on 18 June 2023) and literature (Hamaguchi and Sakaizumi, 1992; Kondo et al., 2001; Koga et al., 2002; Matsuda et al., 2003; Hamaguchi et al., 2004; Shiga and Suzuki, 2004; Shinomiya et al., 2006; Kamei et al., 2007; Kato et al., 2010, 2011; Masaoka et al., 2012; Wang et al., 2017; Dong et al., 2020, 2021; Li et al., 2022a; Yao et al., 2022; Gao et al., 2023). We have made every effort to gather all relevant published literature and publicly available data. For the occurrence data collected in the three ways, we first eliminated duplicates and outliers. In order to avoid overfitting, we created a 1km × 1km grid in ArcGIS 10.7 (Esri, Redlands, CA, USA), and reserved only the point closest to the center in each grid. Finally, 38 valid GPS sites were obtained and used for input occurrence data to the model (Figure 1; Supplementary Table 1).

Climate variables and processing

To investigate the impact of climate change on euryhaline fish distribution in tropical regions, a set of 19 bioclimatic factors (Table 2)

TABLE 1 Information from our comprehensive field survey conducted between 2015 to 2018 on the spatial distribution of *O. curvinotus*.

Sites	Longitude	Latitude	Date	Habitat type	Water body type
Fucheng Town, Leizhou City,China	110.1500°E	20.91667°N	April 26, 2015	Mangrove	Saltwater
Donghaidao Mangrove, Zhanjiang City, China	110.3167°E	21.38333°N	March 20, 2016	Mangrove	Saltwater
Gaoqiao Mangrove, Lianjiang, China	109.7617°E	21.56796°N	January 08, 2016	Mangrove	Saltwater
Tuolin Town, Raoping County, China	117.0833°E	23.56667°N	March 29, 2017	Estuary	Brackish Water
Niutianyang Stream, Shantou City, China	116.7167°E	23.31667°N	March 27, 2017	Stream	Freshwater
Niutianyang Mangrove, Shantou City, China	116.5667°E	23.31658°N	March 27, 2017	Mangrove	Saltwater
Niutianyang Farm, Shantou City, China	116.6897°E	23.35955°N	March 25, 2017	Pond	Freshwater
Haojiang Estuary, Shantou City, China	116.6167°E	23.35000°N	March 26, 2017	Estuary	Brackish Water
Mangroves near the Donghai Chemical plant, Zhanjiang, China	110.3167°E	21.38333°N	March 20, 2017	Mangrove	Saltwater
Mangroves in Huguang town, Zhanjiang City, China	110.2833°E	21.10000°N	March 04, 2017	Mangrove	Saltwater
Liushawan Mangrove, Leizhou City, China	109.9167°E	20.45000°N	May 10, 2017	Mangrove	Saltwater
Huguang Stream, Zhanjiang City, China	110.3213°E	21.10629°N	March 04, 2017	Stream	Freshwater
Sanniangwan Mangrove, Qinzhou City, China	108.7167°E	21.66667°N	April 13, 2017	Mangrove	Saltwater
A stream near Sanyangwan salt farm, Qinzhou City, China	108.7625°E	21.62845°N	April 13, 2017	Stream	Freshwater
Dongzhaigang Mangrove, Haikou City, China	110.5833°E	19.9500°N	May 27, 2017	Mangrove	Saltwater
Hongshuwan Mangrove, Chengmai County, China	109.9833°E	19.9000°N	May 23, 2017	Mangrove	Saltwater
Caihong Valliage, Lingao County, China	109.5667°E	19.86667°N	May 24, 2017	Stream	Freshwater
Bamenwan mangrove, Wenchang County, China	110.8099°E	19.86117°N	May 26, 2017	Mangrove	Saltwater
Sanya Mangrove, Sanya City, China	109.7525°E	18.40005°N	March 27, 2018	Mangrove	Saltwater

with 2.5 arc-minutes spatial resolution were selected as environmental variables for the model, which were downloaded from the WORLDCLIM 2.0 database (https://www.worldclim.org/data/bioclim.html, accessed on June 18, 2023). The downloaded climate variable layer was converted into ASCLL format in ArcGIS 10.7 for MaxEnt model analysis. The climate variables used in this study include historical (the LGM), current and future climates (Fick and Hijmans, 2017). The future climate includes four carbon emission levels (SSP1-2.6: the low-end level, 376 ppm CO_2-equivalent level; SSP2-4.5: the low-moderate level, 650 ppm CO_2-equivalent level;

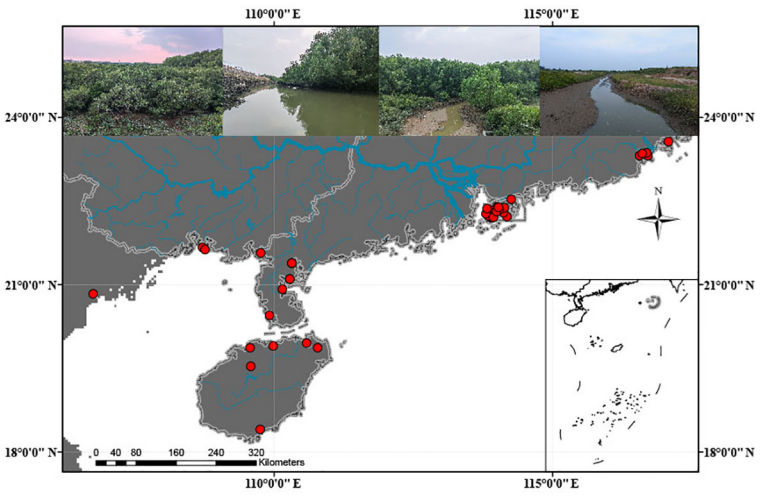

FIGURE 1
Current occurrence sites of *O. curvinotus* and its main habitats photos.

TABLE 2 The 19 climate variables used in this study.

Climate Variables	Unit	Symbol
Annual mean temperature	°C	bio1
Mean diurnal range of temperature	°C	bio2
Isothermality	×100	bio3
Temperature seasonality	×100	bio4
Max temperature of warmest month	°C	bio5
Min temperature of coldest month	°C	bio6
Temperature annual range	°C	bio7
Mean temperature of wettest quarter	°C	bio8
Mean temperature of driest quarter	°C	bio9
Mean temperature of warmest quarter	°C	bio10
Mean temperature of coldest quarter	°C	bio11
Annual precipitation	mm	bio12
Precipitation of wettest month	mm	bio13
Precipitation of driest month	mm	bio14
Precipitation seasonality	mm	bio15
Precipitation of wettest quarter	mm	bio16
Precipitation of driest quarter	mm	bio17
Precipitation of warmest quarter	mm	bio18
Precipitation of coldest quarter	mm	bio19

SSP3-7.0: the medium-high level, 1011 ppm CO_2-equivalent level and SSP5-8.5: the high level, 1228 ppm CO_2-equivalent level) (Meinshausen et al., 2020; Liao et al., 2022) and different future decades (2040, 2060, 2080, and 2100) (Fick and Hijmans, 2017).

In order to avoid the multicollinearity of climate factors leading to overfitting of the model, we conducted a variance inflation factor analysis (VIF) (Liao et al., 2023). We first used ArcGIS 10.7 to convert the GPS site distribution data (*csv* format) into raster (*shp* format), then extracted 19 climate variable values at each site using the extraction function of the spatial analysis tool in the toolbox, and performed VIF analysis on 19 climate factors at all sites. We removed 12 multicollinearity climate variables (VIF > 10) by using USDM version 1.1-18 package in R 4.1.3 (Naimi et al., 2014), and 7 variables were left for modeling: bio2, bio7, bio8, bio9, bio12, bio15 and bio17.

Potential habitat modeling and statistical analysis

The potential suitable habitat of *O. curvinotus* was simulated using the maximum entropy model by MaxEnt version 3.3.3k (Phillips et al., 2006). The input data included optimized climate variables and occurrence data. Among them, 25 percent of the occurrence data was randomly selected for the test dataset and 75 percent for the training dataset (Yuan et al., 2015; Yi et al., 2016; Liao et al., 2022, 2023; Xiao et al., 2022). The program ran at least 1000 iterations until it converged (threshold 0.00001) (Zhang et al., 2018; Liao et al., 2022). The robustness of the MaxEnt model is assessed by the AUC value of the threshold-independent receiver-operating characteristic (ROC) analysis: above 0.9 is defined as excellent, between 0.8 and 0.9 is defined as good, between 0.7 and 0.8 is considered acceptable, between 0.6 and 0.7 is defined as poor, and below 0.6 is considered inadequate (Phillips et al., 2006; Liao et al., 2022). Simulating the probability of occurrence of O. curvinotus in a certain location as its suitability value to distinguish different levels of potential habitat (Phillips et al., 2006). The potential suitable habitats obtained through modeling were categorized into four levels based on their suitability values: highly suitable habitats, moderately suitable habitats, lowly suitable habitats, and unsuitable habitats. The suitability values ranged from 0.6 to 1 for highly suitable habitats, from 0.4 to 0.6 for moderately suitable habitats, from 0.2 to 0.4 for lowly suitable habitats, and from 0 to 0.2 for unsuitable habitats (Zhang et al., 2018; Liao et al., 2023). The area of each part was counted in the 3D analysis tool in ArcGIS, and then the area change chart was drawn by HIPLOT online server (https://hiplot.cn/) (Li et al., 2022b). During the LGM, habitat suitability exceeding 0.9 was defined as Refugium (Gathorne-Hardy et al., 2002). The contribution rate, permutation importance of climate variables and their response curve were completed by Jackknife test in MaxEnt software (Phillips et al., 2006).

Results

Model performance, variable contribution, and response curves

The AUC values of both the training (0.999) and test (0.998) sets were greater than 0.9, indicating that the simulation results were reliable and even excellent. The results of the Jackknife test revealed relevant information about the contribution and importance of climate variables (Table 3). For contribution, annual precipitation (bio12, 35.32%) explained the current potential range of *O. curvinotus* to the greatest extent, followed by the mean diurnal range (bio2, 24.91%). Climate factors bio7 (Temperature annual range), bio8 (mean temperature of wettest quarter), bio9 (mean temperature of driest quarter), bio15 (Precipitation seasonality), and bio17 (precipitation of driest quarter) contributed a total of 39.77%. The permutation importance index identified two of the most important climate variables, bio8 (mean temperature of wettest quarter, 46.35%) and bio2 (mean diurnal range, 35.51%). Considering the contribution rate and permutation importance, bio2 is a key climate factor for the potential distribution of *O. curvinotus*. For the most important variables and those that contributed the most, bio2 was used for further analysis. The mean diurnal temperature range varied from 6.9 to 7.9 degrees Celsius, indicating a habitat of low suitability for *O. curvinotus*. When the mean diurnal temperature range falls between 6 and 6.9 degrees Celsius, the habitat suitability for *O. curvinotus* is considered moderate. In areas where the mean diurnal

TABLE 3 The contribution rate, permutation importance of filtered climate factors used in the model prediction, and relevant information of the Jackknife test.

Variable	bio2	bio7	bio8	bio9	bio12	bio15	bio17
Contribution (%)	24.909	0.261	11.618	4.321	35.317	14.350	9.226
Permutation importance (%)	35.506	7.123	46.345	10.922	0.008	0.057	0.040
Training gain without this variable	5.121	5.303	5.117	5.287	5.32	5.312	5.293
Training gain with only this variable	1.408	2.092	2.314	2.022	2.407	1.250	1.733
Test gain without this variable	5.396	5.442	5.405	5.449	5.461	5.465	5.424
Test gain with only this variable	1.532	2.445	2.743	2.355	2.665	1.599	1.939
AUC without this variable	0.998	0.998	0.998	0.998	0.998	0.998	0.998
AUC with only this variable	0.924	0.971	0.980	0.969	0.976	0.934	0.944

temperature range is below 6 degrees Celsius, *O. curvinotus* exhibits a high degree of suitability (Figure 2).

Current habitats

The distribution of potential habitat in the current situation is shown in Figure 3. The total potential habitat area is 17.82×10^4 km^2, including 1.44×10^4 km^2 of highly suitable habitats, 3.91×10^4 km^2 of moderately suitable habitats, and 12.47×10^4 km^2 of lowly suitable habitats. The potential habitats are mainly distributed in the coastal areas of northern Vietnam, the northeastern Hainan Province, the coastal areas of Guangdong Province and Guangxi Zhuang Autonomous Region, and a small part of Taiwan Province in China. Highly suitable habitats are mainly distributed in Hai Phong, Nam Dinh and Thanh Hoa areas of Vietnam, the central area of Leizhou Peninsula and the west bank of the Pearl River Estuary of China. The moderately suitable habitat extends from the highly suitable habitat to Hanoi of Vietnam, the whole Leizhou Peninsula, the two sides of the Pearl River Delta, and the northeast coast of Hainan Island in China (Figure 3). On the basis of moderately suitable habitat, the lowly suitable habitat extended further to inland areas, especially the southern Guangxi Zhuang Autonomous region has a large area of low potential habitat.

Habitats in the LGM

Our simulations revealed that during the historical period (the LGM), *O. curvinotus* had a wide range of habitats, which were located in tropical and subtropical regions and were therefore less affected by glacial periods. The present study reveals that during the LGM, the habitat of *O. curvinotus* was mainly located in the northern margin of Sundaland, including Guangdong Province, Guangxi Zhuang Autonomous Region and Hainan Province in South China, as well as the northern part of the South China Sea and the Beibu Gulf (Figure 4). The total potential habitat area reached 126.85×10^4 km^2, of which 30.83×10^4 km^2 were highly suitable. In addition, during the LGM, there were three refuges (Refugium 1, Refugium 2 and Refugium 3). Refugium 1 was located in Beibu Gulf, Refugium 2 was located near Guanghai Town, Taishan County, Jiangmen City, Guangdong Province, and Refugium 3 was located in the east of Hong Kong (Figure 5).

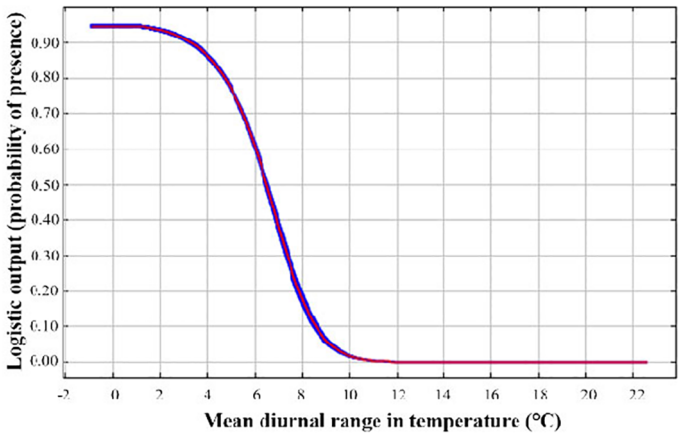

FIGURE 2
Response curves of climatic suitability of bio2 [Mean diurnal range (mean of monthly max temperature-min temperature)].

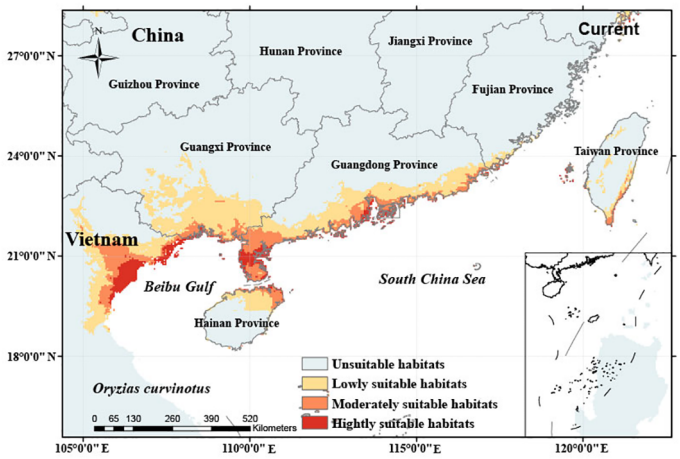

FIGURE 3
Simulation of potential distribution areas of *O. curvinotus* with varying suitability in the current climate based on occurrence records.

Time series analysis in the warming future

We simulated the potential habitat shift process of *O. curvinotus* under four climate warming scenarios with different carbon emission levels, as shown in Figures 6–9. Under the background of a low-end level carbon emission scenario (SSP1-2.6), the potential habitats will expand from the current to 2080 (for example, the lowly suitable habitats at the border of Guangdong Province and Guangxi Zhuang Autonomous Region in China are obviously expanding northward), but it will shrink by 2100. By 2100, the habitats in the border area between Guangdong Province and Guangxi Zhuang Autonomous Region, east Guangdong region and the coast of Fujian decreased significantly, but the highly suitable habitats in Leizhou Peninsula, northeast Hainan Island and southwest Taiwan Island increased slightly (Figures 6A–D). Under the scenario of low-moderate level carbon emission (SSP2-4.5), there is a trend of habitat expansion from the current to 2040, and then a trend of retreat until 2100 (Figures 7A–D). During this period, the highly suitable habitats in Leizhou Peninsula and northeast Hainan will increase (Figure 7D). Under the scenario of medium-high or high levels of carbon emissions, the potential habitats of *O. curvinotus* show oscillating changes, expanding from the present to 2040, then slightly shrinking in 2060, recovering in 2080, and shrinking again in 2100 (Figures 8A–D). As in the previous cases, highly suitable habitats in Leizhou Peninsula, northeastern Hainan, and southwestern Taiwan are expected to expand by 2100 (Figures 9A–D). In terms of area change, from the current to 2100, the four warming scenarios under carbon emission levels caused the potentially suitable habitat (including highly, moderately and lowly suitable habitats) of *O. curvinotus* to first expand, then stabilize, and finally retreat to a slightly higher area than the current area (Figures 10A–D).

Discussion

O. curvinotus is a typical small tropical fish mainly found in the northern coast of the South China Sea. Generally, species with

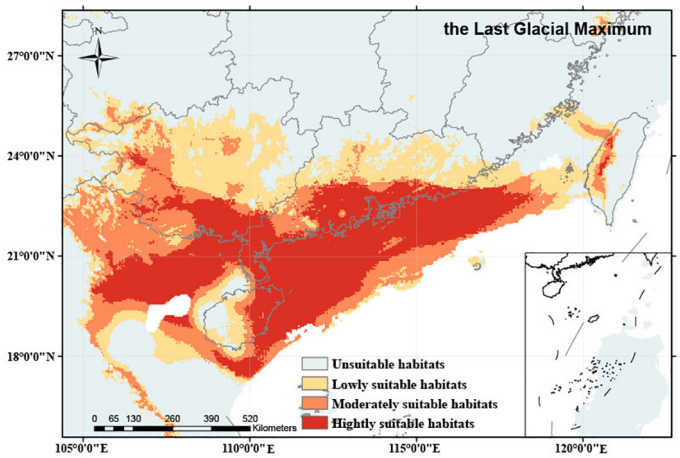

FIGURE 4
Potential distribution areas of *O. curvinotus* with different suitability under paleoclimate (the LGM).

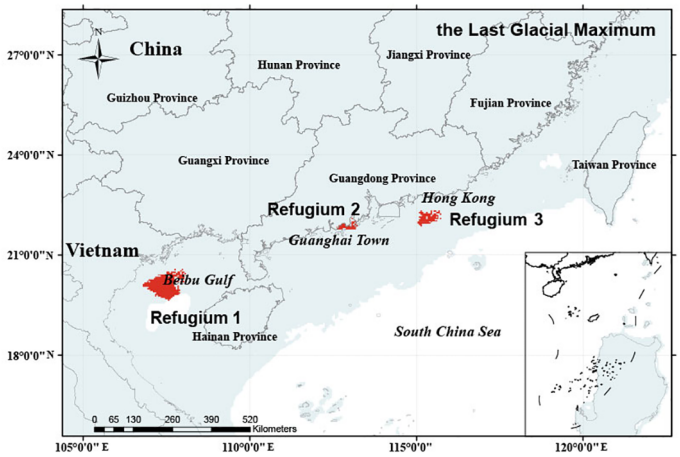

FIGURE 5
Location of *O. curvinotus* refuges during the LGM.

limited distributions tend to have narrower ecological niches, such as smaller temperature variations within their range, making them more susceptible to climate change (Liao et al., 2022). The habitats of species in tropical regions are typically characterized by high humidity and warmth (Skendžić et al., 2021). For instance, *Neurobasis chinensis* inhabits the hot and humid tropical regions of East Asia and is projected to expand its range northward under future warming climates (Skendžić et al., 2021; Liao et al., 2022). However, humidity is not a significant factor for underwater species throughout their lives. In this study, we determined that a mean diurnal temperature range of 8 °C is the critical point for the distribution range of *O. curvinotus*. In areas where the mean diurnal temperature exceeds 8 °C, *O. curvinotus* has virtually no suitable habitat. This is consistent with its status as a tropical species. Tropical species, especially tropical plants, are affected more by climate change than by topographic gradients (Toledo et al., 2012).

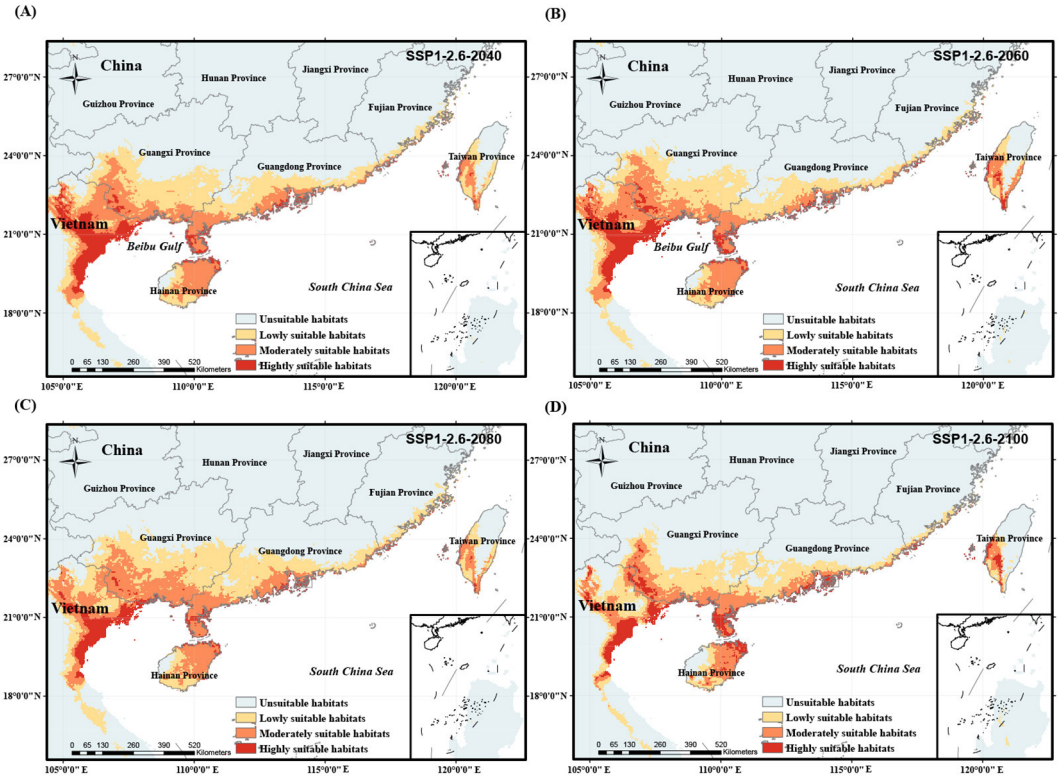

FIGURE 6
Potentially suitable habitat of *O. curvinotus* under future climate warming scenario with the low-end level carbon emission from 2040 to 2100. **(A)** SSP1-2.6-2040; **(B)** SSP1-2.6-2060; **(C)** SSP1-2.6-2080; **(D)** SSP1-2.6-2100.

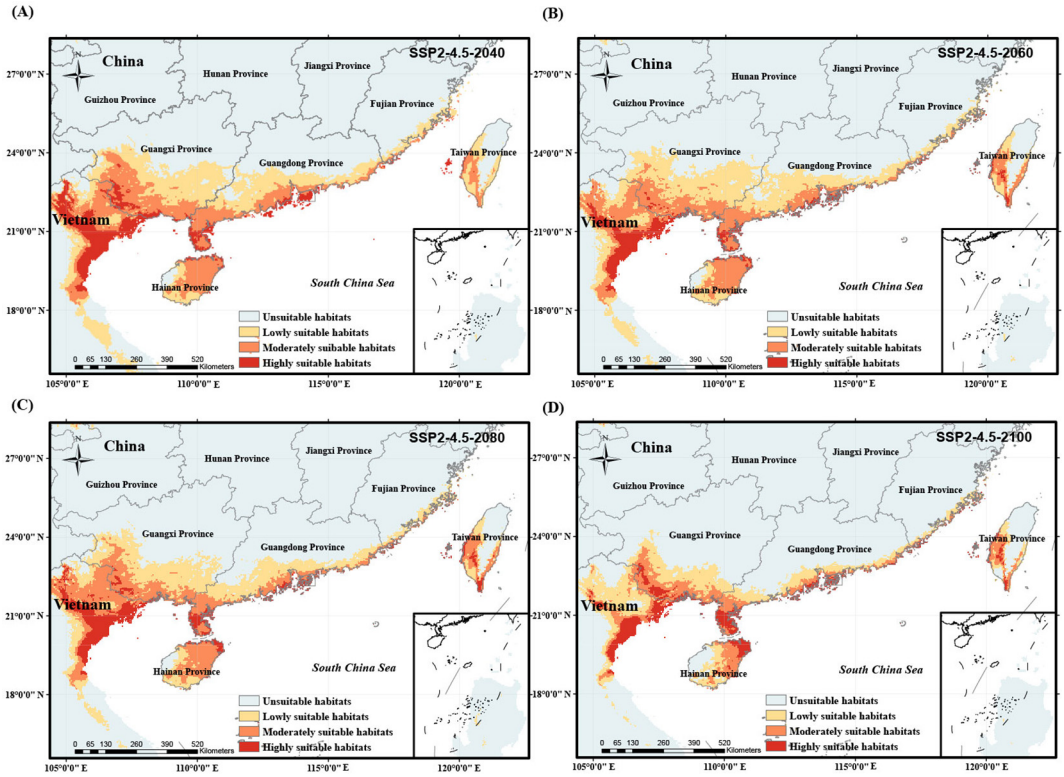

FIGURE 7
Potentially suitable habitat of *O. curvinotus* under future climate warming scenario with the low-moderate level carbon emission from 2040 to 2100. **(A)** SSP2-4.5-2040; **(B)** SSP2-4.5-2060; **(C)** SSP2-4.5-2080; **(D)** SSP2-4.5-2100.

Climate is a strong driver of species distribution, with 72% of tropical species affected by temperature (Toledo et al., 2012). In this study, the habitat of *O. curvinotus* has typical characteristics of tropical species, and only inhabits within the range of mean diurnal temperature of 8°C, especially within 6°C, which is a highly suitable habitat for it. This reveals that one of the habitat characteristics of *O. curvinotus* is a small range of the mean diurnal temperature. Another relatively important climatic factor shaping the distribution of *O. curvinotus* is the mean temperature of wettest quarter (bio8, contribution 11.62%, permutation importance 46.34%). The mean temperature of wettest quarter in the habitat area of *O. curvinotus* is more than 25 °C, with the highly suitable habitat exceeding 28 °C. These findings again confirm the habitat properties of *O. curvinotus* as a tropical species.

Our results revealed that the current distribution area is mainly concentrated in northern Vietnam, northeastern Hainan Province, the coast of Guangdong Province and Guangxi Zhuang Autonomous Region, and a small part of Taiwan Province, in total, covered ca. 17.82×10^4 km^2. Within these ranges, a small number of simulated habitats exist in Taiwan Province of China, which is unexpected and requires further field work to confirm. In addition, it is worth noting that our field work experience confirmed the existence of a large population of *O. curvinotus* in Sanya, Hainan, and we brought the population of *O. curvinotus* in this area back to the laboratory for morphological and DNA barcoding identification, confirming the identity of *O. curvinotus* (Yao et al., 2022). However, the simulation results of this study suggest that Sanya in Hainan Province is not a suitable habitat for *O. curvinotus*. We speculate that the Sanya population may have undergone adaptive evolution in order to meet the changing climate environment, but the evolution has not yet reached the species level. Our earlier study corroborated these results across various dimensions (Dong et al., 2021; Yao et al., 2022). In our previous research, we discovered that the Sanya population lacked the sex determination gene "*dmy*" when compared to other populations (Dong et al., 2021). Additionally, Yao et al. (2022) revealed a significant level of genetic differentiation between the Sanya population and others, without indicating species diversification. Currently, the Sanya population is experiencing a bottleneck phase (characterized by a small population size), confirming that it has undergone intense environmental selection (Yao et al., 2022). All of these evidences indicate that the Sanya population is a unique group, exhibiting genetic variations that have emerged as adaptations to the challenging environment of Sanya, located in the China's Hainan province. Regarding the relationship between the unique physiological response mechanism of *O. curvinotus* populations in Sanya and climate change, we have conducted a thorough analysis of the species' resilience or vulnerability in the face of climate change. Firstly, as a euryhaline fish, *O. curvinotus* possesses physiological characteristics that endow it with remarkable tolerance to salinity fluctuations. Against the backdrop of climate change, the rise in sea level and fluctuations

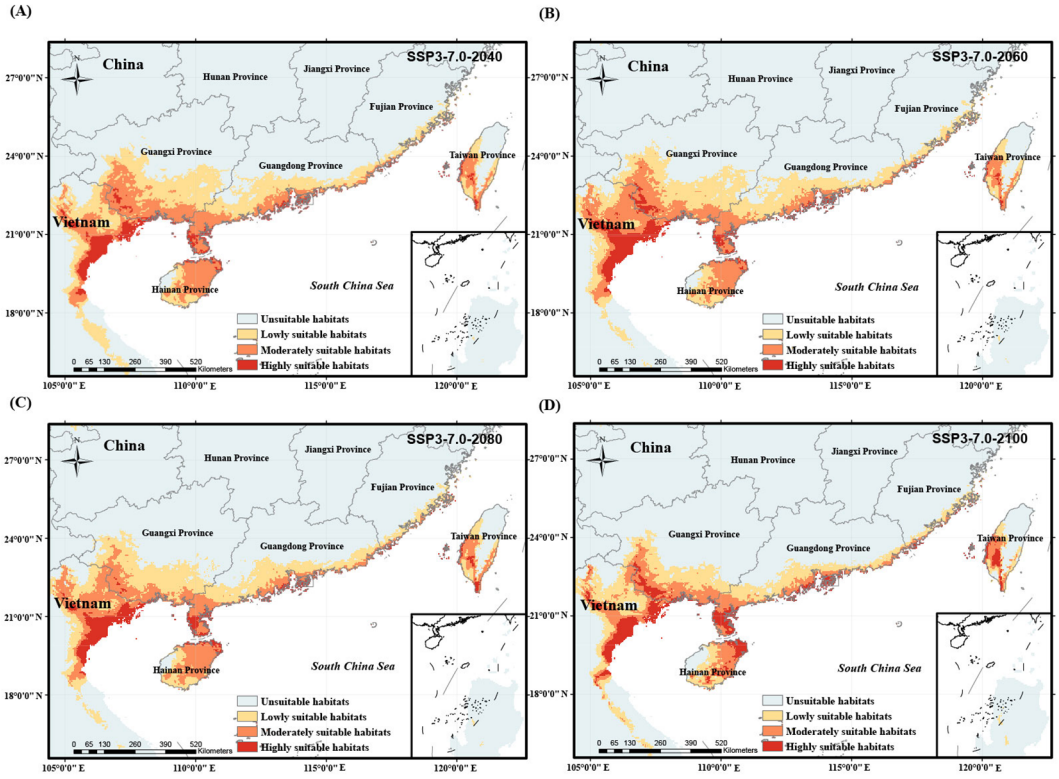

FIGURE 8
Potentially suitable habitat of *O. curvinotus* under future climate warming scenario with the medium-high level carbon emission from 2024 to 2100. **(A)** SSP3-7.0-2040; **(B)** SSP3-7.0-2060; **(C)** SSP3-7.0-2080; **(D)** SSP3-7.0-2100.

in freshwater input may lead to drastic changes in salinity levels in mangrove tidal creeks and streams. Nevertheless, through a series of unique physiological response mechanisms, such as the fine-tuned regulation of ion transport proteins, *O. curvinotus* effectively maintains the balance of salts within its body, ensuring the continuation of normal physiological functions even in varying salinity environments. This genetic adaptability provides significant resilience to *O. curvinotus* in the face of salinity fluctuations, facilitating its survival and reproduction in diverse environments.

However, the impact of climate change on *O. curvinotus* is not entirely positive. With the persistent increase in global temperatures and the frequent occurrence of extreme climate events, these environmental factors may exceed the adaptive range of *O. curvinotus*. For instance, high-temperature environments may significantly increase the metabolic rate of *O. curvinotus*, subsequently escalating its demand for food and oxygen. Under resource-limited conditions, such an elevation in metabolic rate could pose a threat to the survival of *O. curvinotus*. Furthermore, extreme climate events like heavy rainfall or drought can directly destroy the habitats of *O. curvinotus*, leading to severe degradation of its living environment. In such scenarios, the genetic adaptability of *O. curvinotus* may be insufficient to fully cope with these drastic changes, thus exhibiting a degree of vulnerability. However, the adaptation of *O. curvinotus* to this sudden climate change requires at least several generations of natural selection. Therefore, we believe that the genetic adaptability of *O. curvinotus* exhibits both resilience and vulnerability in response to climate change. To gain a more comprehensive understanding of this relationship, further research is needed to explore the interaction between genetic variations in *O. curvinotus* and climate change, as well as to delve deeper into its adaptive mechanisms. This will aid us in providing a more scientific basis for the conservation and utilization of *O. curvinotus*, while also serving as an important reference for addressing the biodiversity challenges posed by climate change.

The historical species distribution pattern in the Quaternary largely determines their current species range. The conservatism of climatic niches, combined with the cycles of glacial and interglacial periods, has forced many species to reduce their ranges in order to survive under the advance of Pleistocene ice sheets. Refugia provide geographical opportunities for species to retreat, survive, and later recolonize under favorable environmental conditions (Morales-Barbero et al., 2018). Our research has revealed three refugia, all located in the northern part of Sundaland (the northern edge of the South China Sea). Among them, the largest one, Refugium 1, is speculated to be the starting point of the dispersal of highly suitable habitats in the northern part of Vietnam and Leizhou Peninsula. While Refugium 2 and Refugium 3 are speculated to be the sources of species migration for the highly suitable habitats in the Pearl River Delta region. Typically,

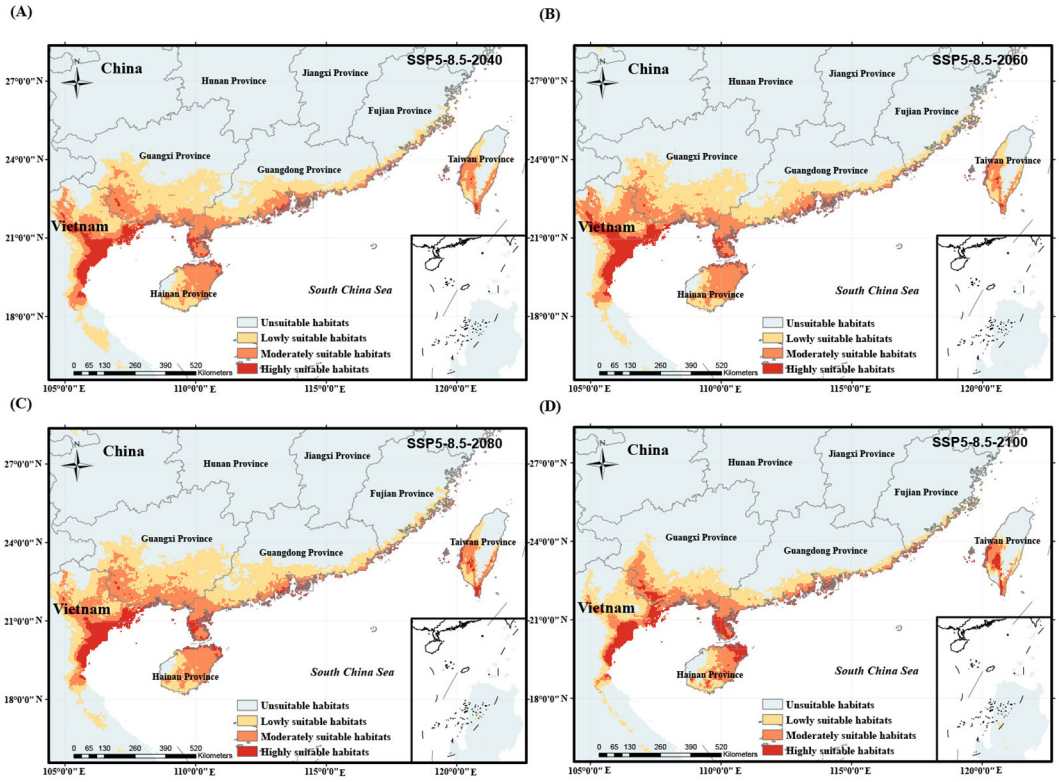

FIGURE 9
Potentially suitable habitat of *O. curvinotus* under future climate warming scenario with the high level carbon emission from 2040 to 2100. **(A)** SSP5-8.5-2040; **(B)** SSP5-8.5-2060; **(C)** SSP5-8.5-2080; **(D)** SSP5-8.5-2100.

species range may expand or contract based on the suitability of climate change for its ecological niche (Morales-Barbero et al., 2018). Migrant species may be geographically restricted to a particular location, or continue their colonization route through a habitat matrix, depending on the suitability of climatic conditions (Hewitt, 2000; Petit et al., 2003; Barnosky, 2005). Due to the disappearance of Sundaland after the glacial period, many habitats of *O. curvinotus* sank into the sea, and highly suitable habitats migrated to neighboring northern Vietnam, Leizhou Peninsula, and a small part of the Pearl River Delta region. Overall, the habitats of *O. curvinotus* have been in a stage of retraction from the Quaternary to the present day.

Future warming is an undeniable reality. Over the past century, the global temperature has risen by 0.6°C and is continuing to change at an accelerated pace. Projections indicate that by the end of the 21st century, the minimum temperature increase is expected to be between 0.3°C and 1.7°C, with a maximum increase of 2.6°C to 4.8°C (Root et al., 2003; Kumar and Rawat, 2022; Liao et al., 2022, 2023). Climate warming is inevitable, and it will undoubtedly alter the current distribution patterns of various species. The impacts of warming have already been observed in numerous organisms, including plants, dragonflies, butterflies, grasshoppers, lacewings, spiders, reptiles, woodlice, ground beetles, longhorn beetles, soldier beetles, harvestmen, millipedes, aquatic bugs, freshwater fish, birds, and mammals (Parmesan and Yohe, 2003; Root et al., 2003; Hickling et al., 2005, 2006; Lenoir and Svenning, 2015). Tropical species with narrow ecological niche are theoretically vulnerable to the stress of climate warming and migrate northward like most species. However, the subjects studied in this research did not follow this typical pattern. In our study, climate warming under four different carbon emission levels caused the current habitat of *O. curvinotus* to expand within a short timeframe (by 2040). After a period of adaptation (by 2100), the expansion trend was mitigated, and the expansion area retreated to slightly larger than the current climate scenario. The increase of habitats primarily occurred in northern Vietnam, southern Guangxi, Hainan Island and Taiwan Island, with a notable increase in highly suitable habitats, such as the Red River Delta in Vietnam and the central part of Leizhou Peninsula. Contrary to the typical northward migration pattern observed in other species under the influence of warming (Hickling et al., 2006), the highly suitable habitats for *O. curvinotus* did not shift latitudinally but instead increased their area around 21°N. East Asia, at 21 degrees north latitude, is a global biodiversity hotspot, and the region's geological history has shaped a complex climate and geological environment in this area (Hekinian and Walker, 1987; Marchese, 2015), resulting in a complex network of biological and abiotic factors. Numerous species have come to rely on this hotspot habitat, making it a crucial ecosystem for various organisms (Gathorne-Hardy et al., 2002; Gorog et al., 2004). Our subject, *O. curvinotus*, despite its adaptability, is currently found only in a small area along the northern coast of the South China Sea, including coastal freshwater extending inland. Hayakawa et al. (2015) discovered this species in mangrove plantations and inland paddy fields in Bang La, Do

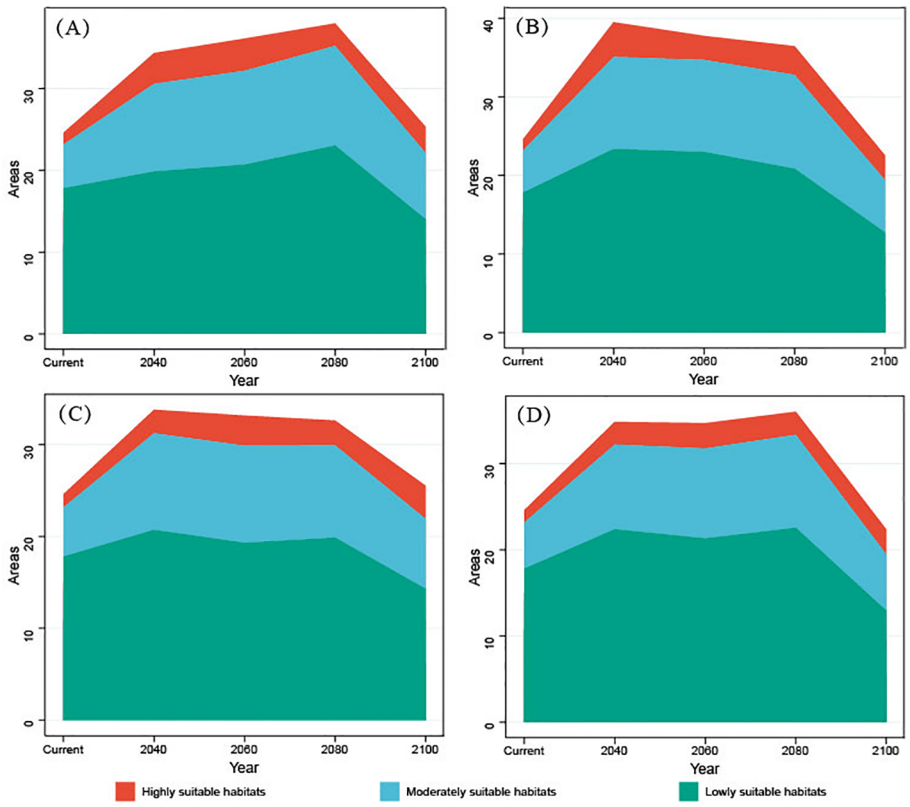

FIGURE 10
Time series analysis of potential habitat areas (x10^4 km^2) of *O. curvinotus* from current to future 2100. **(A)** SSP5-8.5-2040; **(B)** SSP5-8.5-2060; **(C)** SSP5-8.5-2080; **(D)** SSP5-8.5-2100.

Son, Vietnam, and conducted population genetics studies, recognizing it as a promising experimental model species in tropical Asia (Hayakawa et al., 2015). These provide valuable insight into the dispersal of *O. curvinotus* into inland freshwater habitats at the same latitude. Indeed, our simulations of *O. curvinotus* habitats in the context of future climate warming support this notion and underscore the need for further investigation into the species' ecological niche and potential adaptability to changing environmental conditions.

Despite our optimistic findings regarding the recent survival status of this species, proactive conservation measures must still be implemented to secure its long-term survival. To this end, we propose the following conservation strategies: Firstly, monitoring and surveillance: We plan to establish a regular monitoring program to closely track the species' population dynamics, habitat utilization, and any emerging threats. This will involve conducting surveys, monitoring breeding habitats, and collecting crucial data using remote sensing techniques. These data will not only aid in evaluating the effectiveness of our conservation efforts but also guide future actions. Secondly, habitat restoration and enhancement: We prioritize the restoration and enhancement of the species' existing habitats, including contaminant removal, controlling invasive species, and promoting native vegetation growth. Additionally, we aim to establish new habitats in suitable areas to mitigate the potential negative impacts of predicted habitat shifts.

Conclusions

This study summarizes the habitat attributes, potential distribution areas and its long-term temporal changes of a small euryhaline fish species. Results show that *O. curvinotus* is currently mainly distributed along the coastal areas of northern Vietnam, northeastern Hainan, Guangdong and Guangxi Zhuang Autonomous Region, as well as in a few areas of Taiwan Province, China, covering a total area of 17.82 ×10^4 km^2. Highly suitable habitats are mainly found in northern Vietnam, central Leizhou Peninsula, and the western coast of the Pearl River Delta. Three refugia existed in historical times, with the largest one, Refugium 1, speculated to be responsible for the dispersal and establishment of highly suitable habitats in northern Vietnam and central Leizhou Peninsula. Refugium 2 and Refugium 3 are hypothesized to be the sources of immigrant individuals with highly suitable habitats in the Pearl River Delta, with only Refugium 2 remaining to current. Climate warming in the future is not expected to pose a threat to the species' distribution. Instead, it may lead to a rapid expansion of its habitat in a short period of time, followed by a stabilization and gradual decrease to slightly above the current habitat area. The expansion of its habitat will not shift northward as most species do, but will expand around the 21°N latitude. This study provides valuable insights for the conservation of such small euryhaline fish species and the development of model species suitable for ecological environmental research in the region.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

JL: Data curation, Investigation, Formal analysis, Conceptualization, Methodology, Software, Writing – original draft. HC: Data curation, Investigation, Writing – review & editing. J-YL: Writing – review & editing. G-CL: Writing – review & editing. XG: Writing – review & editing. C-FL: Data curation, Writing – review & editing. Y-SG: Investigation, Methodology, Writing – review & editing. Z-DD: Writing – review & editing. Z-DW: Conceptualization, Investigation, Data curation, Supervision, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1391800/full#supplementary-material

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Spatio-temporal analysis of potential factors explaining fluctuations in population size of *Spisula subtruncata* in the Dutch North Sea

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Bivalves play a key role in coastal ecosystems by supporting food web, modifying habitats, and their economic value for fisheries. Many bivalve species are under pressure, showing large variations in population sizes and distributions, with climate change and human activities considered as important drivers. The Dutch North Sea hosts high densities of bivalve species, dominated by the cut trough shell *Spisula subtruncata*, with strong interannual variations and a patchy distribution. To explore the causes of this variation, data of an extensive long-term spatial benthic monitoring program (1995-2021) was analysed using a Bayesian spatio-temporal hurdle model. We considered indicators related to human activities, biological processes, climate change and habitat preference as explanatory variables for the observed long-term temporal and spatial variations. Results revealed that medium sediment grain size was key determinant of *S. subtruncata* occurrence and density. Increasing sea water temperatures during winter and the post-settlement phase positively affected annual population densities, while strong north-westerly winds led to lower densities. These climate change related factors had an overall positive effect on this species in the region. Human activities like shellfish dredging and sand nourishment had no measurable impact. However, shrimp and flatfish beam trawling overlapped with *S. subtruncata* occurrence and were negatively related to densities, suggesting higher beam trawling intensity in these areas may negatively impacts densities. Overall, the effects were stronger at medium to finer sediments where the highest densities occurred, indicating a strong habitat-dependent effect. Despite identifying multiple drivers, unexplained annual variation suggests other not included factors like predation pressure, also play a role. More

detailed studies on the combined effects of climate change-driven environmental stressors and human activities are needed to fully understand the population dynamics. This knowledge is essential for developing more adequate fisheries and coastal management strategies to sustain biodiversity.

KEYWORDS

anthropogenic impacts, bayesian statistics, climate change, Dutch North Sea, population dynamics, *Spisula subtruncata*

Introduction

Many marine species exhibit large spatiotemporal variations in population sizes, distributions or other traits, driven by biological processes (e.g., predation, competition), local human activities (e.g., fisheries and coastal developments) and global climate change (oceanic warming and acidification, sea level rise and intensification of extreme weather events). Human-induced changes, including the global process of climate change and local activities, increasingly negatively affect marine ecosystems (Halpern et al., 2008; Waycott et al., 2009; Trégarot et al., 2024). Climate change effects often interact with local human related stressors that can be managed locally (Scheffer et al., 2015; Gissi et al., 2021). For example, reducing local fishing pressure can ensure that populations remain resilient to critical levels of climate change (e.g. Carpenter et al., 2017; Ramírez et al., 2021). The determination of boundaries, at which populations can withstand pressures due to climate change and ongoing intensification of local human activities, requires insights in which main factors are driving populations.

Bivalves, key benthic species in coastal ecosystems, are susceptible to effects of climate change and local human activities (Kroeker et al., 2010; Philippart et al., 2011; Gobler et al., 2014). They play important roles in ecosystems as food source and altering their physical environment (Norkko and Shumway, 2011; Sospedra et al., 2017; Ysebaert et al., 2019), facilitating themselves and many associated species (i.e. ecosystem engineers) (Bruno and Bertness, 2001; Rullens et al., 2019). Many bivalves are economically valuable for fisheries and often harvested in large amounts (Smaal et al., 2019). Without adequate local management measures, stocks are often at risk of overexploitation (Smaal et al., 2019; Huang et al., 2023). In addition, coastal development and pollution have resulted in decline of bivalve populations in the past (Lotze et al., 2006; Mackenzie, 2007). Besides local human activities, rising seawater temperature, linked to climate change, negatively affect recruitment and survival in many bivalve species (Sampaio et al., 2021; Kruft Welton et al., 2024). Despite considerable research, drivers of population dynamics particularly for sublittoral bivalve, remain unclear (but see: Weinberg, 2005; Narváez et al., 2015; Hofmann et al., 2018).

The cut trough shell *Spisula subtruncata* is a common bivalve in European sublittoral waters, from Norway, British Isles to northern Mediterranean (Hayward and Ryland, 2017). The species has an important role in the food web and is of economic value for fisheries, especially along the Dutch coast (Smaal and Lucas, 2000; Baptist and Leopold, 2009). Once dominant in Dutch coastal waters, its population collapsed after 2000, with a strong recovery in 2017 (Troost et al., 2023). Similar strong interannual variation has been observed for *Spisula* spp. in other regions (Fraschetti et al., 1997; Weissberger and Grassle, 2003; Degraer et al., 2007), likely driven by varying recruitment and mortality rates. The highest mortality occurs shortly after settlement, as in many bivalves (Gosselin and Qian, 1997), which is also the case for *S. subtruncata* (Ambrogi and Occhipinti Ambrogi, 1987; Degraer et al., 2007; Deval and Gokturk, 2008). In the Dutch North Sea, intensified human activities (such as coastal protection, harbour development, and shrimp fisheries) and climate change (Weijerman et al., 2005; Capuzzo et al., 2018; Herman et al., 2021; Wijsman et al., 2023) may drive the species' dynamics, but their precise role remains uncertain.

Seawater temperature increases in the North Sea, a well-documented effect of climate change (Dulvy et al., 2008; Høyer and Karagali, 2016), plays a key role in bivalve recruitment success in temperate waters (e.g. Dekker and Beukema, 1993; Philippart et al., 2003; Beukema et al., 2009). Spawning is triggered by a water temperature threshold in spring (Cardoso et al., 2007; Nicolle et al., 2013). Variations in seawater temperature may then cause temporal shifts with regard to optimal conditions for the larvae and juvenile bivalves, such as food availability and/or predation pressure (Beukema et al., 2002; Philippart et al., 2010; Poloczanska et al., 2016). While wind conditions can affect the dispersal off pelagic eggs and larvae (Thiébaut, 1996; Ellien et al., 2004), increase mortality due to displacement during storms and reduce food uptake and subsequently growth (Witbaard et al., 2005; Raven, 2022).

With respect to biotic factors, juvenile and adult *S. subtruncata* are food sources for shrimp, starfish, demersal fish and diving sea ducks, potentially affecting the local population size (Braber and de Groot, 1973; Pihl and Rosenberg, 1984; Camphuysen et al., 2002; Fox, 2003). Interspecific competition for space and food with other

bivalves may also influence the population dynamics of *S. subtruncata*. In the late 1970s, for example, the invasive razor clam *Ensis leei* established itself to become dominant across the northwest European coastline, after being presumably introduced as larvae from ballast water (Tulp et al., 2010). *S. subtruncata* may be affected locally by interspecific competition with *E. leei* and other co-occurring burrowing bivalve species with similar filter-feeding behaviour. Currently it is unclear whether these species interact by competing for space and food.

Shellfish dredge fisheries on *S. subtruncata* began in 1985 but were halted in 1999 after a strong decline in the local stocks (Craeymeersch et al., 2001). While shellfish dredging has been speculated to locally deplete *S. subtruncata* banks (Leopold, 1999; Camphuysen et al., 2002), its influence on the total Dutch population remains unclear. Beam trawl fisheries for shrimp and flatfish also physically impact the seabed (e.g. Eigaard et al., 2016; Hiddink et al., 2017; Tulp et al., 2020), affecting *S. subtruncata* densities (Bergman and van Santbrink, 2000).

Sand extraction and coastal nourishment, which increased in the past decade (Baptist and Leopold, 2009; van der Veer et al., 2015), can negatively affect the benthic biodiversity (Herman et al., 2021; Dauvin et al., 2022; Saengsupavanich et al., 2023). Some studies suggest benthic communities may take years to recover after nourishment (Wijsman et al., 2023), though others indicate a faster recovery (van Dalfsen and Essink, 1999). A large spatial link between sand nourishments and *S. subtruncata* could not be demonstrated (Baptist and Leopold, 2009).

To gain insight into the factors driving the dynamics of the *S. subtruncata* population in Dutch coastal waters we investigated i) the spatial patterns and temporal trends of *S. subtruncata* densities, and ii) the potential contributions of biotic-, anthropogenic- and climate-related factors. Using data from an annual benthic survey along the entire Dutch North Sea coast, we present two analyses covering different periods: one excluding fisheries effort (1995-2021) and one including fisheries effort (2009-2020). We gathered all relevant available data on a high spatiotemporal resolution and a statistical model was used to assess the effects of climate conditions (temperature, wind), habitat (sediment and tidal current), and human disturbance (fishing intensities and sand nourishments). Additionally, we explored the relationship between predation (e.g., shrimp, fish and birds) and *S. subtruncata* densities in a descriptive manner, as information on these parameters was not available at the same spatial resolution. We discuss how our findings offer insights for improving adequate fisheries and coastal management strategies to sustain biodiversity.

Methods

Benthic survey

Since 1995, an annual survey of shellfish stocks is carried out by Wageningen Marine Research, covering all Dutch North Sea coastal waters. The main aim of the survey is to monitor densities and biomass of exploited shellfish species for stock assessments. The number of benthic sampling stations differs between years due to logistic circumstances (756-1405 stations; min - max), spread out along transect perpendicular to the coast (Figure 1). Samples were taken either with a towed bottom cutting dredge or with a modified hydraulic dredge (see for details: Troost et al., 2023). Mesh size was

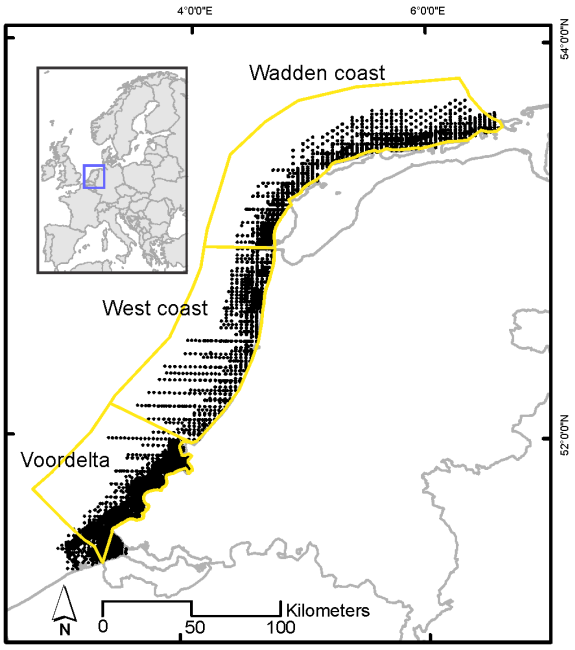

FIGURE 1
Study area with sampling grid with total sample stations (1995-2021) and coastal areas: Voordelta, West coast and Wadden coast.

5 millimetres and sampling depth 10 centimetres. Sampling distance was at most locations about 150 meters, width either 10 cm (towed dredge) or 20 cm (hydraulic dredge), covering 15 to 30m^2 respectively. Surveys were carried out from April to June except in 2020 when the sampling was delayed due to the COVID restrictions and was conducted between 25 May and 9 June (Troost et al., 2023). For our analyses, sampling stations were linked to a 5km hexagonal grid resolution (Supplementary Figure A1) which enables us to spatially link all explanatory variables, available on different scales, to the survey data.

Living bivalves were identified to species and representative subsamples were taken when the sample size was too large to process as a whole (see Troost et al., 2019). Species were grouped into length classes and weighted (fresh shell and flesh wet-weight to the nearest 0.1 gram). Broken shells were included when flesh and both sides of the hinge ligament was present, enabling species and length class determination. To test the potential effect of interspecific competition between *S. subtruncata* and other filter-feeding bivalve species, we included densities of *Ensis* spp., *Lutraria lutraria, Donax vitattus* and *Chamelea striatula* into the statistical analyses. Numbers of *Ensis* spp. and *L. lutraria* are underestimated in the survey as these species often burrow deeper than the sampling depth of 10 centimetres but relative comparison between years is possible as same methodology was used during the entire survey period (Troost et al., 2023).

Spatiotemporal covariates

Tidal current velocity and sediment median grain size

Tidal current velocity data were obtained from a hydrodynamical model with a resolution of 0.02° longitude and 0.05° latitude (~2.3×3.5 km) (van der Molen et al., 2016) (Supplementary Figure A2). For our analyses we used the annual total mean current velocity m s^{-1} for each sampling point. Sediment median grain size (D50) was obtained from TNO Geological Survey of the Netherlands from Deltares OPeNDAP (https://opendap.deltares.nl/thredds/catalog/opendap/tno/ncp/catalog.html) (Supplementary Figure A2).

Sea surface temperature and wind conditions

Sea surface temperature (SST) was used in our analyses, assuming that the coastal waters in our study area are permanently mixed and so that there are no differences in temperatures throughout the water column (van Leeuwen et al., 2015). Data on sea surface temperature (°C) was derived from daily values from 1995-2021 on a 0.05°× 0.05° spatial resolution (~5.5×3.5 km) from European Space Agency (ESA) SST Climate Change Initiative (CCI) project downloaded from the Copernicus Climate Change Service (Merchant et al., 2019) and linked to the hexagon grid. Following Cardoso (2007), we assume that *S. subtruncata* started to spawn at the day of the year (*DY*) when water temperature reached 16°C. At this temperature, egg development time takes about 3 days from fertilization until hatching, and the subsequent pelagic larval stage takes approximately 24 days, until settlement (Cardoso et al., 2007). Thus, we assume that the pelagic phase (from spawning to settlement) lasts 27 days. At *ad libitum* food availability, larval growth and survival correlates positively with seawater temperature (Verween et al., 2007; Enricuso et al., 2018). Therefore, we used the mean water temperature (daily values) between spawning and settlement as a proxy for the growth conditions during the pelagic phase (*SSTp*, subscript refers to larval pelagic stage).

Brown shrimp *Crangon crangon* is a dominant benthic predator on bivalve recruits in marine systems (Hamerlynck et al., 1993; van der Veer et al., 1998) affecting post-settlement survival rates (Hiddink et al., 2002; Andresen and van der Meer, 2010). For *S. subtruncata*, it has been estimated that once settled, it takes 77 days to reach a length of 4 mm, the size at which *S. subtruncata* has outgrown shrimp predation (Cardoso et al., 2007; Campos and van der Veer, 2008) (see Supplementary Figure A3). Therefore, we used the mean water temperature of 77 days after the settlement as a proxy for post-settlement growth conditions (SST_S, subscript refers to post-settlement).

We used mean sea surface temperature from November to February (*SSTw*) as a proxy for winter temperatures as a factor potentially impacting adult mortality by low temperatures or starvation at high temperatures when metabolic rates increase but phytoplankton densities are low (Compton et al., 2007).

The index for local wind-driven wave stress was calculated as the total number of days with strong winds (> 10 m s^{-1}) per year from the northwest (direction between 280° and 10°). In our study area, north-western winds have the longest fetch for waves to build up, creating the most turbulence in coastal waters (Witbaard et al., 2005). Wind data was derived from The Copernicus European Regional ReAnalysis (CERRA) datasets (Schimanke et al., 2021).

Bathymetry was downloaded from EMODnet bathymetry portal at a resolution of 0.05°× 0.05° (https://emodnet.ec.europa.eu/en/bathymetry) and linked to the hexagon grid.

Fishing intensity

Fishing intensity was based on Vessel Monitoring system (VMS) and fishery logbook data to produce spatial data layers on fishing intensity of different categories expressed in Swept Area Ratio (SAR) (see for methods: Eigaard et al., 2016; ICES, 2021). Data was available from 2009 until 2020 at a spatial resolution of 0.05°×0.05° and converted to hexagon resolution. For the intensity of fisheries on molluscs, fisheries data for *Ensis* spp. and *S. subtruncata* are combined, as there is no species-specific fishing effort data available. Beam trawling on shrimp and flatfish (mainly sole and plaice) and demersal otter trawl differ in sea bottom surface impact, varying from sliding over the bottom surface (shrimp trawl) to completely overturning the upper layer of the sediment (flatfish beam trawl) (Eigaard et al., 2016). Because we assume that different fishing gears have different impacts on the benthos including *S. subtruncata*, we differentiate between four gear groups, being mollusc dredge (SARdredge), shrimp beam trawl (SARshrimp), flatfish beam trawl (SARdmf) and otter trawl (SARotter).

Sand nourishments

Data on coastal sand nourishments was supplied by ministerial institute Rijkswaterstaat (Supplementary Figure A4). Sand nourishment activities were conducted at the coastline and did not overlap with sampling points, however, sand from coastal nourishment is known to be redistributed along the coast and to deeper waters due to tidal currents and waves. Therefore, we calculated the distance from each benthos sampling point to the nearest active nourishment site (spatial polygon) on a yearly basis, and used this minimal distance as a covariate in the analyses to detect a possible effect. Sand extraction may also affect the benthos community, however, available data were insufficient to include in our statistical analyses.

Temporal descriptive data

Common scoter

Common scoter *Melanitta nigra* numbers were estimated from aerial midwinter surveys (since 1993) combined with ship based surveys and counts from the coast (Sluijter et al., 2022). Densities could not be converted to the hexagon grid spatial resolution due to the lack of resolution of the data at that scale. As there are large differences on larger spatial scale, we aggregated the data per coastal area (Figure 1).

Demersal shrimp and flatfish

Indices for predation pressure by shrimp and flatfish was derived from the demersal fish survey (DFS). The DFS has been conducted annually since 1970 in September-October and covers the entire Dutch coastal waters, down to 25 meters depth (Beek, 1997). A 6m-wide beam bottom trawl was used at low speed (2-3 knots) with a fine mesh of 20 mm which selects brown shrimp > 20 mm. Species densities were calculated from total shrimp *C. crangon* and flatfish (*Pleuronectes platessa*, *Limanda limanda*, *Platichtys flesus* and *Solea solea*) per haul (see for details: Tulp et al., 2012; Aarts et al., 2019). No correction for net selectivity was applied. Data on shrimp and flatfish densities were aggregated per coastal area and could not be converted to the hexagon grid spatial resolution due to the lack of small-scale resolution of the data.

Spatiotemporal modelling

Data exploration showed that the abundance data of *S. subtruncata* was spatially clustered and contained a high proportion of zero observations, on average per year 35.4% (sd=10.7%). We assume all zeros are from structural source (true zeros). To analyse these zeros and accommodate for zero inflation within the data, we used a two-step modelling approach (hurdle model) (Feng, 2021). The hurdle model fits two distributions; a probability of occurrence assuming a binomial distribution or Bernouilli (presence and absence) and a Gamma distribution (because the values were on a continuous scale in numbers m^{-2}) at locations where *S. subtruncata* was present. This approach allows to separate effects on the occurrence (presence/absence, binomial part) and on the actual densities once *S. subtruncata* is present (gamma part). The combined distribution model is called a zero-altered Gamma (ZAG):

$$Spisula_{is} \sim ZAG\,(\mu_{is}, \pi_{is}, r)$$

$$E(Y_{is}) = \mu_{is} \text{ and } var(Y_{is}) = \mu^2_{is}/r$$

$$Logit(\pi_{is}) = intercept + covariates_{is} + f(year_i)_{AR1} + u_i$$

$$Log(\mu_{is}) = intercept + covariates_{is} + f(year_i)_{AR1} + u_i$$

$$u_i \sim N(O, \Omega)$$

where $Spisula_{is}$ (Y_{is}) is the density of *S. subtruncata* (m^{-2}) at location *i* in year *s*. Covariates described in the previous section are used in the model are either used in the year *i* or the year before *i-1* as some covariates have an effect on *S. subtruncata* during pre- and post-settlement phase the year before (Table 1). The ZAG distribution has three parameters: π is the Bernouilli part which denotes the probability of presence, μ and r are parameters of the Gamma part resembling the mean and the shape of the distribution respectively. The estimated value is linked with a logit link for the binomial part and a log-link for the Gamma part. Both sides of the hurdle model use the same fixed and random effects. For the analysis prior information is incorporated in the model. For the intercept and fixed effect these are the default priors (N(0,1000)). All covariates are modelled linearly, but year trend with non-linear smoother to describe the temporal dependence. To account for temporal correlation between samples, the non-linear year smoother is modelled with an autoregressive process AR1 and incorporated a Penalized Complexity Prior scaled on the mean and SD×3 of the *S. subtruncata* density (Wang et al., 2018). To account for residual spatial correlation a first order intrinsic conditional autoregressive random effect (iCAR) is used to model the data (Blangiardo and Cameletti, 2015; Zuur et al., 2017). On the spatial resolution of the hexagonal grid a spatial structured term u_i is added where (first order) spatial adjacency defines the variance-covariance structure. In this hierarchical structure, information from neighbouring areas is utilized, leading to a smoothing effect that reduces extreme values and produces more balanced predictions.

Models were compared according to the Watanabe-Akaike's Information Criterion (Watanabe, 2010), where the model with the lowest WAIC was considered as having the best support. Models of which WAIC differed less than 2 ΔWAIC from the best model are considered to be equally good (Zuur et al., 2017). Confidence intervals are reported as Bayesian Credibility Intervals (BCI) between 2.5–97.5%. When the BCI of an estimated coefficient does not contain zero we consider that an covariate has an effect on density or occurrence of *S. subtruncata*, and to be relevant of 'significance' in a Bayesian context (McElreath, 2020). Statistical modelling was performed in a Bayesian framework with INLA (Rue et al., 2009; Lindgren and Rue, 2015) in R (R Core Team version 4.1.1, 2021).

Our sea surface temperature covariates exhibited interdependence and showed correlation. Therefore, to investigate the potential effect of

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TABLE 1 Overview of the exploratory variables used in this study.

Covariable	Description (unit)	Spatial scale/resolution	Temporal resolution	Period in analyses (t=sampling year)
D50	Sediment median grain size (μm)	grid/0.05°	static	–
Tidalcur	Tidal current velocity (m s^{-1})	grid/0.02°x0.05°	static	–
DY	Day of the year of onset of spawning SST > 16°C	grid/0.05°	annual/daily	t-1
SSTp	SST during pelagic phase (°C)	grid/0.05°	annual/daily	t-1
SSTs	SST during post-settlement (°C)	grid/0.05°	annual/daily	t-1
SSTw	SST during previous winter (°C)	grid/0.05°	annual/daily	Winter prior to t
DensC	Summed density of intraspecific competitive bivalves (ind. m^2)	sample grid	annual	t-1
Winddays	North-West wind days > 10 m s^{-1} (# days)	grid/0.05°	annual/daily	April-March in t-1
distNour	Minimum distance shoreface sand nourishment activity (meters)	Polygons	annual	t-1
SAR	Fishery intensity, swept area ratio (SAR: shrimp, dmf, otter and dredge)	grid/0.05°	annual	t-1

Median grain size and tidal current velocities were collinear, and therefore not used together in the same model (see text). Most time series span the period from 1995 to 2021, except for the time series on SAR (2009-2020).

sea surface temperature related to timing of spawning (*DY*), the pelagic phase (*SSTp*) and the post-settlement phase (*SSTs*) in relation to all other covariates, three models with other independent covariates were considered. VMS fishery intensity was only available for the period 2009-2020. To make optimal use of the available data, we analysed two different sets of the temperature-related models: one covering the entire data period excluding fisheries effort (1995-2021) and one shorter series including fisheries effort (2009-2020).

Tidal current velocity and median grain size showed high correlation, as they are both related to hydrodynamic processes (Supplementary Figure A5). Due to the collinearity and interdependence, it was not possible to include both covariates in the analyses. Median grain size is known to be an important variable for *S. subtruncata* occurrence and was therefore included in the analyses (Table 1). To show predicted relative effects of a covariate, we used the lower and the upper values for median grain size (150-250 μm) where the highest densities of *S. subtruncata* occur and all other covariates were standardized with a mean of zero in each covariate plot.

Temporal trends of all covariates were analysed with a linear regression in R (R Core Team version 4.1.1, 2021).

Results

S. subtruncata dynamics

The *S. subtruncata* population in the Dutch North Sea coastal zone showed strong interannual fluctuations, with different average densities but similar trends in the three coastal areas (Figure 2). High densities were observed from 1995 to 2000 in the West and Wadden coast, and between 1995 to 1997 in the Voordelta, with a strong decrease to lower densities thereafter. In all coastal areas, densities remained low until 2015 and increased again from 2016. Densities stayed rather high in subsequent years, but showed a general decrease in the Wadden coast (Figure 2) after 2018. During the entire period, persistently high-density clusters of *S. subtruncata* occurred in the northern part of the Voordelta, the northern part of the West coast area and north of the Wadden islands Terschelling and Ameland (Figure 3).

Spatial-temporal covariates

Climate factors

The spawning threshold temperature of 16°C showed temporal and spatial variation, and was reached on average between 10 June (in 2017) and 22 July (in 1996) during the study period. The day at which the threshold was reached declined between 1995 and 2020 with 0.57-day $year^{-1}$ ($F_{1,25}$ = *8.97, P<0.01;* Figure 4A) and tended to be later in deeper- and more northern waters (Supplementary Figure A6). For the pelagic larvae phase (defined as 27 days after the spawning date) no clear significant trend in average sea surface temperature was detected ($F_{1,25}$ = *0.38, P=0.54;* Figure 4B), but sea surface temperature during post-settlement phase (defined as 77 days after settlement, that starts 27 days after spawning) increased significantly, with 0.05°C $year^{-1}$ ($F_{1,25}$ = *6.21, P<0.05*; Figure 4C). Winter sea surface temperature also showed an increasing trend, with 0.04°C $year^{-1}$ ($F_{1,25}$ = *5.68, P<0.05*; Figure 4D). The annual number of days with strong (> 10 m s^{-1}) north-western winds increased over time, but this increase was just not significant ($F_{1,25}$ = *3.42, P=0.08;* Figure 4E).

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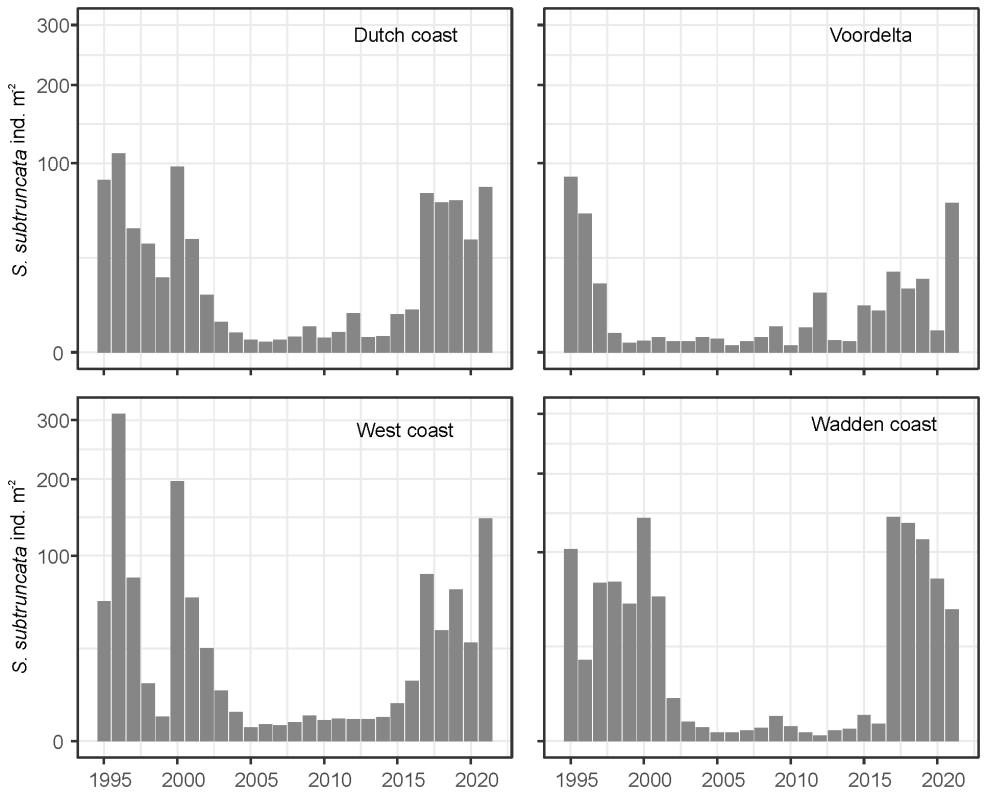

FIGURE 2
Total annual average *S. subtruncata* densities for the entire shallow Dutch North Sea coast (above left) and sub areas: Wadden coast, West coast and Voordelta.

Trend in other filter feeding bivalves

The total density of suspension-feeding bivalve species increased during the study period with a yearly increase of 0.85 ind. m^{-2} to on average of 22.2 ind. m^{-2} ($F_{1,25}$ = *21.22, P<0.001*, Figure 5A). This trend was mainly due to the exponential increase of the invasive *E. leei* since 2000, with average densities reaching up to 100 m^{-2} in the Wadden coast area. Densities of *E. leei* fluctuated strongly between years for all coastal areas, but in general showed a decreasing trend after 2016 (Supplementary Figure A7).

Human activities

Fishing intensities (SAR) differed over time and between coastal areas between 2009 and 2020. Mollusc dredge fishery intensity differs between years ($F_{1,27}$ = *19.66, P<0.001*) and coastal areas ($F_{2,27}$

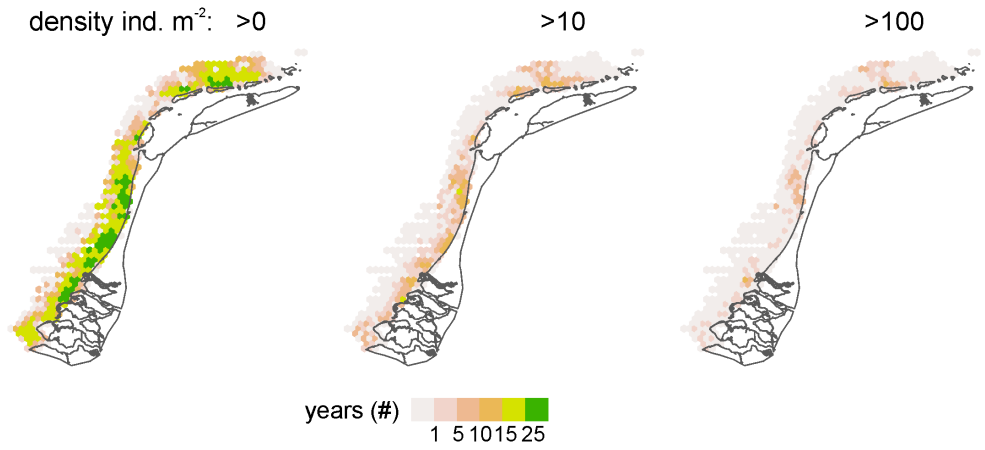

FIGURE 3
Spatial plots of the number of years when *S. subtruncata* densities reached >0, >10 or >100 individuals m^2 per hexagon. Zero observations in grey.

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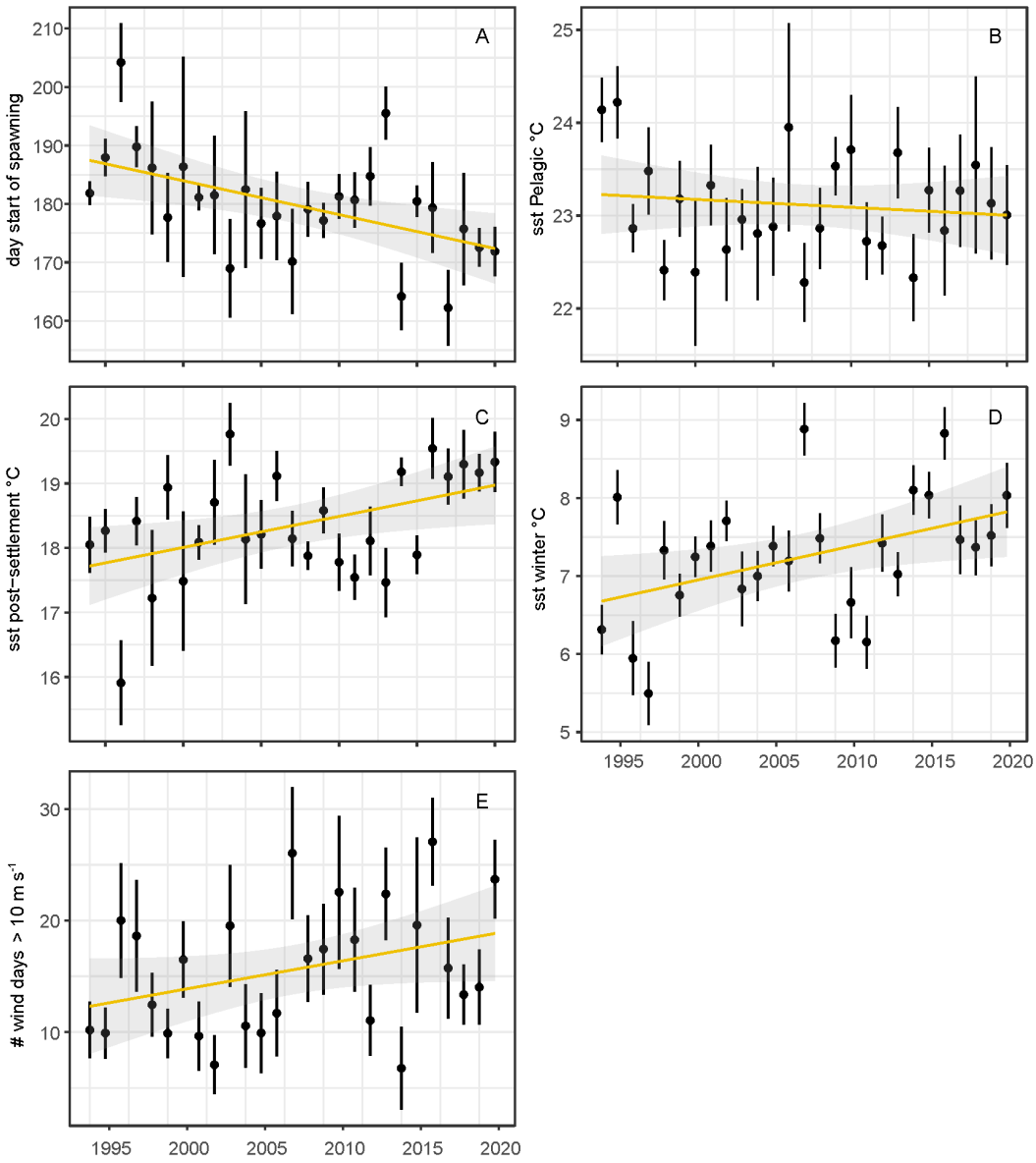

FIGURE 4
Average day of the year when the threshold for spawning was reached (16°C) **(A)** and average sea surface water temperature during pelagic phase (day: 0-27) **(B)**, post settlement phase (day: 28-77) **(C)**, sea surface water temperature in winter **(D)** and wind days with strong North-West winds > 10 m s^{-1} **(E)**. Error bars represent standard errors.

= *34.28, P<0.001*). Trends were different between coastal areas ($F_{2,27}$ = *18.74, P<0.001*), increased in the Voordelta and were stable in the West and Wadden coast (Figure 6A). Sole and place beam trawl fishing intensity declined over the years ($F_{1,30}$ = *30.18, P<0.001*) between areas ($F_{2,30}$ = *74.74, P<0.001*), were highest in the West coast, low and stable in the Voordelta over the years and very low in the Wadden coast ($F_{2,30}$ = *17.04, P<0.001*) (Figure 6B). Shrimp beam trawl intensity had the highest intensity of all fisheries, however no showed significant trend over the years ($F_{1,32}$ = *0.32, P<0.57*) but differed between coastal areas ($F_{2,32}$ = *43.16, P<0.001*). The fishing intensity was generally highest in the Wadden coast and was quite low in the West coast (Figure 6C). Total otter trawl fishing intensity declined over the years ($F_{2,30}$ = *23.78, P<0.001*) and differed between coastal areas ($F_{2,30}$ = *8.45, P<0.01*). Otter trawl fishing intensity was relatively high in the Wadden coast but strongly decreased after 2010 and fishing intensity was relatively low in the West coast and Voordelta (Figure 6D). Shore nourishment increased over the years along the entire Dutch coastline ($F_{1,26}$ = *7.76, P<0.01*), especially since 2000 (Figure 5B).

Temporal descriptive data

Predation

Annual average shrimp densities and trends differed between coastal areas. In the Voordelta, shrimp densities increased over the

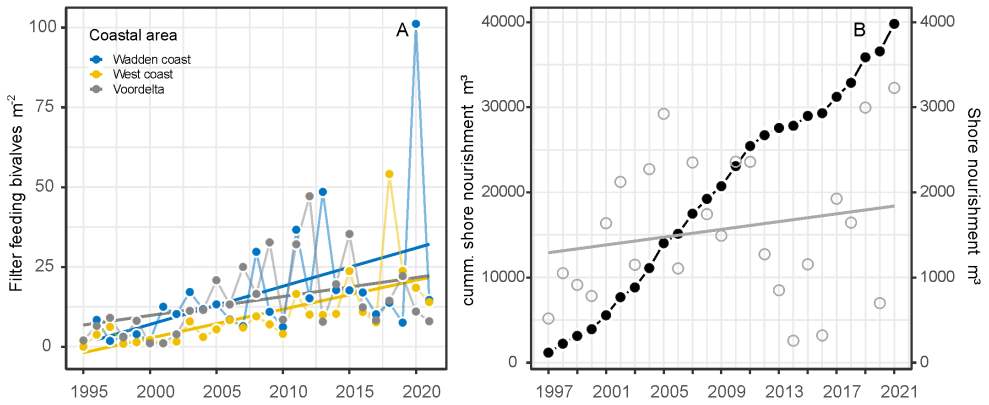

FIGURE 5
Trends of average densities of the sum of filter feeding bivalves (*Ensis* spp., *Lutraria lutraria, Donax vitattus* and *Chamelea striatula*) **(A)** and cumulative sand nourishment over the years (black dots) and yearly total shore nourishment volumes (grey circles) **(B)**.

years, while in the West coast and Wadden coast area they decreased (Figure 7A). Similar to shrimp, total flatfish numbers slightly increased in the Voordelta and decreased in the West and the Wadden coast (Figure 7B). The flatfish species plaice and dab were the numerically dominant species in the survey (Supplementary Figure A8). Common scoters are commonly found in all coastal areas but highest numbers were found in the eastern Wadden coast (Figure 7C). Incidentally, high numbers were also found in the other coastal areas.

Spatial-temporal statistical ZAG model

Model selection and performance

To investigate the effect of sea surface temperature from the moment of spawning three models (with respective temperature-effects at the moment of spawning, the pelagic phase and the post-settlement phase) were considered for the analyses for both sets of time series (Table 2). Based on the WAIC values model 1 and 2 were assumed similarly supporting the data for both time series, as they did

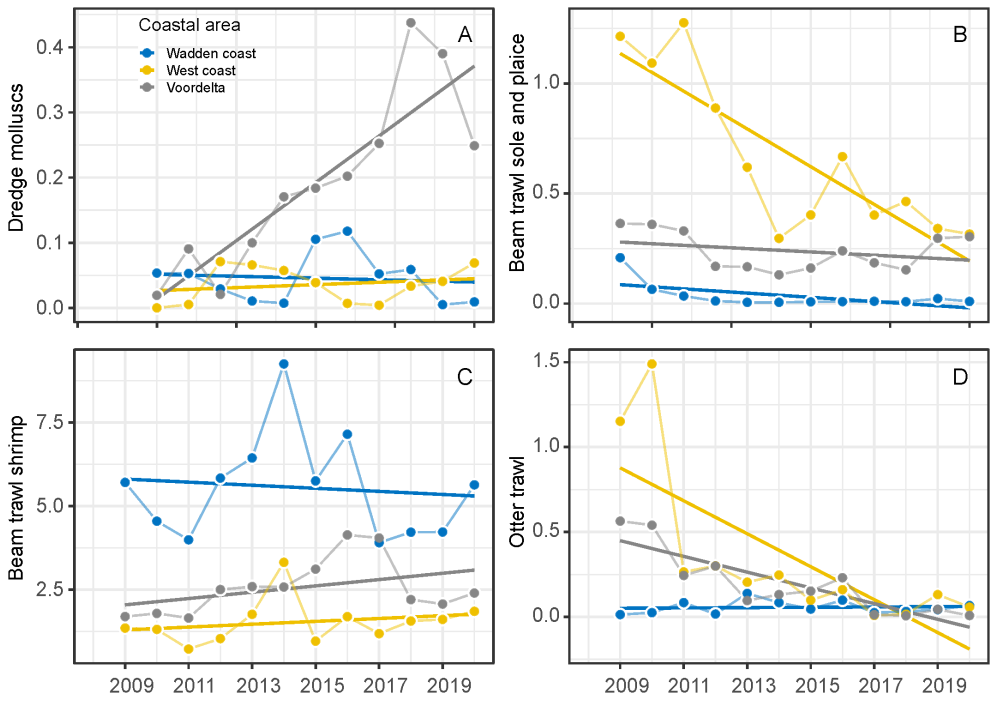

FIGURE 6
Fisheries intensity in the coastal areas expressed in Swept Area Ratio (SAR) in the coastal areas from 2009-2020. Dredge mollusc (*S. subtruncata* and *E. leei*) **(A)**, beam shrimp trawl **(B)**, beam sole and plaice trawl **(C)** and otter trawl fisheries **(D)**.

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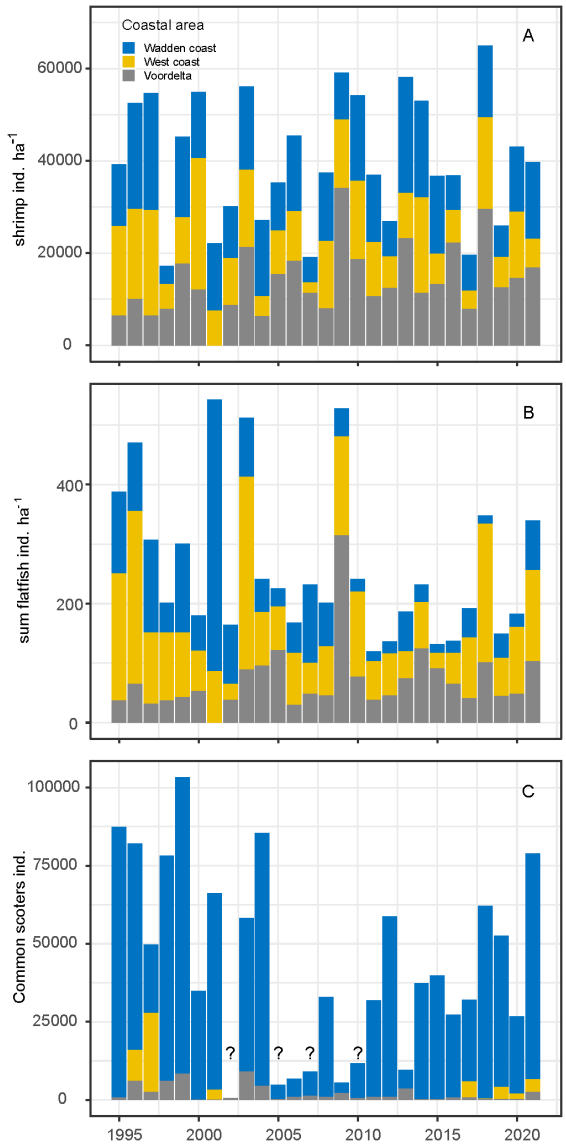

FIGURE 7
Trends of average densities of shrimp **(A)** and total number of flatfish species **(B)** and common scoter, uncomplete surveys are indicated with question mark (source: Sluijter et al., 2022) **(C)**.

not differ more than 2 ΔWAIC (Table 2). Based on model performance we conclude that model 2 had a satisfactory fit and correctly estimates occurrence and densities of *S. subtruncata* (Supplementary Material B). In addition, we considered this model biologically the most relevant and interpretable, because it includes average sea surface temperature in the post settlement phase (*SSTs*) instead the start of spawning date *(DY)*. The post settlement phase is a critical period during which biological processes likely influence mortality and survival of *S. subtruncata* recruits, providing interpretability and stronger basis for causal understanding.

Covariates effects (1995-2021), excluding fisheries

Model 2 shows that median grain size (D50) had the largest effect on densities and occurrence (Figure 8). The highest densities of *S. subtruncata* were at median grain sizes of 160-280 µm (Figure 9A). We used this range to standardise the effects of all other contributing covariates, as it indicates the preferred habitat for *S. subtruncata* based on median grain size (Figure 9A, between the blue and yellow lines). Median grain size showed a negative association (when all other variables were standardised) with occurrence and density, indicating higher abundances of *S. subtruncata* at intermediate fine compared to coarse sediments (Figure 9B). Sea surface temperature during the post settlement phase (*SSTs*) showed a positive association with densities (Figures 8, 9C). This effect became stronger with decreasing median grain size (Figure 9C). Likewise, increasing water temperature during winter had a positive effect on *S. subtruncata* densities (Figure 8) which also became stronger with decreasing median grain size (Figure 9D). The number of NW-wind days above 10 m s^{-1} (winddays) showed a negative effect on *S. subtruncata* densities and

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TABLE 2 Models ranked according Watanabe-Akaike information criterion (WAIC), with the ΔWAIC of the best (equally good) models printed in bold.

model	WAIC	ΔWAIC
Time series: 1995-2021 (excluding fishing efforts)		
1. D50+**DY**+SSTw+densC+winddays+distNour+f(year$_i$)	78991.36	**0.00**
2. D50+**SSTs**+SSTw+densC+winddays+distNour +f(year$_i$)	78991.63	**0.27**
3. D50+**SSTp**+SSTw+densC+winddays+distNour +f(year$_i$)	78997.70	6.34
Time series: 2009-2020 (including fishing efforts)		
1. D50+**DY**+SSTw+densC+winddays+disSupp+ SARshrimp+SARdmf+SARotter+SARdredge+f(year$_i$)	34485.82	**0.00**
2. D50+**SSTs**+SSTw+densC+winddays+disSupp+ SARshrimp+SARdmf+SARotter+SARdredge+f(year$_i$)	34486.16	**0.34**
3. D50+**SSTp**+SSTw+densC+winddays+distNour+ SARshrimp+SARdmf+SARotter+SARdredge+f(year$_i$)	34493.49	7.67

Models include fixed factors: median sediment grain size (D50), day of the year start of spawning (DY), sea surface temperature pelagic phase (SSTp), SST settlement phase (SSTs), SST winter (SSTw), density competing bivalves (densC), number of days NW-wind > 10 m s^{-1} (winddays), distance to sand nourishment (distNour) and Swept Area Ratio for fishing intensity (SARshrimp, SARdmf, SARotter and SARdredge) and smoother year (f(year$_i$)). Distinctive covariables in bold.

no effect on occurrence as the 95% confidence intervals overlap with zero (Figure 8). A negative association was found between densities and NW-wind days at high grain size, but a positive association at low grain size (Figure 9E). The cumulative density of filtering bivalves (densC) showed a positive effect on *S. subtruncata* densities but no effect on occurrence, as the 95% confidence intervals overlapped with zero (Figure 8). This positive effect with other filter-feeding bivalve species and *S. subtruncata* densities became stronger with increasing median grain size (Figure 9F). Shoreface sand nourishment (DistNour) did not contributed importantly to the models, as the 95% confidence intervals overlapped with zero (Figure 8).

Covariates effects (2009-2020), including fisheries

To investigate the effect of fishery intensity in combination with other covariates we used model 2, which was the most parsimonious model based on WAIC and included average sea surface temperature during the post settlement phase (*SSTs*) (Table 2). The fisheries covariates showed different effects in both parts of the model (Figure 10). Beam shrimp fishing intensity showed a positive association with occurrence of *S. subtruncata* but a negative with densities (Figure 10). This indicates that shrimp fisheries are associated with the species' occurrence, but at locations where *S. subtruncata* is present, there is a negative association that became stronger with lower median grain size (Figure 11A). The effect of beam trawl fishing intensity on sole and plaice showed a similar association on occurrence and densities (Figure 10), with a negative association on *S. subtruncata* densities that was stronger at lower median grain size (Figure 11B). Otter trawling did not show a relevant association on occurrence as the 95% confidence interval overlapped with zero, implying no strong overlap between otter trawl fishing intensity and the presence of *S. subtruncata* (Figure 10). However, a weak positive effect of otter trawl fishing intensity on *S. subtruncata* densities was found (Figures 10, 11C). Mollusc dredge fisheries showed a positive association with the occurrence of *S. subtruncata* but no effect on densities (Figures 10, 11D). Most other (non-fishery) covariates within this model (DistNour, DensComp, SSTs and SSTw) showed similar results to the first model analyses on the longer time series (Figure 10). Only the number of NW-wind days above 10 m s^{-1} showed a positive association with *S. subtruncata* occurrence and no association with densities (Figure 10).

Year effect

Although several covariates were considered important in our models, the relative effect of the smoother year was high and captured the temporal trend of *S. subtruncata* densities to a large extent (Supplementary Material B). This was less apparent for the binomial part of the models. Year has no direct biological meaning as such. Therefore, there is some unexplained annual variation in densities and other factors which could not be captured by our model covariates should be considered.

Discussion

Our study suggests that both local human activities and climate conditions are important factors influencing the *S. subtruncata* population dynamics in the Dutch North Sea. Water temperature in winter and after settlement, were positively linked to *S. subtruncata* occurrence and densities, while strong north-westerly winds (>10 m s^{-1}) had a negative effect. Overall, recent climate conditions seem to have benefited the population. Shellfish dredging and sand nourishment showed no apparent effect in recent years. However, our analyses shows that shrimp and flatfish beam trawling were positively associated with *S. subtruncata* occurrence but negatively with densities, suggesting higher trawling intensity where the species is found, which then negatively affects densities. An unexplained year effect, indicates additional unknown factors may also affect recruitment and survival. While our observational, correlative analysis is no proof of causality, it sheds light on factors potentially driving the population. Further discussion of our model results, the year effect and, possible mechanisms is provided below.

Sediment grain size

Our analyses shows that medium sediment grain size (D50) is an important determinant explaining occurrence and the density of *Spisula subtruncata*, with highest densities found at medium fine sediments (160-280 µm), aligning with earlier studies (Degraer

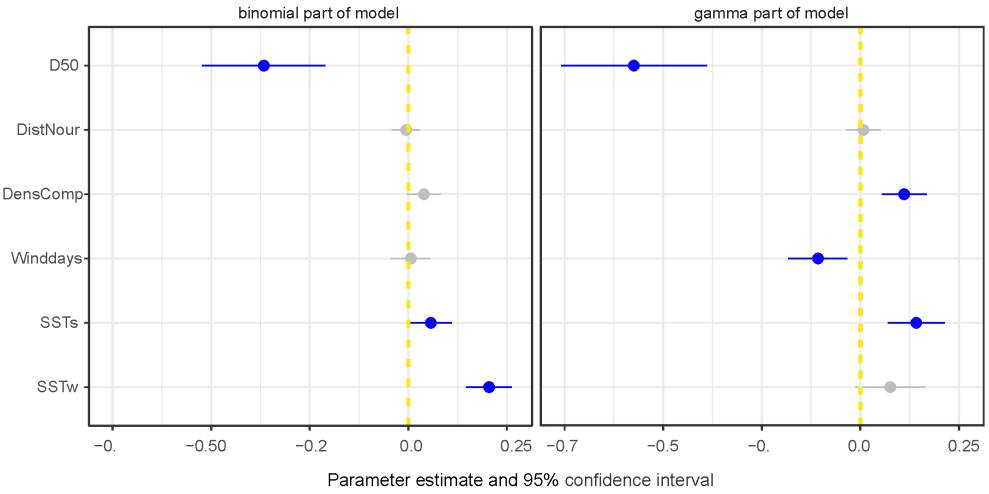

FIGURE 8
Estimated weights of the covariate effects indicated with posterior means with 95% confidence interval (CI) plotted for most parsimonious model excluding fisheries (for the dataset 1995-2021) for binomial and gamma part (best model in Table 2), blue points and lines show effects differing from zero with 95% CI. Median sediment grain size (D50), SST settlement phase (SSTs), SST winter (SSTw), density competing bivalves (DensCom), number of days NW wind > 10 m s^{-1} (winddays), distance to sand nourishment (DistNour).

et al., 2006, 2007). Sediment grain size, shaped by tidal current velocities and wave action, is commonly linked to the distribution of macro zoobenthos (Ellis et al., 2017; Bosco Gusmao et al., 2022). Our study indicates that habitat, as indicted by grain size, is a good proxy for habitat preference for *S. subtruncata*, with stronger effect of stressors at lower sediment grain size. Similar sediment-related effects on benthic communities have been observed in the North Sea (van Denderen et al., 2014; Rijnsdorp et al., 2018; van der Reijden et al., 2018).

Changes in sediment texture can affect *S. subtruncata* densities, with beach and foreshore sand nourishment altering sediment texture and impacting benthic communities (Herman et al., 2021; Dauvin et al., 2022; Saengsupavanich et al., 2023; Wijsman et al., 2023). While our analysis treated median grain size as an annual static variable, potential changes from nourishment were not fully accounted for. Although no direct effect of sand nourishment was detected (cf., Baptist and Leopold, 2009), we may were unable to assess its potential impact as it is currently unknown how to examine nourishment effects on the spatiotemporal scale of our study. In addition, the lack of detailed sand extraction data hindered a comprehensive assessment of its impact on *S. subtruncata* population.

Winter temperatures

We found a positive association between winter temperatures and the occurrence and densities of *S. subtruncata*. Warmer winters may reduce mortality by increasing mobility, allowing *S. subtruncata* to bury themselves faster in the sediment to escape from storms and predation. Moreover, the absence of prolonged sub-zero water temperatures may avert direct mass mortality of shellfish as has been observed during severe winters (Armonies et al., 2001; Baptist and Leopold, 2009). Thus, increasing winter temperatures may led to higher adult survival of *S. subtruncata*.

Spring and summer temperatures

The positive association between water temperature during the post-settlement phase (77 days after settlement) is likely related to increased survival of recruits. Warmer seawater increases growth rates of *S. subtruncata*, helping juveniles to outgrow predators like brown shrimp (van der Veer et al., 1998; Hiddink et al., 2002; Andresen and van der Meer, 2010), which feed on recruits up to 4 mm in size (Cardoso et al., 2007; Campos and van der Veer, 2008). Faster growth shortens the duration of the shrimp predation window, enhancing survival (Hiddink et al., 2002; Andresen and van der Meer, 2010). While shrimp reproduction and shoreward migration are also temperature-dependent (Boddeke, 1976; Beukema, 1992; Penning et al., 2021), rising North Sea temperatures could create a mismatch between shrimp and prey, potentially benefiting *S. subtruncata*. However, warming may also shift predator communities, with increasing cold water species in the coastal zone, negatively effecting bivalves. For example, flatfish such as sole and plaice, appear to be move from the Wadden Sea to the cooler coastal zone in the North Sea (van der Veer et al., 2022).

The positive association between post-settlement water temperature and *S. subtruncata* densities may also be related to food availability. Phytoplankton blooms play a crucial role for benthic fauna, driving rapid growth and changes in benthic communities (Zhang et al., 2015). There are indications that changes in North Sea phytoplankton have occurred in the recent and more distant past.

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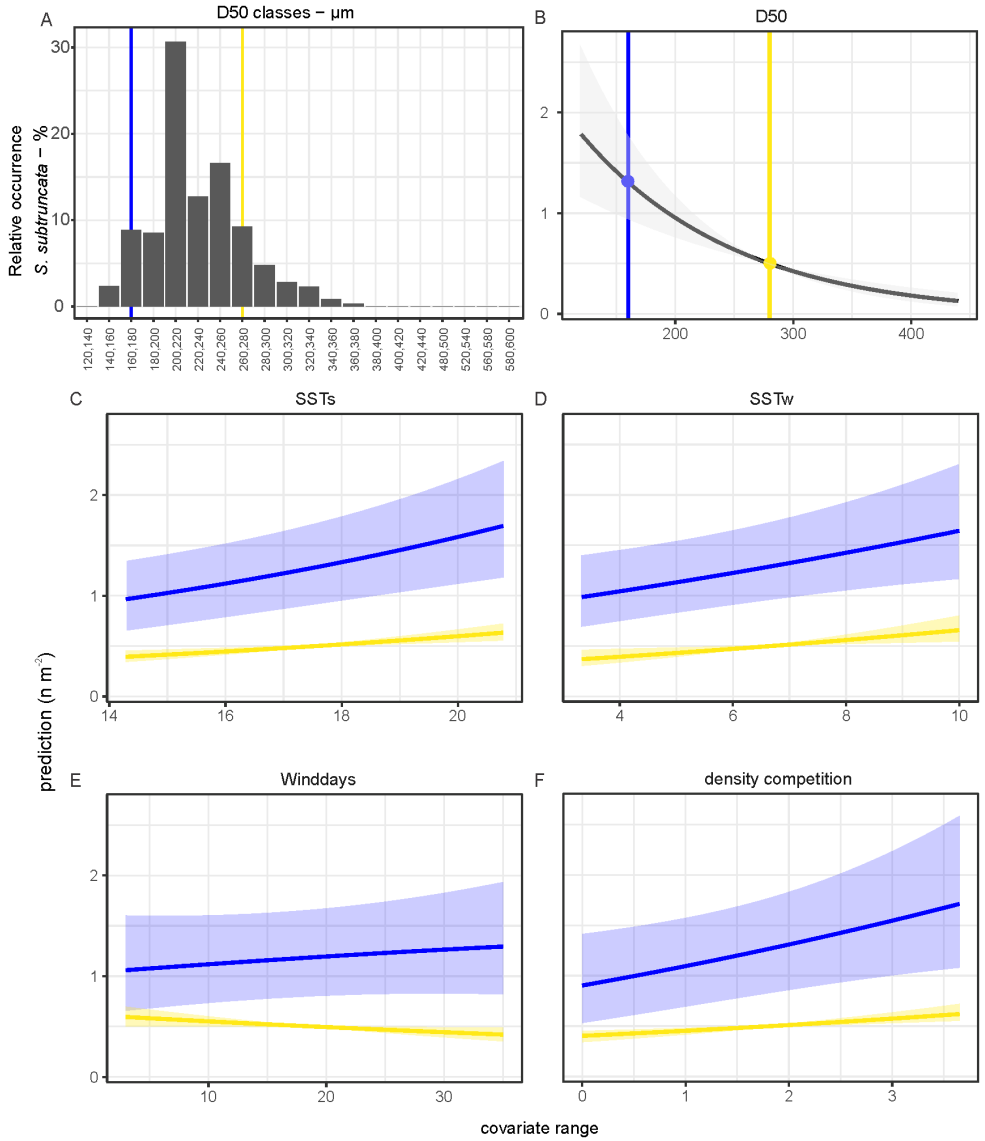

FIGURE 9
Frequency plot of sediment grain size where *S. subtruncata* occurred **(A)**. Predicted contribution of covariates from the hurdle model. **(B–F)** Prediction per measured range of covariates with minimum (blue) and the maximum (yellow, for values see **B**) of the optimal range of occurrence of *S. subtruncata* for median grain size while all other covariates standardized with a mean of zero. Shaded areas represent 95% confidence interval around the prediction.

Over the last century, for example, it is estimated that a reduced water transparency resulted in a delay of the spring bloom by 3 weeks (Opdal et al., 2019). Between 1988 and 2016, however, phytoplankton biomass declined and the timing of the spring bloom advanced (Desmit et al., 2020). While, shifts in phytoplankton species composition that have occurred (Baretta-Bekker et al., 2009), may have affected growth and survival of juvenile bivalves in Dutch North Sea coastal waters. Currently, the net consequences of altering phytoplankton bloom as a food source for benthic animals in the North Sea are difficult to evaluate due to the multifaceted changes in phytoplankton and unknown food preferences of the bivalves.

Strong north-western winds

Strong north-westerly winds affected *S. subtruncata* densities negatively. Strong winds cause resuspension of fine sediments which might reduce filtering efficiency of feeding bivalves, hampering their growth (Witbaard et al., 2005). Additionally, the disturbance of waves can disturb the buried *S. subtruncata* and release them from the seafloor. As *S. subtruncata* live at the sediment surface, they are also vulnerable to strong under water currents which can transport them to the beach or other unfavourable habitat. Mass mortality events due to strandings are

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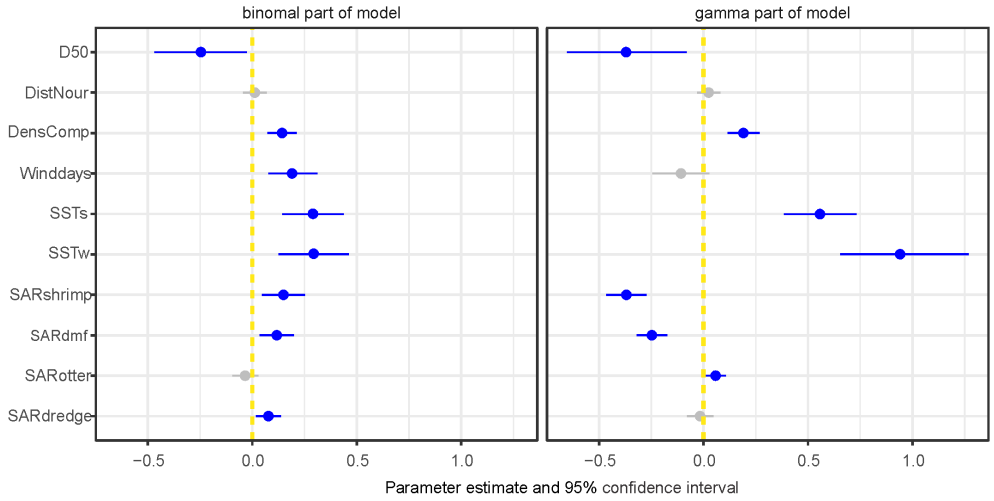

FIGURE 10
Estimated weights of the covariate effects indicated with posterior means with 95% confidence interval (CI) plotted for most parsimonious model including fisheries (for the dataset 2009-2020) for binomial and gamma part (best model in Table 2), blue points and lines show effects differing from zero with 95% CI. Median sediment grain size (D50), SST settlement phase (SSTs), SST winter (SSTw), density competing bivalves (DensComp), number of days wind > 10 m^{-s} (Winddays), distance to sand nourishment (DistNour) and Swept area ratio for fishing intensity (SARshrimp, SARdmf, SARotter and SARdredge).

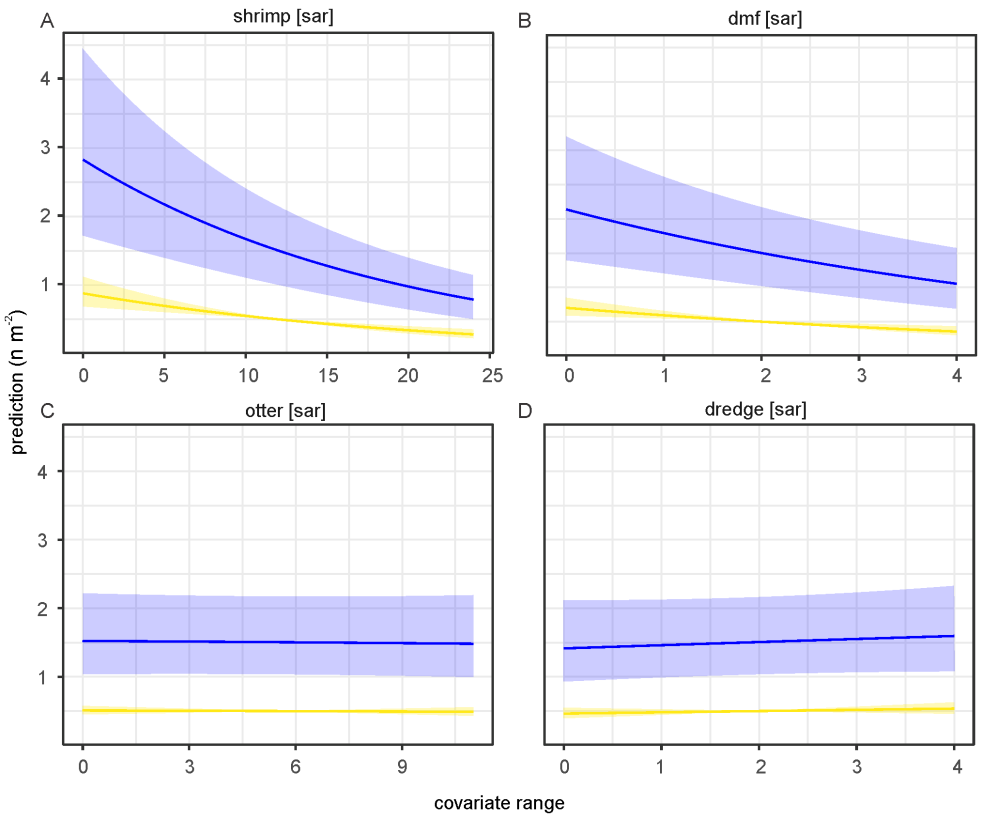

FIGURE 11
Predicted contribution of covariates the hurdle model. **(A–D)** Prediction per measured range of covariates with minimum (blue) and the maximum (yellow, for values see Figure 9B) of the optimal range of occurrence of *S. subtruncata* for median grain size while all other covariates standardized with a mean of zero. Shaded areas represent 95% confidence interval around the prediction.

known to happen after strong north-westerly winds followed by wind from the land creating a reversed current at the bottom (Raven, 2022).

Fishery impact

Our analyses showed a positive association between beam trawling for shrimp and flatfish and the presence of *S. subtruncata*, indicating that areas where the species is abundantly present, were more frequently fished. This aligns with observations that areas rich in bivalves attract shrimp and flatfish, and thus fisheries (van der Reijden et al., 2018; Hintzen et al., 2020). We also found a negative association between intensity of beam trawling for shrimp and flatfish and *S. subtruncata* density. While flatfish trawling, which penetrates the seabed, is known to increase bivalve mortality and affecting benthic communities (Tillin et al., 2006; Eigaard et al., 2016; Hiddink et al., 2017; Rijnsdorp et al., 2018), shrimp trawling, which lightly disturbs the seabed, is more frequent in the study area (Figure 6). However, studies on the impact of shrimp trawling on the benthic community in coastal waters are very limited (Tulp et al., 2020; Sala et al., 2023; van der Meer et al., 2024). The limited studies on the effects of shrimp beam trawling suggest it may shift benthic communities in the Wadden Sea (Tulp et al., 2020). This shift as observed in dredge sampling was mainly due to an increase in *E. leei* densities, likely able to relocate and quickly colonise disturbed shrimp trawl areas (Tulp et al., 2020), though a follow-up study based on box-core sampling within the same study did not find support for this hypothesis (van der Meer et al., 2024). A similar observation was found in an experimental study in the Wadden Sea, where *E. leei* preferred the manipulated unstable sediments (van der Heide et al., 2014).

The impact of bottom trawling on the benthic community varies between habitats. In highly dynamic habitats, with larger median grain size, benthic communities are less affected by trawling (van Denderen et al., 2014; Rijnsdorp et al., 2018; van der Reijden et al., 2018). Our study also found a stronger negative association between *S. subtruncata* and flatfish and shrimp trawl fisheries in areas with lower median grain size (Figures 11A, B), suggesting potential trawling effects are habitat dependent. In fine-medium sediment grain size, the bottom trawl gear may impact the seabed more strongly as it penetrates deeper into the seafloor, potentially increasing shellfish mortality and disrupting larval settlement. To disentangle the causal relationships and potential mechanisms, empirical research on the effects of beam trawl, especially shrimp fisheries, is needed, considering sediment characteristics.

Intensive fisheries on *S. subtruncata* can have strong effects on local abundances (Leopold, 1999; Smaal et al., 2001; Camphuysen et al., 2002), however, within our study, we did not find a relation between bivalve dredging and *S. subtruncata* densities. The absence of an effect may be because our analyses, covering fisheries data from 2009-2020, only includes two years of bivalve fisheries (2019-2020). In addition, the harvested quantities of adult *S. subtruncata* in these years were low, at 5.0 $\times 10^6$ kg in 2019 and 6.5$\times 10^6$ kg in 2020, representing 0.3% and 0.6% of the estimated standing adult stocks respectively (Perdon et al., 2019; Troost et al., 2023). In earlier years (1995-1999), fishing pressure was much higher (1% to 22% of the total estimated standing adult stock) which might have contributed to the population decline at the end of the 1990s (estimated harvest data supplied by A. Seinen, Meromar; Troost et al., 2023).

Window of opportunity

The relative effect of the smoother year in our models was high and captured the temporal trend to a large extent. This means that the unexplained annual variation in densities is likely related to yearly recruitment fluctuations (Fogarty et al., 1991) which were not captured by our model covariates. Therefore, additional factors during pre- and post-settlement are likely responsible for the observed variation. Recruitment success of shellfish is highly dependent on factors that must be optimal during a critical 'window of opportunity' (Balke et al., 2011; Capelle et al., 2019). Here, we discuss factors not included in our model analyses that are potentially related to recruitment success.

Larval settlement largely depends on the wind conditions for survival, dispersal and local settlement conditions. Wind-induced mixing of the water column can affect the vertical distribution of phytoplankton, influencing food availability for fish and invertebrate larvae and in turn their survival (Corten and van de Kamp, 1996; Turley and Rykaczewski, 2019). Wind direction and force during the pelagic larval phase determine the dispersal and location of shellfish larvae settlement (Belgrano et al., 1995; Armonies et al., 2001). The optimum conditions for *S. subtruncata* during the pelagic and settlement phases are unknown, however the pelagic phase for *S. subtruncata* larvae is relatively long, making them vulnerable to predation and environmental fluctuations, leading to high recruitment variability (Fogarty et al., 1991; Cardoso et al., 2007).

Predation

We used shrimp densities in the North Sea (Tulp et al., 2012) (Figure 7A) and energy requirements of shrimp (Jung et al., 2017) to estimate shrimp predation pressure (Supplementary Figure A3). Based on average estimated shrimp densities of 1.35 m^{-2} (13.500 shrimp ha^{-1}), with a maximum observed of 22 m^{-2} (220.000 ha^{-1}) (Tulp et al., 2012) (Supplementary Figure A3), we estimate that brown shrimps reduce *S. subtruncata* densities by 1.800 to 30.000 recruits m^{-2} over a 77 day predation window respectively. The net effect depends on the starting settlement density of *S. subtruncata* recruits. For example, a recruit density of 15.000 m^{-2} may lead to a local reduction ranging from 10% to a potential complete depletion of recruit density. However, based on the maximum observed *S. subtruncata* recruit densities of 150.000 m^{-2} (Degraer et al., 2007), we estimate a local potential predation mortality by brown shrimp ranging from 1% to 20%. The trends in our descriptive data on shrimp predation did not provide a clear indication that they can explain the unexplained year effect. However, there is a large uncertainty on shrimp densities and are likely underestimated

(Aarts et al., 2019; Supplementary Material A3). For other bivalve species it was shown that a predation pressure of this order of magnitude can drive population dynamics (Hiddink et al., 2002; Andresen and van der Meer, 2010; Weerman et al., 2014).

Flatfish also prey on bivalves, especially for dab and plaice it can be an important prey (Braber and de Groot, 1973; Rijnsdorp and Vingerhoed, 2001; Tulp et al., 2010). Stomach content analyses showed that *S. subtruncata* can be the dominant prey for plaice (Rijnsdorp and Vingerhoed, 2001). The same uncertainties as for brown shrimp apply for the estimation for flatfish densities. Moreover, larger flatfish (> 150 mm) are underrepresented in the DFS survey (Aarts et al., 2019) because the gear is not suited for larger, faster swimming fish, and diets are poorly known. Therefore, reliable estimates of flatfish predation pressure cannot be made.

Diving ducks, particularly common scoters, feed on adult *S. subtruncata* during winter in Dutch coastal waters (Camphuysen et al., 2002; Fox, 2003). Common scoters can potentially consume 4% to 20% of the local adult *S. subtruncata* (van de Wolfshaar et al., 2023). Since the ducks prefer larger specimens and are mainly present in winter, we can assume that scoter predation pressure on recruits during autumn is relatively low.

Implications for research and management

Our results showed that *S. subtruncata* was spatially aggregated on a large scale, occurring in high densities in distinct areas year after year. This spatial aggregation offers opportunities for conservation management. While European Union directives (e.g. Species and Habitats Directive 92/43/EEC and Birds Directive 79/409/EEC) permit anthropogenic activities within protected areas in the Dutch North Sea, provided that they do not significantly impact designated species and habitats. However, currently shrimp trawl fisheries, mollusc dredge fisheries and sand nourishment are occurring within protected areas (Natura 2000) and in areas with high densities of *S. subtruncata* (Hintzen, 2021; van de Wolfshaar et al., 2023), raising concerns about their potential impacts. Apart from the uncertainty about the impacts of shellfish dredging, shrimp trawl fisheries, there are uncertainties about the effects of sand extraction and nourishments. Due to the limitations of available data and methodological challenges for sand extraction and nourishments, we were unable to investigate potential impact over large spatiotemporal scales. The potential for climate effects to interact with local anthropogenic activities may complicate management, as they may amplify, neutralize or counteract each other's impact on the benthic community (Wakelin et al., 2015). The net outcome of such interactions is currently unknown and may contribute to the strong temporal variations of the unexplained year effect.

The effects of potential drivers in our study appear to be context-dependent, with sediment grain size serving as a proxy for habitat. This implies that a nuanced understanding of habitat dependency at finer spatial scales could be critical. Additionally, further insights into what determines the critical window of opportunity driving *S. subtruncata* population dynamics are needed. Questions remain about how climate change and intensifying local human activities may significantly affect the *S. subtruncata* population. Addressing these uncertainties would benefit from focused empirical research, particularly observational and experimental studies during the early recruitment phases. This more in-depth empirical research on (a)biotic and anthropogenic effects, and their cumulative impacts is essential to develop adequate fisheries and coastal management strategies, to sustain biodiversity.

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 manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

JdF: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Supervision, Validation, Visualization, Writing – original draft. PvH: Conceptualization, Data curation, Formal analysis, Methodology, Software, Visualization, Writing – review & editing. JC: Data curation, Investigation, Methodology, Writing – review & editing. ML: Data curation, Investigation, Methodology, Writing – review & editing. JP: Data curation, Investigation, Writing – review & editing. KT: Data curation, Investigation, Methodology, Project administration, Writing – review & editing. IT: Data curation, Investigation, Methodology, Writing – review & editing. JvZ: Data curation, Investigation, Writing – review & editing. CP: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1476223/full#supplementary-material

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Responses of Indo-Pacific humpback dolphins (*Sousa chinensis*) to construction of the Hong Kong–Zhuhai–Macao Bridge

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The location of offshore and coastal marine engineering projects often shows considerable overlap with the foraging and breeding grounds of marine mammals. Lingding Bay, located in the Chinese Pearl River Delta, is home to the world's largest known population of Indo-Pacific humpback dolphins (*Sousa chinensis*). The bay is also the site of the Hong Kong–Zhuhai–Macao Bridge mega-engineering project. This study assessed the responses of the dolphins to the bridge construction. Data were collected on dolphin sightings by survey vessels following standard line-transect tracks, with surveys conducted during the pre-construction (2005–2006), construction (2015–2016), and post-construction (2020–2021) phases. The dolphin distribution patterns, density, group sizes, and presence of calves were compared across these three periods. Additionally, the range patterns of the dolphins were analyzed following the identification of individuals during the post-construction phase. The average distance at which humpback dolphins were sighted from the bridge was significantly shorter after the completion of the bridge than during the pre-construction and construction phases. Furthermore, the density of humpback dolphins in the southern region of the bay—where the bridge is located—was significantly higher post-construction compared with that recorded during the pre-construction and construction phases. A noticeable increase in dolphin group sizes post-construction may indicate a shift in foraging strategy. The post-construction phase coincided with the COVID-19 pandemic lockdown period, and the resultant reduced human activity in Lingding Bay may have influenced the distribution of dolphins and other animals to some extent.

Individual identification results demonstrated that the waters near the bridge remained an integral habitat for the dolphins post-construction, as they freely traversed underneath the bridge. The results of this study hold considerable importance within the realm of marine engineering, offering valuable guidance and references for informed decision-making and operational practices in associated domains.

KEYWORDS

Indo-Pacific humpback dolphin, line-transect survey, distribution, behavior, marine engineering, Lingding Bay

1 Introduction

With the rapid development and transformation of coastal areas, over 40% of the world's population currently resides in these regions, and an increasing number of people are expected to migrate there in the future (Small and Nicholls, 2003; Lotze et al., 2006). This spatial pattern of human settlement, coupled with an increasing demand for resources and trade, has exerted tremendous pressure on coastal ecosystems and biota (Lotze et al., 2006). Coastal development involves the construction of bridges, waterways, docks, wind farms, and other structures, and the locations of such projects often overlap with the distribution ranges of marine mammals. However, research on the responses of dolphins to large-scale ocean engineering projects is limited, which hinders the development of effective protective environmental policies (Wright et al., 2011; Dähne et al., 2013; Pirotta et al., 2013).

Early research on the responses of marine mammals to construction primarily focused on their short-term behavioral adjustments and shifts in distribution range. A comprehensive examination of the historical distribution patterns of bowhead whales (*Balaena mysticetus*) revealed a notable shift in their habitat usage following exposure to offshore construction, reflecting the avoidance of areas characterized by heavy industrial activity (Richardson et al., 1995; Schick and Urban, 2000). In a study on bottlenose dolphins (*Tursiops truncatus*) and harbor porpoises (*Phocoena phocoena*) in northeast Scotland, the bottlenose dolphins were shown to spend less time in the vicinity of construction works that involved either impact or vibration piling (Graham et al., 2017). Furthermore, the abundance of female Australian humpback dolphins (*Sousa sahulensis*) in the southern regions of the Great Barrier Reef decreased significantly in response to port construction activities and a major concurrent flood; however, at the completion of this development project, the abundance of females returned to reflect original numbers (Cagnazzi et al., 2020). Additionally, notable changes in the swimming speed of Indo-Pacific humpback dolphins (*Sousa chinensis*) have been observed during piling operations and in the presence of marine vessels in the waters off Hong Kong (Würsig et al., 2000; Piwetz et al., 2012). In the early to mid-1990s, the waters of northwest Hong Kong were key areas frequently visited by humpback dolphins (Jefferson, 2000); however, since then, dolphin sightings have significantly declined (Jefferson et al., 2023). A previous study on humpback dolphins in Lingding Bay (LDB), an estuary of the Pearl River Delta in southern China, also suggested that the dolphins may have altered their habitat selection in the last 20 years, adapting to coastline disturbances caused by human activities (Wang et al., 2022).

The Hong Kong–Zhuhai–Macao Bridge (HZMB) is a bridge–tunnel system connecting Hong Kong with the cities of Zhuhai and Macao on the Chinese mainland. Located in LDB, the HZMB is the longest bridge across the sea in the world. It has been hailed as a mega-engineering project and represents a world-class cross-sea passage. The eastern end of the bridge is located on an artificial island near Hong Kong International Airport, from where the bridge spans the LDB westward to an artificial island near the port of Zhuhai–Macao (Figure 1). Construction of the bridge began in December 2009, and the HZMB was officially opened for trial operations in October 2018. Of note, LDB is a key habitat of the Indo-Pacific humpback dolphin (*Sousa chinensis*), also known as the Chinese white dolphin and hereafter referred to as the humpback dolphin, an animal under state protection in China. Humpback dolphins' health status, population dynamics, trophic relationships, and levels of pollutants within their bodies comprehensively reflect the ecological health and environmental changes of estuaries and their surrounding marine areas. As top predators highly sensitive to changes in water quality, food resources, and habitat conditions, monitoring these factors provides critical insights into ecosystem health, the presence of pollutants, the condition of the food web, and the impacts of human activities on the environment.

The Indo-Pacific humpback dolphin—listed as Vulnerable in the IUCN Red List— is a small, toothed cetacean residing in coastal and estuarine habitats and is predominantly found in the coastal waters of the Eastern Indian Ocean and Western Pacific Ocean (Jefferson et al., 2017). Its distribution extends from the northern coast of China (with the northernmost sighting record located in the Yellow Sea) southward throughout Southeast Asia and westward to the border between Bangladesh and Myanmar

(Jefferson and Rosenbaum, 2014; Jefferson and Smith, 2016; Jefferson et al., 2017; Lin et al., 2022). In China, humpback dolphins primarily inhabit the coastal regions of Xiamen, the western coasts and estuaries of Taiwan, the waters around Nanao Island in Shantou, the coast of the Pearl River Estuary up to the Moyang River, Leizhou Bay in Zhanjiang, the Beibu Gulf in Guangxi, and the waters around Sanya in Hainan (Chan, 2019; Chen et al., 2008; Chen et al., 2010; Chen et al., 2016; Jefferson, 2000; Li et al., 2019; Li et al., 2016; Peng et al., 2020; Wang et al., 2016a; Wang et al., 2016b; Xu et al., 2015). Among these regions, the largest known population is found between the Pearl River Estuary and the Moyang River (PRE-MR), boasting an estimated 2,600 individuals, which significantly surpasses the populations of the other regions (Jefferson, 2018; Chan, 2019; Li et al., 2019). Therefore, the population of this flagship species in PRE-MR serve as an ecological indicator for the Guangdong–Hong Kong–Macao Greater Bay Area, thereby playing a pivotal role in biodiversity conservation and ecosystem health assessments.

The construction of the HZMB has provided an opportunity to investigate the potential impact of marine construction on humpback dolphins in LDB. Due to the lack of research addressing the effect of bridge construction on humpback dolphins, wildlife conservation authorities still require insight into the potential adverse effects of such a mega-marine project on these animals. This study, inspired by the "opportunistic experiment" of Richardson et al., investigated the distribution of humpback dolphins before, during, and after construction of the HZMB (Richardson et al., 1985). Our research objectives encompassed assessments of the following three aspects: (1) the distribution and density of humpback dolphins in areas associated with the HZMB project, comparing these values with historical data; (2) group structure changes, such as calf presence or aggregations into large groups; and (3) whether humpback dolphins traversed underneath the completed bridge.

2 Methods

2.1 Study area

The study area covered most of the humpback dolphin distribution in the LDB and was bordered by Humen to the north, Dong'ao Island to the south, the boundary of Guangdong–Hong Kong waters to the east, and the coastlines of Zhuhai, Macao, and Hengqin Islands to the west. Previous surveys have shown that humpback dolphins are unevenly distributed in the LDB (Chen et al., 2010). Dividing the study area into four regions allows for a more accurate reflection of the humpback dolphins' density and distribution characteristics in each region, thereby improving the precision of the survey results. Additionally, subdividing the area helps balance the sample size across regions, reducing sampling errors. Consistent survey efforts were maintained across these

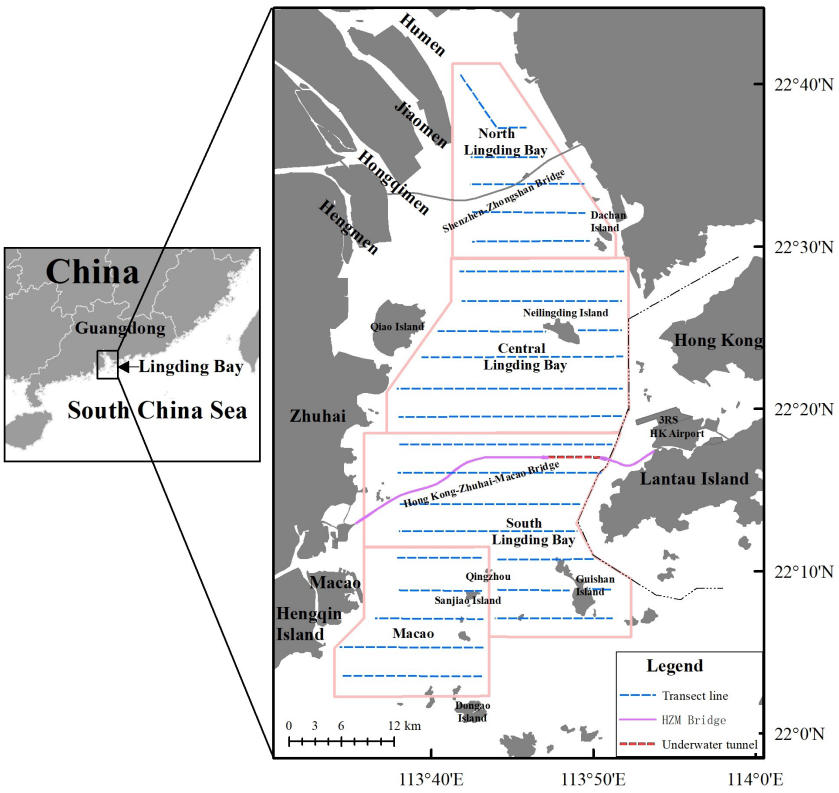

FIGURE 1
Map of the Lingding Bay study area in China, showing the locations of four line-transect survey regions—northern Lingding Bay, central Lingding Bay, southern Lingding Bay, and Macao. The pink-shaded area represents the boundary lines of the four survey regions.

regions to ensure unbiased data collection and analysis. Our study area was subdivided into four regions: northern Lingding Bay (NLDB), central Lingding Bay (CLDB), southern Lingding Bay (SLDB), and Macao (MA). The exact geographic locations of all monitoring zones and observation transects are illustrated in Figure 1.

2.2 Vessel survey

A survey team used standard line-transect methods to conduct regular vessel surveys (Buckland et al., 2001). To ensure the continuity and comparability of observational data, these surveys comprised the same visual observation and operational protocols as previous dolphin surveys in the Pearl River Estuary (Jefferson, 2000; Chen et al., 2010).

The observation vessel was a shrimp trawler with an observation platform fitted to its foredeck, approximately 4-5 m above the waterline. Under suitable observational conditions (0-5 on the Beaufort scale, no heavy rain, and visibility ≥1200 m), the survey vessel traveled along predetermined transects at 7-8 knots. Data were recorded simultaneously by a team of two observers, consisting of a primary observer using marine compass binoculars (7 × 50; Bushnell, Overland Park, KS, USA) and a secondary observer conducting naked-eye observations. To alleviate fatigue, the primary and secondary observers exchanged roles every 30 min. Both observers underwent training in observation and recording methods, visual distance estimation (corrected using a laser rangefinder), and dolphin species identification, and both had experience in offshore cetacean surveys.

For each line-transect, the following data were recorded: the times at which transect observations began and ended; the geographic location of the transect; boat speed; boat heading; sea state; visibility; and total distance covered. The survey vessel approached dolphin groups closely to allow an estimation of the number of individuals, observation of group composition and behavior, and photography of individuals from different angles for identification purposes (using a high-speed SLR camera and telephoto lens). For each dolphin sighting, the following data were collected: initial sighting time, geographic location, sighting angle, distance of dolphins from the vessel (estimated visually by the observers), number of dolphins, group composition, and behavior. A handheld GPS (eXplorist; magellan, San Dimas, CA, USA) was used to determine geographic locations, survey vessel speed, and distance covered, whereas angles were measured using compass binoculars. Group composition was determined according to age classes, comprising unspotted calves (UC), unspotted juveniles (UJ), mottled (SJ), speckled (SS), spotted adults (SA), and unspotted adults (UA) (Jefferson, 2000; Jefferson et al., 2012).

2.3 Photo-identification

Humpback dolphins bear distinctive markings on their bodies, such as notches on the dorsal fin or scar tissue (Chan and Karczmarski, 2024). Occasionally, body coloration patterns can also serve as references that allow researchers to distinguish between individuals. When humpback dolphins were sighted during our line-transect surveys, the survey was paused, and the vessel slowly approached the dolphins from the side and rear to allow accurate photography. Since body coloration and markings are not necessarily symmetrical, efforts were made to capture images of both sides of each dolphin. After the photos had been sorted into a reference library enabling the identification of individuals, they were subsequently used to analyze the movement patterns of individual dolphins.

2.4 Data analysis

The survey data were categorized into three phases relating to the construction of the HZMB: (1) pre-construction (February 2005 to January 2006), (2) construction (August 2015 to August 2016), and (3) post-construction (June 2020 to April 2021). Although the dataset provides important information regarding dolphin activity during the different phases of the HZMB construction, the use of a one-year dataset for each phase presents limitations.

2.4.1 Distribution and population density

Geographic information system (GIS) analysis was employed to determine changes in dolphin distribution in the study area during the three phases of HZMB construction. The data were projected onto the UTM49N coordinate system to minimize distortions in distance and area measurements. A cost/distance grid was created to measure the distance between each grid (400 m^2) and the bridge, allowing a calculation of the distance from each dolphin sighting location to the bridge (Buckstaff et al., 2013). The non-parametric Kruskal–Wallis test was used to test our null hypothesis that the distances from dolphin sighting locations to the HZMB did not differ significantly across the three construction phases.

To assess changes in the density of humpback dolphins in the study area across our three time periods, a distance sampling method was used to evaluate dolphin density in various regions (Buckland et al., 2001). For subsequent data analysis, we used DISTANCE software (Version 6.0, Release 2) to estimate dolphin density and related statistical parameters (Thomas et al., 2009). The formulae used for calculating density and the coefficient of variation were as follows:

$$\hat{D} = \frac{n\hat{f}(0)\hat{E}(s)}{2L\hat{g}(0)}$$

$$C\hat{V} = \sqrt{\frac{v\hat{a}r(n)}{n^2} + \frac{v\hat{a}r[\hat{f}(0)]}{[\hat{f}(0)]^2} + \frac{v\hat{a}r[\hat{E}(s)]}{[\hat{E}(s)]^2} + \frac{v\hat{a}r[\hat{g}(0)]}{[\hat{g}(0)]^2}}$$

where D is the density of the dolphins, n is the number of on-effort sightings (sample size), $f(0)$ is the trackline probability density at zero distance, $E(s)$ is an unbiased estimate of average group size, L is the length of the transect line, $g(0)$ is the trackline detection probability, CV is the coefficient of variation, and var is variance.

2.4.2 large group dolphin distribution and calf occurrence analyses

A frequency distribution of different activities and behaviors can identify whether any LDB regions are associated with distinct behaviors in the humpback dolphins. In terms of group size, larger dolphin groups are closely linked to the availability of food resources and level of human interference: locations containing larger groups are typically indicative of richer food resources and lower levels of human activity (Hung, 2008; Liu et al., 2021). Additionally, the presence and well-being of calves are crucial, affecting the overall health and survival of the population. Calves are generally more sensitive to construction activities, and monitoring changes in their distribution provides a vital indicator of the impact of projects on the dolphin population. Therefore, we overlaid the locations of large dolphin groups (≥10 individuals) and calf sightings with the cost/distance grid, extracted the distances from sighting locations to the bridge for the three construction phases, and assessed changes in dolphin distribution over time.

To analyze the variation in the frequency of dolphin occurrences within specific distances from the bridge, the study separately calculated the distribution of Indo-Pacific humpback dolphins, the presence of calves, and the formation of large aggregations within 0–0.99 km, 1–4.99 km, and 5–9.99 km of the Hong Kong–Zhuhai–Macao Bridge. The differences among these groups were also analyzed at various stages of the bridge's construction.

3 Results

3.1 Dolphin distribution and density

Humpback dolphins were located at significantly different distances from the HZMB during the three phases of its construction (Kruskal–Wallis, H (2, 567) = 14.45, p = 0.0007).

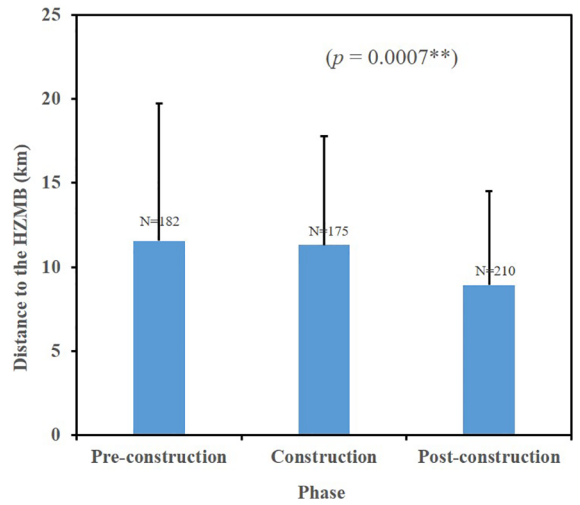

FIGURE 2
The average distance of humpback dolphins from the Hong Kong–Zhuhai–Macao Bridge (HZMB) during different phases of its construction. Error bars indicate *SD*, ** denotes significant differences.

The average distances from sighting locations to the bridge during the pre-construction, construction, and post-construction phases were 11.56 km (SD = 8.16, n = 182), 11.32 km (SD = 6.48, n = 175), and 8.93 km (SD = 5.57, n = 210), respectively (Figure 2). Density overlay maps of dolphin-sighting locations relative to the bridge are presented for these time periods in Figure 3.

The CLDB and SLDB are located in proximity to the HZMB, and the abundance of dolphins in these two areas can be expected to reflect the response of the dolphins to bridge construction most accurately. The population density of dolphins in the CLDB showed little variation over the three investigational phases, remaining at 50-60 individuals/100km^2. In contrast, the SLDB exhibited a significantly higher abundance of dolphins in the post-construction phase, whereas the population density remained relatively stable in the pre-construction and construction phases (Figure 4).

We compared the average humpback dolphin densities between the experimental subregions during the three construction periods. These average densities were significantly different between the CLDB and SLDB areas during the same periods ($p < 0.05$). When considering the CLDB in isolation, humpback dolphin abundance did not differ significantly between the pre-construction and construction phases or between the pre-construction and post-construction phases ($p > 0.05$); however, the dolphin density was significantly different between the construction and post-construction phases ($p < 0.05$). Additionally, when viewing only the SLDB, dolphin density did not differ significantly between the pre-construction and construction phases ($p > 0.05$); however, significant differences were observed between the pre-construction and post-construction phases, as well as between the construction and post-construction phases ($p < 0.05$).

3.2 Group size and calf occurrence

The mean sizes of dolphin groups during the pre-construction, construction, and post-construction phases were 5.03 (SD = 4.43, n = 182), 4.70 (SD = 6.48, n = 175), and 6.18 individuals (SD = 5.15, n = 210), respectively.

Group sizes were initially compared between the pre-construction, construction, and post-construction datasets via analysis of variance (ANOVA) followed by Tukey's honest significant difference (HSD) *post-hoc* test, with the initial assessments including Levene's test for homogeneity of variances. The results from Levene's test indicated that an assumption of equal variances across the three datasets could not be rejected at a significance level (α) of 0.05 (F = 2.7043, p = 0.0682). Subsequent ANOVAs (focusing on the equality of means) similarly failed to reject the null hypothesis at the 0.05 significance level (F = 2.8154, p = 0.0612). However, Tukey's HSD *post-hoc* test identified significant mean differences between the group sizes observed during the construction and post-construction phases (mean difference = 1.4793, p = 0.0476, reject = true). In other words, although overall mean differences did not differ significantly, specific pairwise comparisons revealed significant differences (particularly between the construction and post-construction datasets).

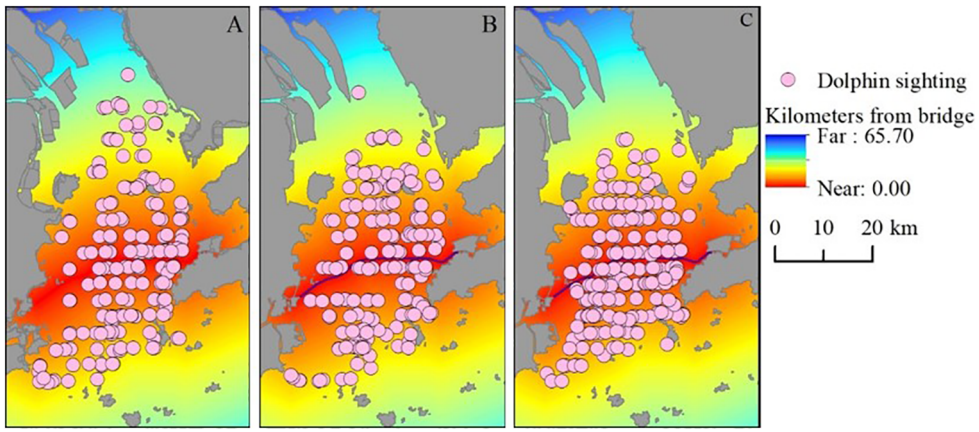

FIGURE 3
Dolphin group sightings during three different phases of the Hong Kong–Zhuhai–Macao Bridge (red line) construction: **(A)** pre-construction, **(B)** construction, and **(C)** post-construction. Sighting locations are overlaid with a cost/distance grid to extract the distances of the sighting locations from the bridge.

Recent studies highlight that environmental pressures, including food scarcity and anthropogenic factors, play a significant role in cetacean group formation. Research suggests that larger dolphin groups are often formed to improve foraging efficiency when food resources are scarce, as highlighted by Bearzi et al. (1999), while environmental factors such as prey distribution can also significantly influence group dynamics, as noted by Gowans et al. (2007).The distribution of humpback dolphin sightings comprising large groups (10 or more individuals) is illustrated for the different monitoring periods in Figure 5. Large groups were observed on both sides of the HZMB during the three construction phases. The distances of these groups from the HZMB did not differ significantly between the three periods (Kruskal-Wallis H (2,85) = 2.85, p = 0.2402). The average distances of large groups from the bridge during pre-construction, construction, and post construction were 11.13 km (SD = 6.35, n = 25), 9.75 km (SD = 5.12, n = 21), and 8.59 km (SD = 5.71, n = 38), respectively. Density overlay maps of large group sightings in relation to the bridge during these three construction phases are shown in Figure 5.

In this study, "calves" refers collectively to the age groups designated UC and UJ. Figure 6 displays the proportion of calves among the different age groups as recorded during the three different phases of bridge construction. Notably, during the construction period, the proportion of calves was the lowest, contrasting with its peak during the pre-construction period.

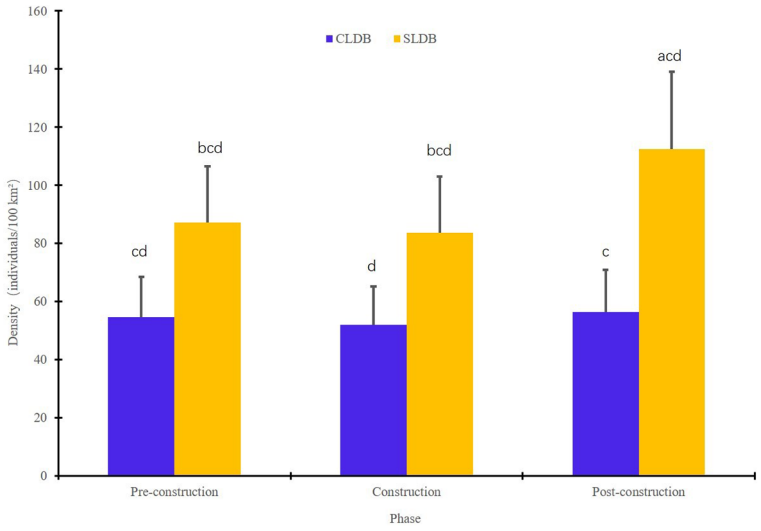

FIGURE 4
Changes in humpback dolphin density in the central Lingding Bay (CLDB) and south Lingding Bay (SLDB) regions during different construction phases of the Hong Kong–Zhuhai–Macao Bridge. Letters above the bars indicate the significance of differences between groups, where the same letter denotes no significant difference (α = 0.05).

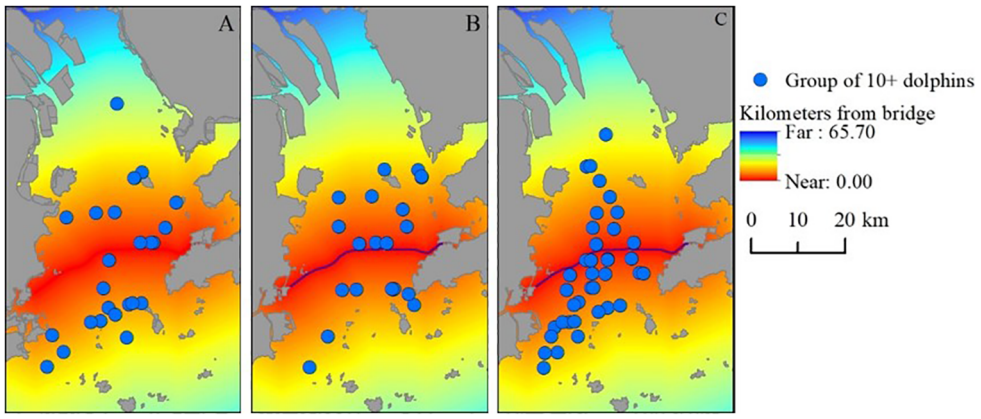

FIGURE 5
Sightings of large humpback dolphin groups (≥10 individuals) during the **(A)** pre-construction, **(B)** construction, and **(C)** post-construction phases of the Hong Kong–Zhuhai–Macao Bridge (red line). Sighting locations are overlaid with a cost/distance grid to extract the distances from sighting points to the bridge.

The distribution of calf sightings as recorded in each construction phase is shown in Figure 7. During the pre-construction phase, calves were observed throughout the LDB. However, during the construction phase, the number of calf sightings significantly decreased, with fewer sightings on both sides of the HZMB and almost none in the NLDB. During the post-construction period, calves were again observed in all regions, with a higher density of sightings near the bridge. Notably, the distances from calf sightings to the bridge did not differ significantly between the three periods (Kruskal-Wallis, H (2, 172) = 5.98, p = 0.0504). During the pre-construction, construction, and post-construction phases, these average distances comprised 11.89 km (SD = 7.29, n = 66), 9.48 km (SD = 5.15, n = 33), and 9.06 km (SD = 5.62, n = 73), respectively. Figure 7 displays the density overlay maps of calf sightings in relation to the HZMB during the three construction periods.

Based on the statistical analysis of three distribution categories—dolphin sightings, large group sightings, and calf sightings—across different time periods (pre-construction, construction, and post-construction) in various distance intervals (0–1, 1–5, 5–10) (Table 1), the Fisher's Exact test results indicate that the differences in the 0-1 interval across different years are not statistically significant (p = 1.0, which is greater than the 0.05 significance level). This suggests no significant changes in dolphin sightings within this interval over time. However, the differences in the 1–5 and 5–10 intervals are highly significant, with p-values of less than 0.05 (p < 0.05), specifically. This indicates that dolphin activity in these farther distance intervals has changed significantly over time.

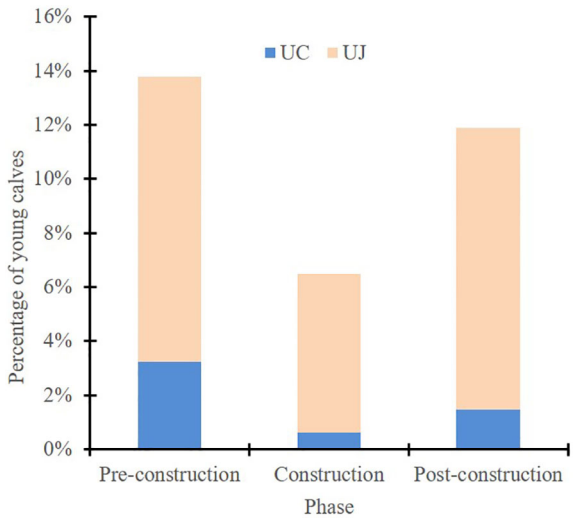

FIGURE 6
Percentages of young calves [i.e., unspotted calves (UC) and unspotted juveniles (UJ)] observed among all dolphin age groups during the three different phases of construction of the Hong Kong–Zhuhai–Macao Bridge.

3.3 Range use and movement patterns

During the post-construction survey, 449 humpback dolphin individuals were identified via photographs. Of these, approximately 174 individuals were sighted twice or more at different locations, accounting for 467 of the total number of sightings throughout the study area and period. The remaining 275 dolphins (61.2%) were photographed only once. Of the repeatedly identified individuals, 19.5% were observed exclusively in the waters to north of the bridge (Figure 8A), ~42.0% were found only in the waters to south of the bridge (Figure 8B), and ~38.5% exhibited a range use that spanned the HZMB (Figure 8C). Additionally, 46.6% of the dolphins displayed an activity range that was consistently close to the bridge, where they were repeatedly sighted (Figure 8D).

4 Discussion

We systematically analyzed the responses of humpback dolphins to various phases of a large-scale marine engineering project by using vessel-based line-transect data to assess changes

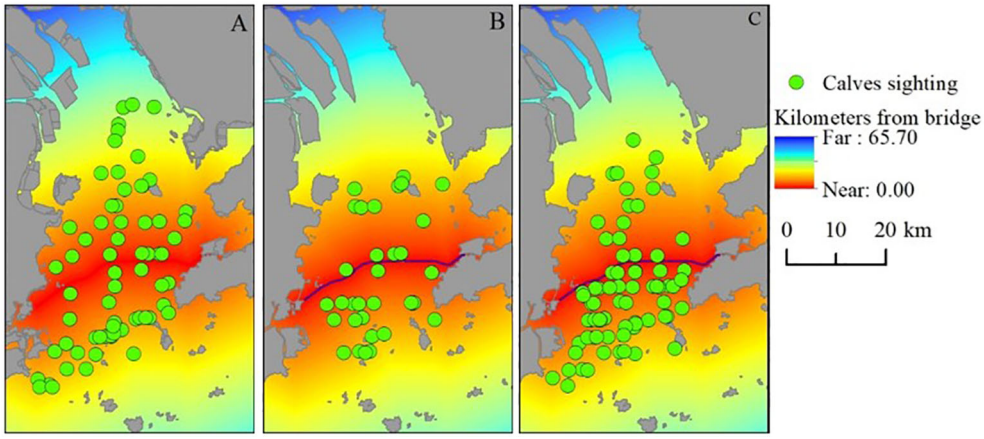

FIGURE 7
Locations of calf sightings during the **(A)** pre-construction, **(B)** construction, and **(C)** post-construction phases of the Hong Kong–Zhuhai–Macao Bridge (red line). These locations were overlaid with a cost/distance grid to extract their distances from the bridge.

in their distribution, density, group size, and group composition. Additionally, we examined the post-construction range use and movement patterns of the dolphins via the identification of individuals.

Dolphin abundance showed little change in the CLDB over periods before, during, and after the construction of the HZMB. In contrast, their abundance increased in the SLDB after the bridge construction. The increased abundance observed in the SLDB may have resulted from alternative causes, such as a reduction in human activities due to the COVID-19 pandemic that may have led to an increase in the number of dolphins entering the SLDB. However, our results suggest that the bridge construction had a minimal impact on the habitat use of humpback dolphins in the LDB, retaining it as a key habitat in their distribution range. During the COVID-19 lockdown, large marine mammals that had not been observed for generations reemerged near coastlines and in marine channels (Bates et al., 2020). This unexpected behavior has been linked to the reduced anthropogenic noise in the environment during human confinement (Rutz et al., 2020; Thomson and Barclay, 2020).

During the post-construction phase, an increased dolphin density near the HZMB could be attributable to two reasons: (1) an increase in food resources (reef effect) and/or (2) a reduction in disturbances (sheltering effect). The introduction of hard substrates on an originally uniform sandy seabed can alter the species composition of the habitat, subsequently increasing the abundance of marine organisms (Pedersen et al., 2006; Petersen and Malm, 2006). Furthermore, with reduced fishing activity near the bridge, the fish community is also likely to change. The waters around the HZMB in the Pearl River Estuary are under significant fishing pressure, especially from bottom and shrimp trawling operations (Liu et al., 2011; Zhou et al., 2019). Safety alert lines were established on either side of the HZMB in January 2020, thereby restricting vessel operations within 5 km of the bridge. In the Guangdong waters around the HZMB, all vessel traffic is prohibited in the bridge waters and a marginal 5 km buffer zone. With the exception of emergency disposal, official duties, and water activities permitted by maritime authorities, no vessels may enter these waters beyond the first-level alert line in bridge channels and tunnel areas. Such restrictions provide a sheltering effect, contributing to the observed increase in dolphin abundance in the SLDB, which is the region in which the HZMB is located. Dolphins dive for longer periods in areas with heavy vessel traffic or in the presence of an oncoming vessel (Ng and Leung, 2003). Therefore, the humpback dolphins may find the protected waters around the HZMB in the SLDB more attractive than other areas.

Additionally, the distance of humpback dolphin sightings from the bridge decreased significantly in the post-construction period. However, distances from the bridge did not differ significantly between large groups and calves during the different construction phases. Indeed, an analysis of the movement patterns of individual dolphins revealed that both sides of the bridge continued to be

TABLE 1 Dolphin sightings, large group sightings, and calf sightings within specific ranges from the bridge during different phases: pre-construction (pre-c), construction (c), and post-construction (post-c).

Phase	Dolphin sightings			Large group sightings			Calf sightings		
	[0-1) km	[1-5) km	[5-10) km	[0-1) km	[1-5) km	[5-10) km	[0-1) km	[1-5) km	[5-10) km
Pre-c	1	50	29	0	5	3	0	14	12
C	0	38	35	0	4	8	0	8	11
Post-c	4	58	55	1	10	12	1	18	23

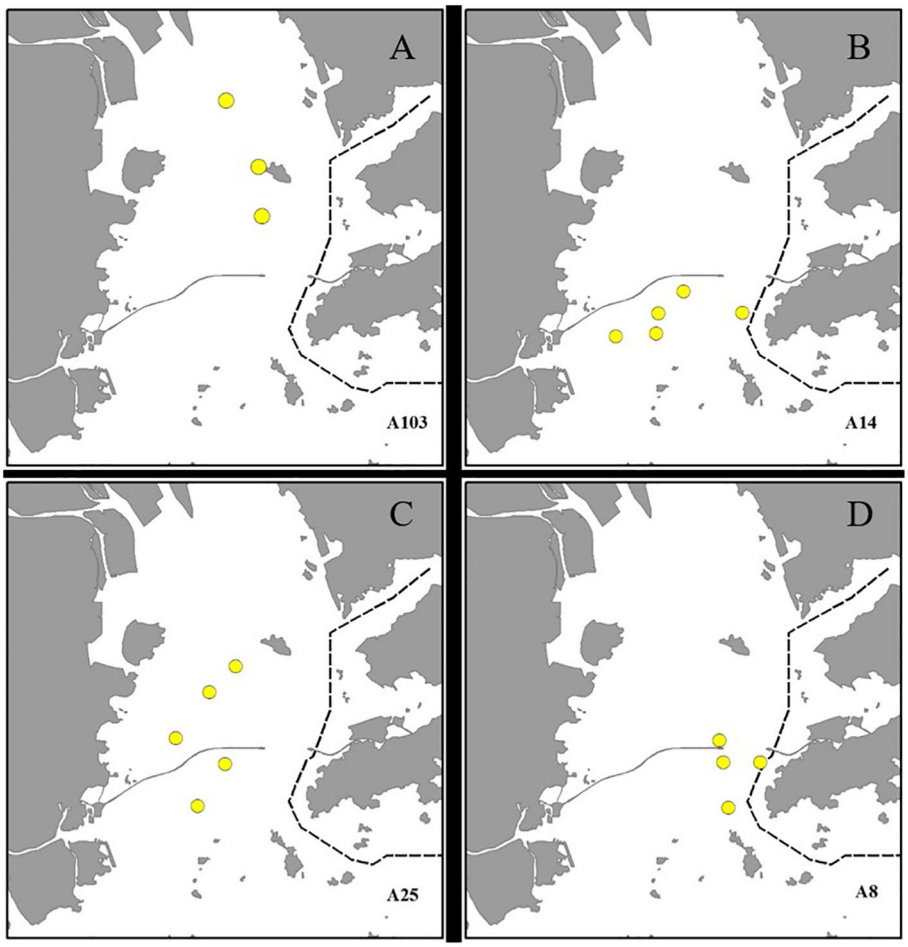

FIGURE 8
Patterns of humpback dolphin range use across the study area. **(A)** Individuals occurring exclusively in the waters to the north of the Hong Kong–Zhuhai–Macao Bridge (HZMB). **(B)** Individuals encountered exclusively in the waters to the south of the HZMB. **(C)** Individuals that were sighted on both sides of the HZMB. **(D)** Individuals that were frequently sighted in waters close to the HZMB.

essential distribution areas for dolphins in the post-construction period. This finding underscores the importance of the marine area around the HZMB as a crucial corridor for humpback dolphins in the LDB, with the regions on both sides persisting as preferred habitats.

Group size plays a vital role in facilitating communication and maintaining social dynamics among marine mammals. In the LDB, the average group size of humpback dolphins was significantly larger during the post-construction period compared to the construction phase. This increase in group size likely reflects a behavioral adaptation to cope with the elevated disturbances caused by shipping traffic, noise pollution, and habitat modifications associated with construction activities. For instance, the heightened shipping activity may have disrupted the dolphins' natural foraging areas, prompting them to form larger groups to improve hunting success and reduce individual energy expenditure (Connor, 2000; Silk, 2007). Furthermore, the alteration in prey availability and distribution due to construction-induced changes in the marine environment could have driven dolphins to form larger groups, as cooperative foraging becomes advantageous when prey is sparse or patchily distributed.

The variation in group sizes across geographical locations likely results from intraspecific trade-offs between the advantages of increased social cooperation—such as enhanced foraging efficiency—and the potential costs, such as increased competition for limited resources (Gygax, 2002; Gowans, 2019). These trade-offs may vary depending on local environmental conditions, leading to different social structures. Coastal dolphins exhibit dynamic social systems that can shift according to temporal changes in environmental pressures, such as seasonal shifts in prey abundance or increased human activities. Such flexibility allows dolphins to adapt their social behavior to fluctuating conditions within their habitats (Gómez de Segura et al., 2006; Sutaria et al., 2019).

In recent years, overfishing has significantly impacted fishery resources in LDB, leading to a 70% decrease in the biomass of coastal fish from 2004 to 2014 in the northern part of the bay (Yu et al., 2016). Additionally, the post-construction monitoring period of our study coincided with the COVID-19 pandemic. As a result, the number of fishing vessels, high-speed passenger ships, and other oceangoing boats was significantly reduced compared with the traffic present during the construction of the HZMB. This

substantial decrease in the interference from various vessels benefits dolphin communication. These factors collectively suggest that alterations in dolphin foraging strategies, driven by the variable availability of prey and the reduction of interference from seafaring vessels, could be linked with fluctuations in group size.

In terms of age groups, the percentage of young calves observed during the post-construction phase was significantly higher than that recorded for the construction period, yet it remained slightly lower than that noted for the pre-construction period. An analysis of stranded dolphin mortalities suggested that pollutants such as polychlorinated biphenyls, Cu, and perfluorooctane sulfonate may contribute significantly to the low calf survival rate in this population (Sun et al., 2022). Calves are more susceptible to anthropogenic disturbances than other age classes. Given the escalating anthropogenic activities in their habitats (including offshore construction projects, vessel traffic, fishing activities, and pollutant discharge), a restoration of the calf sighting ratio to that of the pre-construction period poses serious challenges.

The distances of calf sightings from the bridge did not differ significantly between the three HZMB construction periods. In the NLDB, a higher number of calves were present during the pre-construction phase of the bridge; however, during the construction and post-construction phases, this number decreased noticeably, likely linked to the extensive and prolonged development in this area, such as more than a decade of sand mining. In the CLDB, calf sightings decreased during the construction phase of the bridge, suggesting a potential decline in habitat quality that may stem from diminished food resources or increased human activities. South of the HZMB, an increased presence of calves was recorded during the construction phase, which could be attributed to two factors. Firstly, a decline in NLDB habitat quality may have prompted calves to migrate southward. Secondly, during post-construction, the suspension of ferry services between Hong Kong and MA due to the COVID-19 pandemic resulted in reduced water traffic in the northern waters of MA, possibly leading to the eastward migration of dolphins from the western Pearl River Estuary. However, whether this phenomenon is related to the impact of the HZMB construction requires further investigations utilizing extended monitoring data.

Based on our monitoring results, the construction of the HZMB had a minimal impact on the north–south movement of humpback dolphins in the LDB. The annual average distribution density of dolphins remained at approximately 50-60 individuals per 100km^2 in the CLDB throughout the pre-construction period (2005-2006), construction period (2015-2016), and post-construction period (2020-2021). Humpback dolphins have been shown to exhibit seasonal north–south migration patterns in LDB, moving toward the north during the dry season and toward the south during the wet season (Jia et al., 2000). Currently, the annual average population density of humpback dolphins remains stable in the CLDB. Further monitoring has shown significant seasonal fluctuations in dolphin sightings in the CLDB (unpublished report), again suggesting that the seasonal north–south migration of the dolphins may not have been affected by the bridge construction.

In terms of distribution range, some dolphins were seen both north and south of the bridge at different times. This suggests that the movement of individual dolphins is unlikely to be hindered by the HZMB. One previous study on the ranging patterns of humpback dolphins in LDB found that the estimated mean range size (± SD) of 40 humpback dolphins was 99.5 ± 61.04 km^2 (range: 23.76-303.84 km^2), with several individuals occurring exclusively in LDB (Hung and Jefferson, 2004). A similar study in the waters of Xiamen found that the individual ranges of humpback dolphins along this part of the coastline were similar to those of their conspecifics in the LDB (Chen et al., 2011). Our observation that some humpback dolphins did not traverse the HZMB could be an artefact of their habitual ranging patterns. The presence of the bridge may have also had an influence, leading to a change in distribution. Age class, associations with fishing boats, the distribution and availability of food resources, and human activities and disturbances have all been shown to influence the ranging patterns of humpback dolphins in the Pearl River Estuary (Hung and Jefferson, 2004). Future studies need to assess the significance of short-term behavioral changes relative to long-term survival and reproductive success, although long-term effects should not be assumed (Bejder et al., 2006). It should also be noted that the HZMB had just started operating during the post-construction survey period and was influenced by the COVID-19 pandemic, experiencing a low traffic volume. The habitat use of dolphins near the bridge is still subject to further assessments once the traffic volume increases.

5 Conclusion

The HZMB is a mega marine engineering project conducted within the habitat of the largest known population of humpback dolphins in the world. We evaluated the responses of the dolphins to construction activity via systematic line-transect sampling during various stages of the project. Results revealed a significant decrease in the average sighting distance of humpback dolphins from the bridge during the post-construction period compared to that in both the pre-construction and construction phases. Additionally, a notable increase in dolphin group sizes post-construction indicated a potential shift in foraging strategy. The proportion of calves recorded among the different age groups initially increased, followed by a subsequent decline and eventual recovery.

Monitoring these distribution changes of humpback dolphins over time offers valuable insights into the adaptive capacity of the species and facilitates the development of targeted conservation measures. Future endeavors should prioritize ongoing research and monitoring of humpback dolphins in the vicinity of the HZMB to monitor their long-term responses to the infrastructure and to form adaptive management approaches. Through the incorporation of scientific findings into conservation and management frameworks, stakeholders can collaboratively mitigate potential threats and ensure the enduring survival of this iconic dolphin 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.

Ethics statement

The animal study was approved by Academic Board of South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

ZH: Formal Analysis, Investigation, Methodology, Visualization, Writing – original draft. LF: Formal Analysis, Investigation, Writing – review & editing. HW: Formal Analysis, Investigation, Writing – review & editing. KZ: Formal Analysis, Investigation, Writing – review & editing. XW: Conceptualization, Resources, Supervision, Writing – original draft, Writing – review & editing. TC: Conceptualization, Resources, Supervision, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1407937/full#supplementary-material

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Exploration and implication of green macroalgal proliferation in the Nanhui-east-tidal-flat: an investigation of post-reclamation mudflat wetlands

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The Nanhui-east-tidal-flat (NETF), the largest marginal shoal in the Yangtze River of China, is significantly impacted by human activities. Prior research has not detected the presence of green macroalgae in the NETF, nor has it explored the effects of reclamation on the distribution of macroalgae. However, in 2021, a small-scale aggregated attached algal mats emerged in the NETF, potentially signaling the onset of a green tide and necessitating vigilant monitoring. Morphological and molecular biological identification analysis revealed that all collected green macroalgae were attributed to a single dominant species, *Ulva prolifera*, characterized by broad blades and prominent air bladders, colonizing various substrates. The attached *U. prolifera* exhibited continuous growth from March to May 2021, peaking at a wet weight of 373.6229 g/m^2 and a dry weight of 72.7904 g/m^2 on May 1, 2021, within the accessible sampling period. The rapid proliferation of the "opportunistic" *Ulva* was facilitated by high-level eutrophication and favorable environmental conditions. Furthermore, six potential germplasm sources of *U. prolifera* are summarized. The dominance of *Ulva* in the intertidal zone often indicates high eutrophication and deteriorating ecological conditions. With long-term reclamation and repeated ecological restoration projects, the intertidal vegetation is subjected to a vicious cycle of growth and destruction. Therefore, it is important to recognize that *U. prolifera* germplasm (macroalgae and micropropagules) will persist over the long term, and mudflats with monotonous and eutrophic habitats are highly likely to experience future large-scale algal blooms. Notably, a small-scale floating green tide was observed in the sea area near NETF in July 2023, and such concerns are not unfounded. This study conducts foundational scientific research on the attached green tide algae, a type of research that is relatively scarce in other marine areas. Most studies tend to initiate foundational research only after the outbreak of green tides, lacking early background data from the marine environment, thus rendering this study of significant reference value. Concurrently, this study emphasizes that field surveys remain an essential approach for conducting foundational scientific research on green tide algae in the NETF region, with the need to select appropriate research methods based

on the occurrence and development of algal mats, as required by the situation. Importantly, this study reflects the stability of marine ecosystems as a prerequisite for modern ocean management and services, provides new perspectives on the occurrence and development of green tides, and highlights potential ecological risk factors that should be considered in the implementation of intertidal construction projects.

KEYWORDS

ecological risk, harmful algal bloom, indicator species, ecosystem stability, reclamation, eutrophication, anthropogenic stressors, modern ocean management

1 Introduction

Coastal wetlands are a crucial component of the aquatic ecosystem, serving as a vital link between the ocean, freshwater, and land while providing unique ecological functions (Xu et al., 2024; Levin et al., 2001). They offer food and habitat for diverse ecosystems, and play a critical role in shoreline protection, mitigation of wind and wave impact, pollution control, maintenance of fishery resources, and promotion of carbon sequestration (Barbier et al., 2011; Mcleod et al., 2011). Additionally, wetlands hold significant value for educational, recreational, and tourism purposes (Barbier et al., 2011). The Nanhui-east-tidal-flat (NETF), situated in the southeast of Shanghai between the southern passage of the Yangtze River Estuary and Hangzhou Bay to the south (Figure 1), represents the largest marginal shoal in the Yangtze River Estuary area (Wei et al., 2017). Tides at this location are predominantly semi-diurnal. Positioned on the southern edge of the subtropical zone exposes NETF to the East Asian Monsoon climate.

The intertidal area of the NETF plays a crucial role in providing ecological services, serving as habitat and feeding grounds for intertidal creatures, as well as being an essential resting place for migratory birds along the East Asian–Australasian Flyway (Ge et al., 2007). Various species of vegetation are distributed across the intertidal gradient (Fan et al., 2006; You et al., 2018). *Phragmites australis* and *Spartina alterniflora* dominate the high tide zone, with *S. alterniflora* extending to the upper middle tide zone where it coexists with *Scirpus mariqueter*. The lower middle tide zone is characterized by different salt marsh pioneer species, followed by a bare mudflat. Notably, there are no higher plants present in the low tide zone (Fan et al., 2006; You et al., 2018).

Due to the rapid global population growth and accelerated urbanization, estuaries and coastal wetlands worldwide have suffered varying degrees of loss and degradation (Kennish, 2002; Crain et al., 2009; Barbier et al., 2011; Peter et al., 2024). From 1985 to 2010, a total of 754,697 hectares (ha) of coastal wetlands in China were reclaimed. Shanghai has reclaimed a total of 58,038.8 ha of tidal flats (Tian et al., 2016). The NETF is a post-reclamation mudflat wetland (Figure 1). Before reclamation, it was a nearshore marine ecosystem rather than an intertidal ecosystem. It has now become one of the most significant wetlands in the Yangtze River Estuary area.

The Yangtze River Estuary, the largest estuary system in Asia, is facing significant ecological stress due to a variety of human activities (Wei et al., 2015, 2017; Mei et al., 2018). The development of Shanghai has heavily relied on the natural land resources provided by the estuary (Yang, 2017), with river-driven deposition processes contributing to the expansion of tidal flat land (Figure 1). However, the construction of water conservancy facilities like the Three Gorges Dam has resulted in reduced sediment transport from the Yangtze River (Yang et al., 2011), leading to a slowdown in land deposition near the estuary. In addition to other factors such as rising sea levels and land erosion, the land deposition process near the NETF has slowed down (Wei et al., 2015). Combined with the reclamation projects following urbanization in Shanghai (Figure 1), by 2012, the tidal flats above 0 m in the NETF decreased by 80.8% (Wei et al., 2015). Additionally, reclamation activities have altered vegetation distribution (Han et al., 2010; Tao et al., 2017), zooplankton community composition (Li et al., 2012), waterbird diversity (Zhang, 2012; Niu et al., 2013), and benthic fauna composition (Ma, 2015; Yang, 2017) within the NETF ecosystem. Limited information regarding macroalgal proliferation in this region has been documented.

Marine vegetation, including macroalgae, plays a significant role in carbon sequestration (Liu et al., 2024a), contributing to approximately 50% of the burial of marine sediment carbon while occupying only 0.2% of the ocean area (Duarte et al., 2013; Krause-Jensen and Duarte, 2016). As one of the dominant primary producers in coastal ecosystems, macroalgae cover an area of about 3.5 million km^2 with a global net primary production of 1,521 TgC/yr (Krause-Jensen and Duarte, 2016). Additionally, macroalgae have the potential to mitigate climate change by absorbing CO_2, and their biomass is considered a sustainable feedstock for green energy and other types of blue carbon

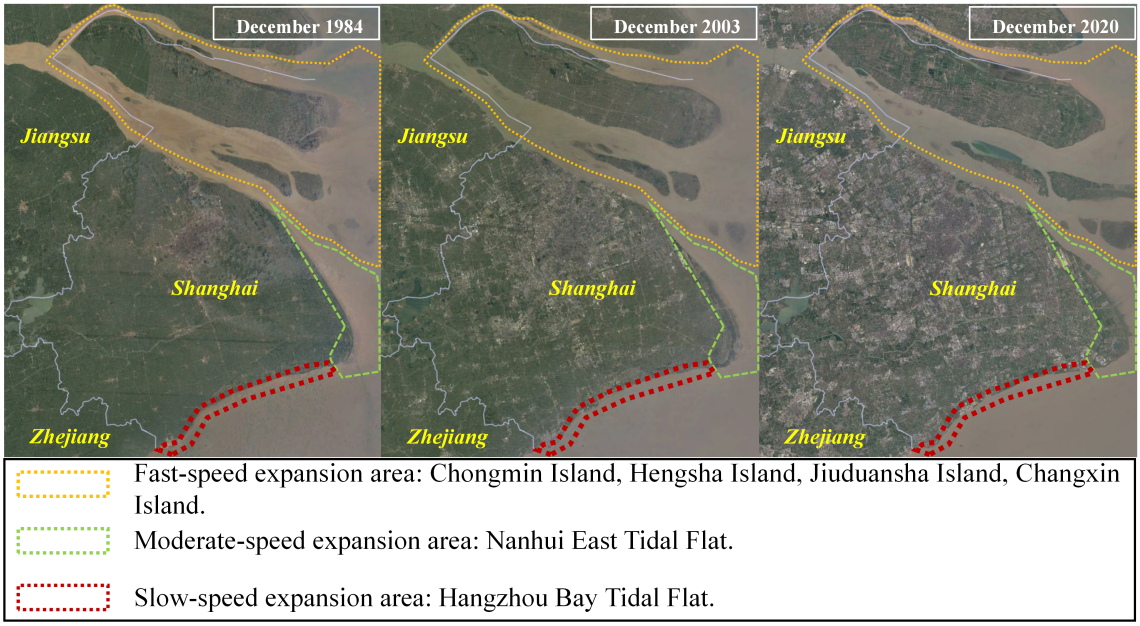

FIGURE 1
Satellite remote sensing imagery captured the expansion of Shanghai's urban area from 1984 to 2020, with data obtained from Google Earth Engine in April 2024. The significant increase in area in the Nanhui-east-tidal-flat occurred primarily between 2002 and 2003, as a result of Shanghai's utilization of land reclamation for the development of a modern coastal satellite city.

economy development (Yong et al., 2022). Chlorophyta (green seaweed) is a group of macroalgae. *Ulva* spp., an important green algae species (Shimada et al., 2008), has been utilized as an indicator of regional eutrophication and heavy metal pollution (Fort et al., 2020; Rybak, 2021; AbouGabal et al., 2023). *Ulva* possesses high nutritional value and is consumed by coastal residents in Asian countries (Sun et al., 2022b). It also serves as a natural source of polysaccharides and holds potential for use as antioxidants in the pharmaceutical industry (Farasat et al., 2014; Raposo et al., 2015; Bodar et al., 2024). However, large-scale blooms of *Ulva* have been occurring along the coast of China (Liu et al., 2013a; Liu et al., 2021a, 2022; Sun et al., 2022a; Xia et al., 2022a, 2024a; Feng et al., 2024; He et al., 2023). Therefore, studying the distribution and species proliferation of green macroalgae is crucial.

The current study investigated the spatial distribution and biomass of green seaweeds in the NETF, utilizing a combination of morphological and molecular biological methods to assess their taxonomic species. Additionally, environmental factors such as sea surface temperature (SST), sea surface salinity (SSS), pH, dissolved oxygen, chemical oxygen demand, inorganic nitrogen, active phosphate, petroleum, and other parameters were analyzed for further analysis and discussion. Overall, this research examines the taxonomy, spatial patterns, and variability of macroalgae in the NETF while also evaluating the potential for future large-scale green tide outbreaks in relation to environmental factors. So far, the occurrence of a small-scale floating green tide near the NETF in 2023 has been observed. The implication of attached green seaweeds in this region is underscored, along with a preliminary ecological risk assessment. This also provides foundational data and guidance for monitoring protocols for subsequent long-term surveillance.

2 Materials and methods

2.1 Distribution of green seaweeds in the NETF

The distribution and species identity of green seaweeds along the coastline of the NETF were systematically investigated from March to May 2021. A Global Positioning System (GPS) was utilized to accurately record the precise geographical coordinates of the green seaweed distribution (Figure 2). Specimens of green seaweeds were meticulously collected, and their respective habitats and types of solid substratum were thoroughly documented. Green seaweeds were observed at designated stations A-H (Figure 2A), with stations A-E forming part of the transect line (Figures 2B, C). The sampling sites were delineated using Surfer 16.0 software (Golden Software, Colorado, USA).

2.2 Green seaweed biomass and dry-wet ratio

Field surveys were conducted in accordance with the "The specification for marine monitoring, Part 7: Ecological survey for offshore pollution and biological monitoring" (National Standard of the People's Republic of China, GB17378.7-2007). Green seaweeds were collected on March 12, March 18, March 27, April 4, April 13, and May 1 of 2021 based on their distribution as described in Section 2.1 and sampling availability. The biomass of green seaweeds was measured at points A, B, C, D, and E along a line transect arranged in the intertidal zone (line transect, Figure 2), with a sampling point set

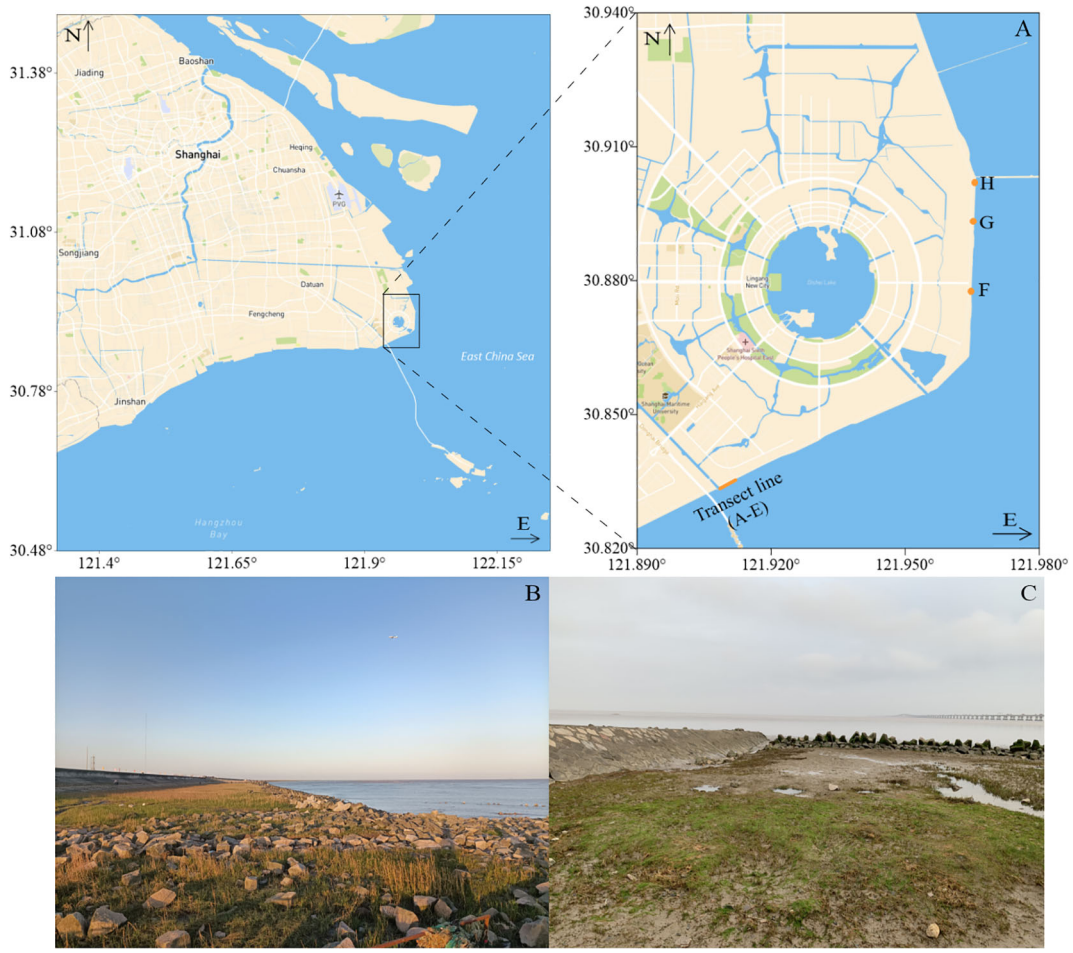

FIGURE 2
(A) Eight sampling sites (stations A-H) were selected, with transect lines consisting of five equally spaced sampling points (stations A-E); **(B)** The habitat characteristics along the transect line were documented; **(C)** The distribution of green seaweed at point E in the transect line revealed attached populations throughout the green areas.

every 250 m. Samples were collected using a quadrat measuring 0.25 m × 0.25 m and immediately transported to the laboratory under cool conditions. Fresh green seaweeds were carefully cleaned of adhering sediment with a brush and dried using an electric thermostatic drying oven until reaching constant weight (Shanghai Yiheng Scientific Instrument Co., Ltd., Shanghai, China). The wet weight (WW) and dry weight (DW) of the seaweeds were measured using an electronic balance (AL-104, Mettler Toledo, Zurich, Switzerland). Origin 2019b (OriginLab, Massachusetts, USA) software was used to plot biomass and dry-wet ratio curves. GraphPad Prism 9 (version 9.5.1) was used for variance analysis. Algal biomass was expressed as mean ± standard deviation (X ± SD).

2.3 Morphology and molecular identification of green seaweeds

The green seaweeds collected were initially classified based on their morphology, and the micro-morphology was observed and photographed using an optical microscope (E200, Nikon, Tokyo, Japan). Three to eight strains of green seaweeds were selected from each station, A-H. Prior to molecular identification, the surface sediment and other impurities were removed by brushing. The Dzup (Plant) genomic DNA isolation reagent (B518203-0025, Sangon Bioengineering Co., Ltd., Shanghai) was utilized for DNA extraction. The internal transcribed spacer (ITS) and 5S ribosomal DNA (5S) primers were utilized for the identification of *Ulva* algae (Liu et al., 2022; Zhao et al., 2023). The polymerase chain reaction (PCR) cycling conditions followed those described by Liu et al. (2022). The PCR reaction mixture consisted of 50 μL, comprising 25 μL of 2× PCR-mix, 19 μL of dd-H_2O, 2 μL (10 mM) of each forward and reverse primers, and 2 μL of DNA template. Amplification was carried out using a PCR machine (Thermo Fisher Scientific, Singapore). Following confirmation via electrophoresis on a 1% gel, the qualified PCR products were submitted to Sangon Bioengineering (Shanghai) Co., Ltd. for Sanger sequencing.

The obtained sequences were corrected using Chromas 2.3 software, which included 31 ITS sequences and 31 5S sequences. Subsequently, the sequences were compared using the Basic Local Alignment Search Tool (BLAST) within the National Center for Biotechnology Information (NCBI, https://www.ncbi.nlm.nih.gov/) to further identify the specific species of macroalgae. The ITS

sequences of similar *Ulva* species, including *U. prolifera*, *Ulva linza*, *Ulva compressa*, and *Ulva flexuosa*, were then downloaded from the NCBI database for comparison. *Blidingia minima* was selected as the outgroup and the 5S sequence of *U. linza* was chosen for further study. Detailed sample information can be found in Table 1.

2.4 Phylogenetic tree construction and genetic diversity analysis

The sequences were aligned using MEGA X software (Kumar et al., 2018), and a maximum likelihood (ML) phylogenetic tree was constructed based on the Kimura two-parameter model (Kimura, 1980). Genetic distances were calculated, and the reliability of each branch was verified through 1,000 bootstrap tests. The constructed trees were further enhanced using the iTOL database (https://itol.embl.de/) (Letunic and Bork, 2021). All 62 sequences have been deposited in the NCBI database (Table 1).

2.5 Data collection and statistical analysis of environmental factors

Data for SST and SSS in the NETF from January 1 to December 31 of 2021 were acquired from the National Marine Data Center of China, while data on pH, dissolved oxygen, chemical oxygen demand, inorganic nitrogen, active phosphate, and petroleum in the NETF from May 2017 to March 2023 were obtained from the Online Water Quality Monitoring System. Seawater quality categories were determined based on the "Seawater Quality Standard" (Ministry of Ecology and Environment of the People's Republic of China, GB 3097-1997). The standard applies to the maritime jurisdiction of China and adopts the single-factor method for assessing seawater quality. According to the standard, seawater quality is categorized into five levels, ranging from high to low: Grade I (excellent water quality: suitable for marine fisheries, marine nature reserves, and reserves for rare and endangered marine life; evaluation criteria include: pH range of 7.8 to 8.5 with a permissible normal fluctuation not exceeding 0.2, $C_{(Dissolved\ Oxygen)} \geq 6$ mg/L, $C_{(Chemical\ Oxygen\ Demand)} \leq 2$ mg/L, $C_{(inorganic\ nitrogen)} \leq 0.20$ mg/L, $C_{(Active\ phosphate)} \leq 0.015$ mg/L, $C_{(Petroleum)} \leq 0.05$ mg/L, etc.), Grade II (good water quality: suitable for aquaculture areas, bathing areas, marine sports or recreational areas with direct human contact with seawater, and industrial water areas directly related to human consumption; evaluation criteria include: pH range of 7.8 to 8.5 with a permissible normal fluctuation not exceeding 0.2, 5 mg/L $\leq C_{(Dissolved\ Oxygen)} <$ 6 mg/L, 2 mg/L$< C_{(Chemical\ Oxygen\ Demand)} \leq$ 3 mg/L, 0.20 mg/L$< C_{(inorganic\ nitrogen)} \leq$ 0.30 mg/L, 0.015 mg/L$< C_{(Active\ phosphate)} \leq$ 0.030 mg/L, $C_{(Petroleum)} \leq$0.05 mg/L, etc.), Grade III (ordinary water quality: suitable for general industrial water areas and coastal scenic tourism areas; evaluation criteria include: pH range of 6.8 to 8.8 with a permissible normal fluctuation not exceeding 0.5, 4 mg/L $\leq C_{(Dissolved\ Oxygen)} <$ 5 mg/L, 3 mg/L$< C_{(Chemical\ Oxygen\ Demand)} \leq$ 4 mg/L, 0.30 mg/L$< C_{(inorganic\ nitrogen)} \leq$ 0.40 mg/L, 0.015 mg/L$< C_{(Active\ phosphate)} \leq$ 0.030 mg/L, 0.05 mg/L$< C_{(Petroleum)} \leq$ 0.30 mg/L, etc.), Grade IV (deviant water quality: suitable for marine port waters and marine development and operational areas; evaluation criteria include: pH range of 6.8 to 8.8 with a permissible normal fluctuation not exceeding 0.5, 3 mg/L $\leq C_{(Dissolved\ Oxygen)} <$ 4 mg/L, 4 mg/L$< C_{(Chemical\ Oxygen\ Demand)} \leq$ 5 mg/L, 0.40 mg/L$< C_{(inorganic\ nitrogen)} \leq$ 0.50 mg/L, 0.030 mg/L$< C_{(Active\ phosphate)} \leq$ 0.045 mg/L, 0.30 mg/L$< C_{(Petroleum)} \leq$ 0.50 mg/L, etc.), and Worse than Grade IV (extremely poor water quality: seawater quality is worse than the above four categories).

The environmental data was analyzed using Microsoft Excel (Excel 2016, Microsoft, Washington, USA). The eutrophication level in the NETF was evaluated using the eutrophication index method. The calculation formula for the eutrophication index is as follows (1):

$$E = C_{(Chemical\ Oxygen\ Demand)} \times C_{(Inorganic\ Nitrogen)} \times C_{(Active\ phosphate)} \times 10^6/4500 \quad (1)$$

where E represents the eutrophication index and C represents the concentration (mg/L). When $1 \leq E \leq 3$, eutrophication is classified as mild; when $3< E \leq 9$, it is classified as medium; and when $E > 9$, it is classified as heavy (Liu et al., 2024b). Additionally, Origin 2019b and Surfer 9 software were employed for data analysis, figure drawing, and assembly.

3 Results

3.1 Vegetation distribution and solid substrate types of green seaweeds in the NETF

During the spring of 2021, green seaweeds were collected from eight designated stations (stations A-H) along the coastline of the NETF, primarily in the intertidal zone with relatively gentle terrain slopes. Stations A-E exhibited a dominance of *S. alterniflora* and *P. australis* among higher plants, with sporadic occurrences of *S. mariqueter*. Four types of solid substrates were identified at stations A-E, including discarded fishing nets, woven bags, and bottles (Figure 3A); hard materials such as crushed stones, broken bricks, and artificial dams (Figure 3B); residual roots from withered higher plants or roots of new plants (Figure 3C); as well as sediment (Figure 3D). In contrast, stations F-G presented a relatively simple habitat where *S. alterniflora* dominated among higher plants. The green seaweeds were mainly dispersed across the mudflat.

3.2 Morphology, molecular identification, and genetic diversity

The samples collected from the NETF exhibited a dark green or bright green coloration (Figure 4A) and were initially identified as *Ulva* spp. The seaweeds displayed numerous branches and an anchorage structure, with wide blades primarily consisting of primary branches and few secondary branches (Figure 4A). During the growth period, the seaweeds in the intertidal zone of the NETF appeared to have developed conspicuous air bladders (Figure 4B). The cells were arranged irregularly in monolayers,

TABLE 1 Detailed information about the macroalgae used to build the phylogenetic tree.

Species Number	Authority	Collection Locality	GenBank Information (ITS)	GenBank Information (5S)	Source	Specimen Location	Reference
2021ESNHA1, 2021ESNHA2, 2021ESNHA3	This study	East China Sea, China	OR543030, OR543031, OR543032	OR544859, OR544860, OR544861	This study	Shanghai Ocean University	This study
2021ESNHB1, 2021ESNHB2, 2021ESNHB3	This study	East China Sea, China	OR543033, OR543034, OR543035	OR544862, OR544863, OR544864	This study	Shanghai Ocean University	This study
2021ESNHC1, 2021ESNHC2, 2021ESNHC3	This study	East China Sea, China	OR543036, OR543037, OR543038	OR544865, OR544866, OR544867	This study	Shanghai Ocean University	This study
2021ESNHD1, 2021ESNHD2, 2021ESNHD3	This study	East China Sea, China	OR543039, OR543040, OR543041	OR544868, OR544869, OR544870	This study	Shanghai Ocean University	This study
2021ESNHE1, 2021ESNHE2, 2021ESNHE3	This study	East China Sea, China	OR543042, OR543043, OR543044	OR544871, OR544872, OR544873	This study	Shanghai Ocean University	This study
2021ESNHH1, 2021ESNHH2, 2021ESNHH3, 2021ESNHH4, 2021ESNHH5, 2021ESNHH6, 2021ESNHH7, 2021ESNHH8	This study	East China Sea, China	OR543045, OR543046, OR543047, OR543048, OR543049, OR543050, OR543051, OR543052	OR544874, OR544875, OR544876, OR544877, OR544878, OR544879, OR544880, OR544881	This study	Shanghai Ocean University	This study
2021ESNHF1, 2021ESNHF2, 2021ESNHF3, 2021ESNHF4, 2021ESNHF5	This study	East China Sea, China	OR543053, OR543054, OR543055, OR543056, OR543057	OR544882, OR544883, OR544884, OR544885, OR544886	This study	Shanghai Ocean University	This study
2021ESNHG1, 2021ESNHG2, 2021ESNHG3	This study	East China Sea, China	OR543058, OR543059, OR543060	OR544887, OR544888, OR544889	This study	Shanghai Ocean University	This study
6XSG-6	*Ulva prolifera*	Xiangshan Bay, Zhejiang province, China	KT802966	KT803042	NCBI	Institute of Oceanology, Chinese Academy of Sciences	(Zhang et al., 2018)
SDA4	*Ulva linza*	Zhanqiao, Qingdao, China	HM584731	HM584773	NCBI	Ningbo Entry-Exit Inspection and Quarantine Bureau Technical Center	(Duan et al., 2012)
SDF12	*Ulva compressa*	Jinshatan, Qingdao, China	HM584738	N.A.	NCBI	Ningbo Entry-Exit Inspection and Quarantine Bureau Technical Center	(Duan et al., 2012)
4X-1	*Ulva flexuosa*	Xiaoyangkou, Subei Shoal, China	KT802910	N.A.	NCBI	Institute of Oceanology, Chinese Academy of Sciences	(Zhang et al., 2018)
MurDG	*Blidingia minima*	Muroran D (Charatsunai), southern Hokkaido, Japan	AF163104	N.A.	NCBI	University of New South Wales	(Woolcott et al., 2000)

N.A., no information.

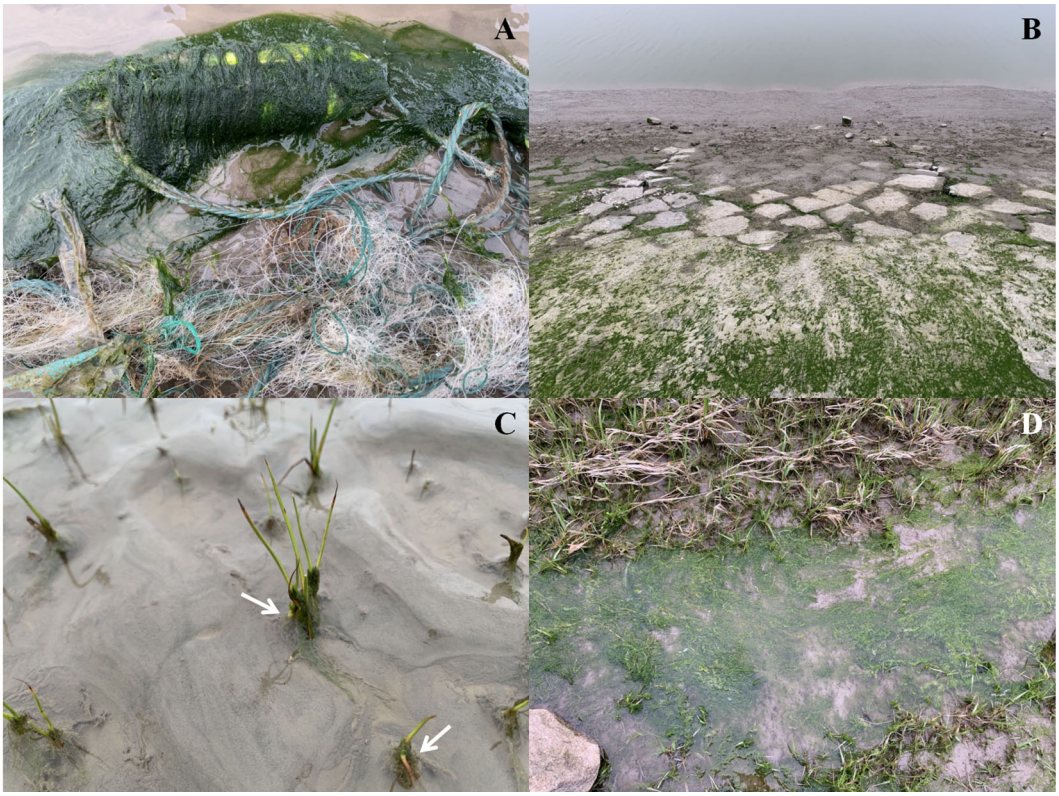

FIGURE 3
Main solid substrate types of green seaweeds in the Nanhui-east-tidal-flat. **(A)** Plastic waste, **(B)** Natural or artificial reef, **(C)** Intertidal plant roots (white arrows), and **(D)** Sediment.

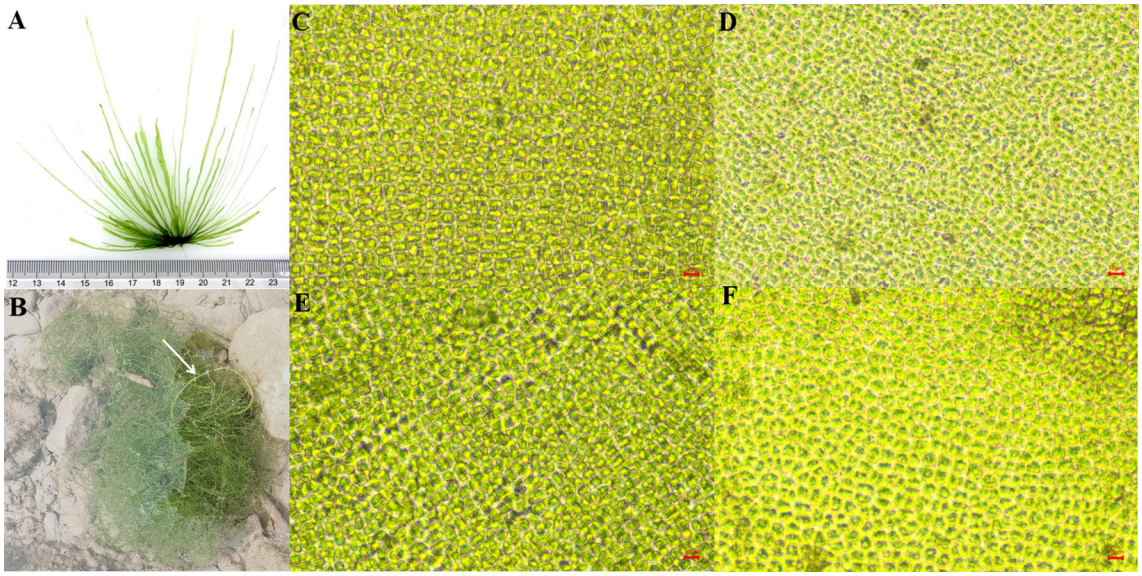

FIGURE 4
(A) The morphology of green seaweeds in the Nanhui-east-tidal-flat; **(B)** The air bladders of the seaweeds (white arrows); **(C)** The cell morphology of seaweeds in the transect line; **(D-F)** The cell morphology of seaweeds at stations F-H.

being oval or polygonal in shape (Figures 4C–F). Based on ITS and 5S sequences, BLAST results indicated that the 31 samples shared more than 98% similarity with *U. prolifera*. Two phylogenetic trees were constructed for further confirmation of the species.

The ML tree constructed based on the ITS revealed that 36 sequences, including outgroups, were clustered into four branches, and 31 samples from the NETF were distinguished from *U. compressa* (HM584738) and *U. flexuosa* (KT802910). However, these 31 samples were grouped into the *U. linza-procera-prolifera* complex group (LPP) with *U. prolifera* (KT802966) and *U. linza* (HM584731) (Figure 5), indicating that the ITS could not distinguish between *U. prolifera* and *U. linza* effectively. Therefore, it is recommended to use the 5S region for better resolution. The ML tree constructed based on the 5S region showed that all 31 samples from NETF formed a main clade with *U. prolifera*, suggesting that they indeed all belong to this species (Figure 6).

3.3 Variation of green macroalgal biomass in the NETF

Overall, the biomass (WW and DW) of attached *U. prolifera* in the NETF exhibited an increasing trend from March to May 2021 (Figure 7). The WW of *U. prolifera* on March 12, March 18, March 27, April 4, April 13, and May 1 of 2021 was measured at 85.9301 ± 30.1555 g/m^2, 96.7104 ± 38.4215 g/m^2, 114.9303 ± 72.7708 g/m^2, 223.8895 ± 124.3791 g/m^2, 225.0913 ± 89.5540 g/m^2, and 373.6229 ± 208.0184 g/m^2, respectively (Figure 7). The DW of *U. prolifera* on March 12, March 18, March 27, April 4, April 13, and May 1 of 2021 measured 11.0117 ± 1.8634 g/m^2, 11.7029 ± 2.4305 g/m^2, 12.6385 ± 6.3048 g/m^2, 27.6035 ± 17.6919 g/m^2, 33.1949 ± 16.4219 g/m^2, and 72.7904 ± 48.1359 g/m^2, respectively (Figure 7). The high SD of *U. prolifera* biomass at various stations on March 27, April 4, April 13, and May 1 of 2021 (Figure 7) was attributed to the heterogeneous distribution of *U. prolifera* in the intertidal zone. As environmental conditions gradually warmed, they became more conducive to the germination and growth of *U. prolifera*. The attached *U. prolifera* in the NETF exhibited continuous growth from March to May of 2021, with an increasing trend in average biomass (Figure 7), reaching 373.6229 g/m^2 (WW) and 72.7904 g/m^2 (DW) on May 1, 2021. The water content of *U. prolifera* in the NETF ranged from 80.5177% to 89.0033% with an average of 86.2548%. Generally, the average water content of *U. prolifera* ranges from 75% to 96.6%, and that of *U. prolifera* collected in the present study fell within this range.

3.4 Assessment of the environmental factors, seawater quality categories, and eutrophication level of the NETF

The annual SST in the NETF ranged from 5.2°C to 29.1°C (Figure 8A). *Ulva prolifera* is capable of year-round survival within

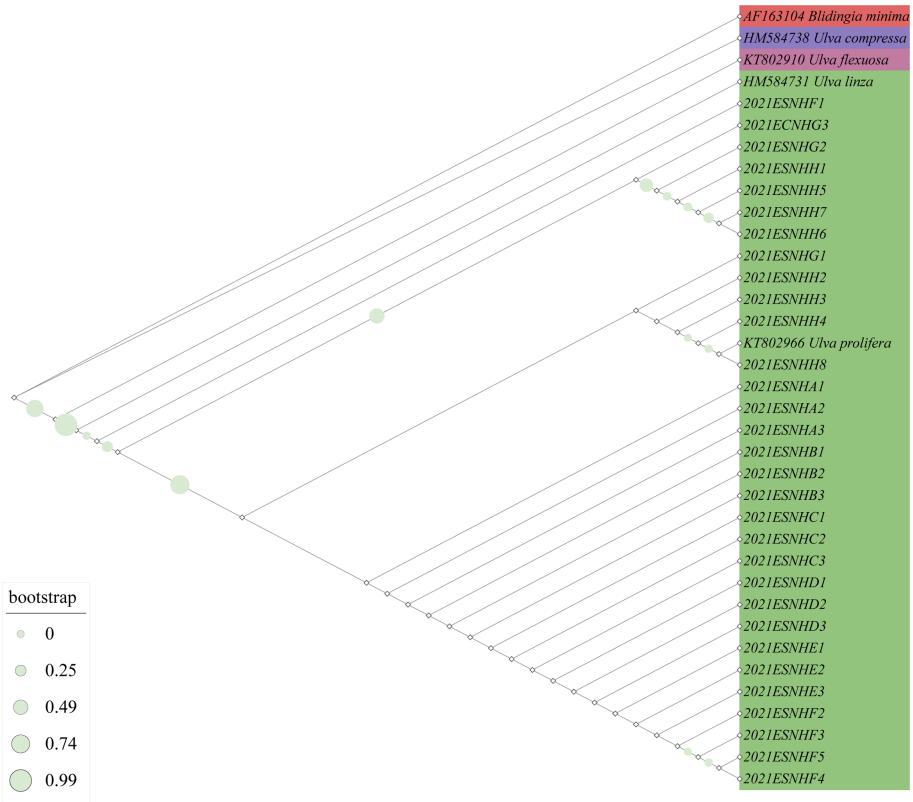

FIGURE 5
Maximum likelihood phylogenetic tree constructed based on ITS sequences.

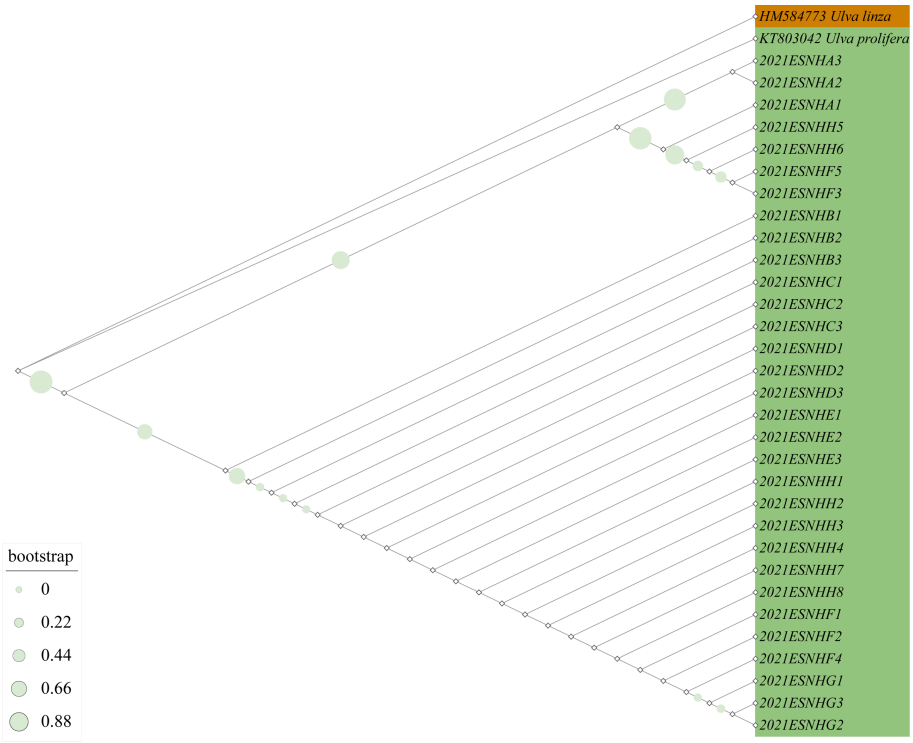

FIGURE 6
Maximum likelihood phylogenetic tree constructed based on 5S sequences.

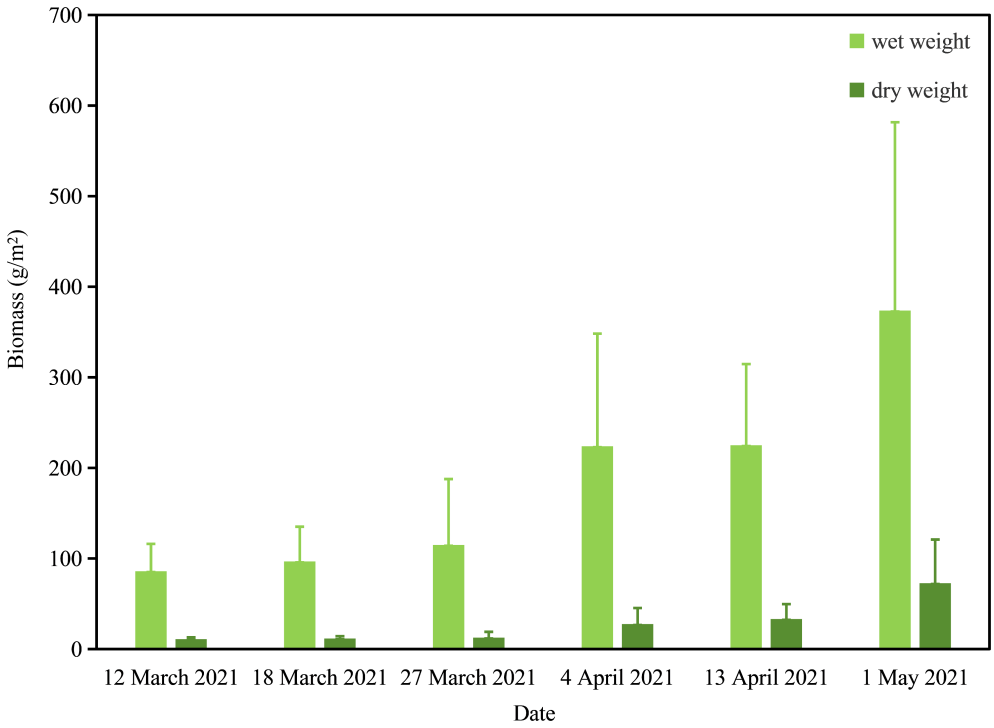

FIGURE 7
The wet and dry weights of attached *U. prolifera* in the NETF from March to May 2021.

this temperature range (Xiao et al., 2016). In the Northern Hemisphere, the SSTs of the NETF in March, April, and May ranged from 9.5°C to 13.4°C, 12.5°C to 17.2°C, and 17.1°C to 21.3°C, respectively. The monthly average SST in March, April, and May measured at about 10.98°C, 14.68°C, and 19.60°C, respectively. Previous studies have indicated that *U. prolifera*'s daily growth rate was highest at temperatures between 15°C and 25°C. The SST in April and May within the NETF was evidently conducive for the growth and biomass accumulation of *U. prolifera* (Figure 7; Figure 8A). In comparison with March and April, the temperature conditions in May were more favorable for *U. prolifera*'s growth. During the monitoring period, the WW and DW of *U. prolifera* per unit area within the NETF reached their peak levels in May (Figure 7).

The annual SSS in the NETF ranged from 12 psu to 27.5 psu (Figure 8B). Despite significant seasonal fluctuations, *U. prolifera* can survive year-round within this range of salinity (Rybak, 2018). The ranges of SSS in the NETF during March, April, and May were 21.8 psu to 24.7 psu, 21.9 psu to 22.1 psu, and 13.9 psu to 19.9 psu, respectively. The monthly average SSSs in March, April, and May were calculated as about 22.87 psu, 22.01 psu, and 16.30 psu, respectively. The SSS of the NETF provides a suitable environment for the growth of *U. prolifera* (Xiao et al., 2016; Li et al., 2017).

The pH at the NETF ranged from 7.79 to 8.12 (Figure 9A) between May 2017 and March 2023, with a monthly average of 7.99, indicating suitable conditions for the growth of *U. prolifera* (Li et al., 2017). The $C_{(Dissolved\ Oxygen)}$ in the NETF ranged from 5.58 mg/L to 8.86 mg/L (Figure 9B), with an average value of 7.63 mg/L. The $C_{(Chemical\ Oxygen\ Demand)}$ ranged from 1.18 mg/L to 3.66 mg/L (Figure 9C), averaging at 2.42 mg/L. The $C_{(Inorganic\ Nitrogen)}$ ranged from 0.377 mg/L to 1.527 mg/L (Figure 9D), with an average value of 0.98 mg/L. The $C_{(Active\ phosphate)}$ ranged from 0.017 mg/L to 0.064 mg/L (Figure 9E), with an average value of 0.04 mg/L, indicating a general declining trend (Figure 9E). The $C_{(Petroleum)}$ ranged from 0 mg/L to 0.051 mg/L (Figure 9F), with an average value of 0.02 mg/L, showing an initial increase followed by a decrease (Figure 9F). Based on these six monitoring indexes, the single factor method identified the seawater quality of the NETF as predominantly Worse than Grade IV (Figure 10). With only Grade III and Grade IV identified in August 2022 and October of 2022 respectively, the seawater quality has been persistently poor for an extended period.

From May 2017 to March 2023, the NETF exhibited significant eutrophication, with E values ranging from about 3.38 to 58.82 and an average of about 25.04. Only in August 2022 was the E value<9 (about 3.38), indicating medium eutrophication. During all other monitoring periods, the E values exceeded 9, indicating heavy eutrophication. For instance, in April 2021, the E value of the NETF was recorded at about 21.26. The presence of seawaters with heavy or medium eutrophication (Figures 9, 10) provided ample nutritional support for *U. prolifera* in the intertidal zone (Figures 2, 3), resulting in its high biomass per unit area within the NETF (Figure 7).

4 Discussion

4.1 Implications of *Ulva* morphology and biodiversity in the NETF

Macroalgae plays a crucial role as habitat-forming organisms in coastal ecosystems of temperate and subtropical regions (Graba-Landry et al., 2018). The genus *Ulva* L. (Ulvales) is widely

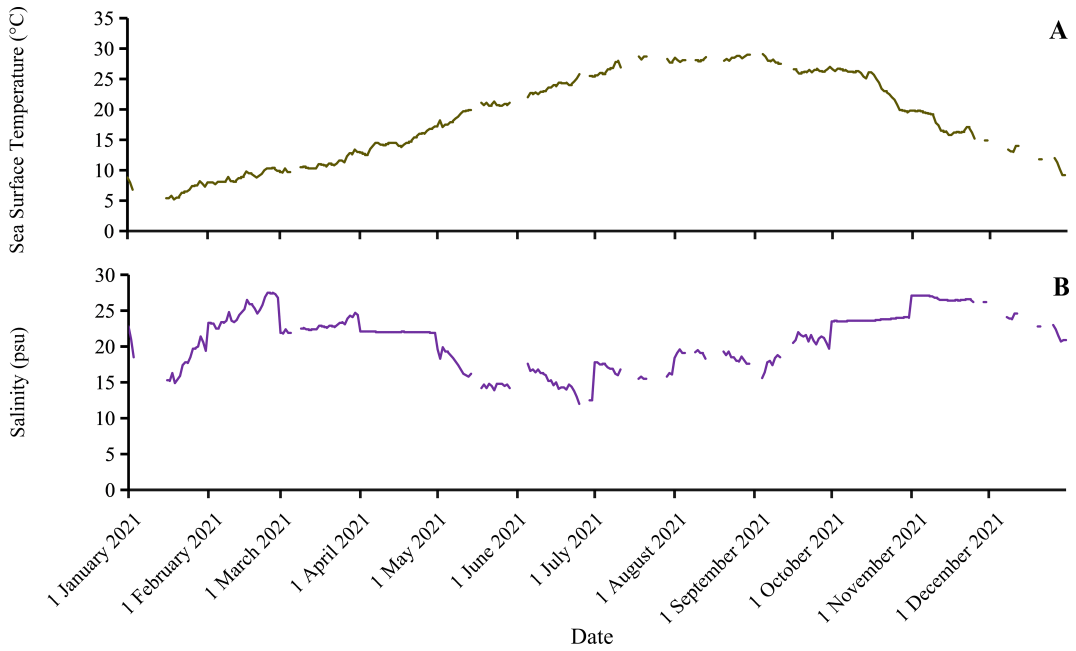

FIGURE 8
Data of sea surface temperature **(A)** and salinity **(B)** in the sea area of the NETF.

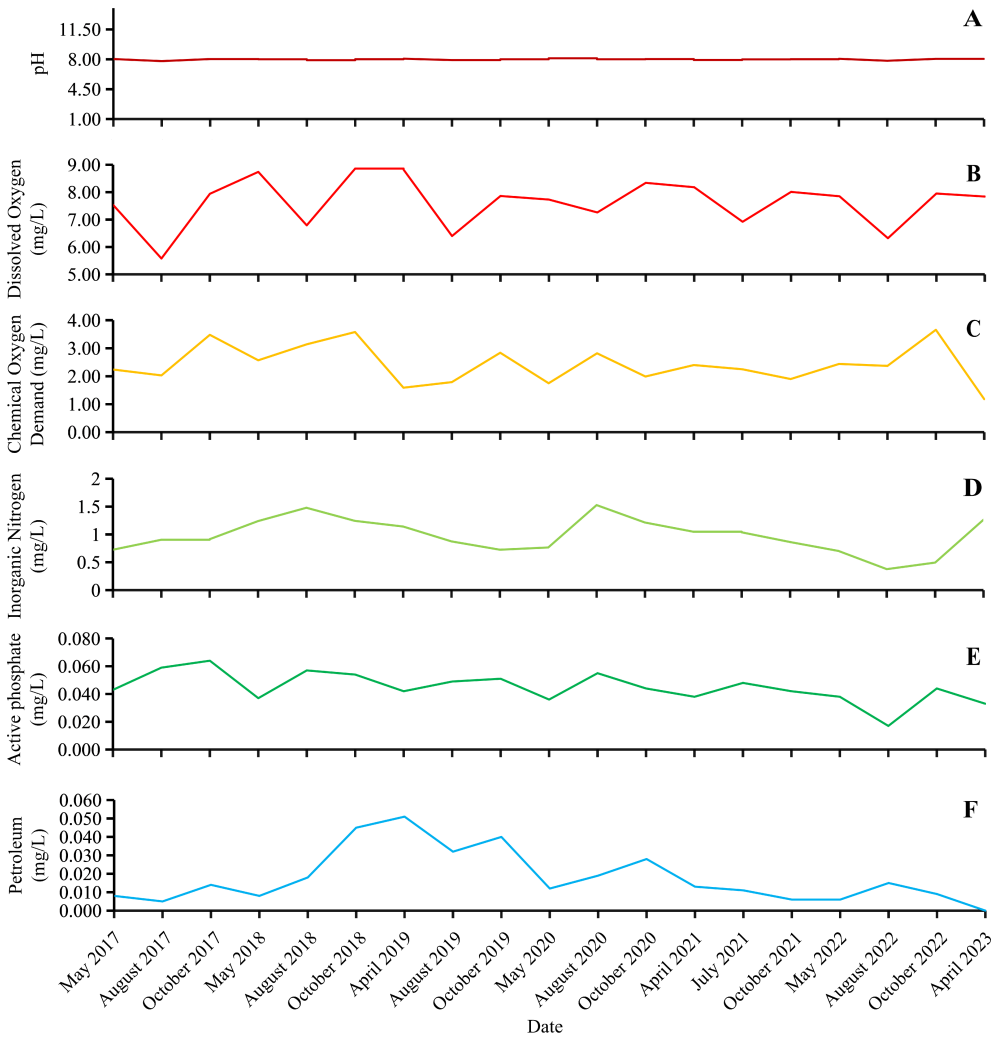

FIGURE 9
Data of pH **(A)**, $C_{(Dissolved\ Oxygen)}$ **(B)**, $C_{(Chemical\ Oxygen\ Demand)}$ **(C)**, $C_{(Inorganic\ Nitrogen)}$ **(D)**, $C_{(Active\ phosphate)}$ **(E)**, and $C_{(Petroleum)}$ **(F)** in the sea area of the NETF.

distributed worldwide, primarily inhabiting estuaries, intertidal zones, and other coastal areas. Species such as *Ulva pertusa* (Chen et al., 2022), *Ulva lactuca* (Human et al., 2016) and *U. prolifera* (Li et al., 2024a; Sun et al., 2022b), *Ulva rigida* (Dartois et al., 2021), and other macroalgae are commonly found in intertidal zones. The NETF is an important wetland in the Yangtze River Estuary area, rich in biological resources. However, the morphology of *U. prolifera* collected in this study appears to be atypical (Figure 4A), possibly influenced by unique environmental factors present on the intertidal mudflat. The morphology of *Ulva* spp. can be influenced by various factors including thallus age, lifestyle (Loughnane et al., 2008; Wolf et al., 2012), microbiology (Wichard, 2015; Chen, 2018; Alsufyani et al., 2020), environmental temperature (Gao et al., 2016), light intensity (Wu et al., 2022), salinity (Gao et al., 2016), nutrient concentration (Blomster et al., 2002), among others. Compared with the floating populations of *U. prolifera* from the green tide in the southern Yellow Sea, the blades of the attached *U. prolifera* collected in this study exhibited greater width and fewer secondary branches. The observed disparity in branching phenotypes may be attributed to the two distinct ecotypes of *U. prolifera* (i.e., attached and floating ecotypes) (Ma et al., 2020).

Environmental factors and volatility in the intertidal zone of the NETF (Figure 8B) may have also contributed to the differences in the morphology of *U. prolifera*. It has been found that at a suitable temperature and higher salinity (from 20 psu to 30 psu), the branches of *U. prolifera* were reduced, and the thalli were wider and well-dispersed (Gao et al., 2016). During the investigation, the salinity of NETF was around 22. The tendency for *U. prolifera* thalli to be leaf-like was similarly observed (Figure 4A). Such morphology facilitates *U. prolifera* to reduce shading, obtain sufficient light and nutrients to maintain high growth rates (Gao et al., 2016), and dominate in complex intertidal habitats. Due to this plasticity in morphological traits (Wichard et al., 2015; Gao et al., 2016), some *Ulva* spp. can often adapt to the variable and harsh environments of the intertidal zone (Innes, 1988).

The morphological variations of the green macroalgae in the genus *Ulva* present significant challenges for traditional morphological identification (Hayden et al., 2003). DNA barcoding

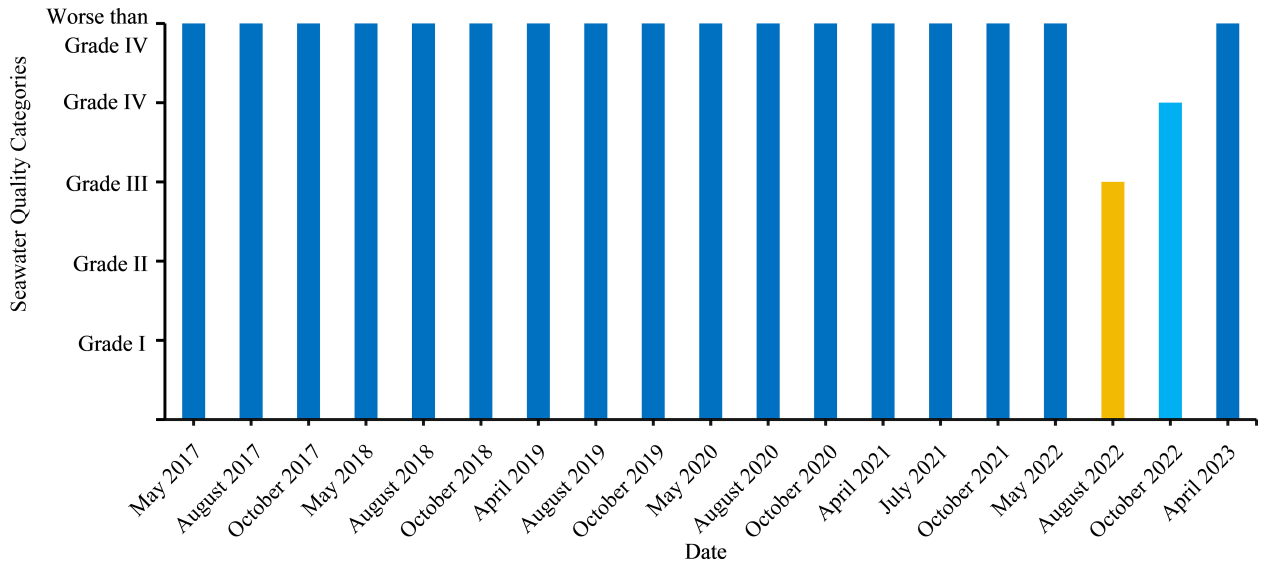

FIGURE 10
Data of seawater quality categories in the sea area of the NETF.

technology has been recognized as an effective approach to the identification of green macroalgae (Du et al., 2014). The combination of ITS + 5S primers identified all the green macroalgae collected in this study as *U. prolifera*, indicating that a single dominant species was prevalent among the green macroalgae distributed in the NETF during spring 2021. Consequently, there was a low biodiversity of green macroalgae in the NETF and relatively simple trophic pathways within this intertidal environment (Riera et al., 2004). Furthermore, being an artificial habitat, the NETF may exhibit lower ecosystem resilience and stability.

4.2 Potential factors influencing the distribution of green macroalgae in the NETF

Due to the significant longitudinal gradient in environmental and biological factors within the intertidal zone, spatial zonation is observed in the population of macroalgae, resulting in low species diversity (Park and Hwang, 2011; Choi and Kim, 2004). For instance, *Ulva* spp. are typically dominant in temperate and subtropical intertidal mudflats (Park and Hwang, 2011; Sun et al., 2022b). The distribution of macroalgae in the intertidal mudflat will be influenced by a variety of environmental factors, including biological and physical elements. For instance, *Ulva* spp. are impacted by interspecific competition and predator behavior (Park and Hwang, 2011), with *Ampithoe* spp. exhibiting high abundance in the NETF (Li et al., 2023a) and playing a crucial role in controlling the biomass of *U. prolifera*. Physical factors encompass irradiance, temperature, nutrient level, tidal heights (Choi and Kim, 2004), and currents (de Guimaraens and Coutinho, 2000). Typhoons, for example, are frequent in the East China Sea, and their waves have adverse effects on the stability of intertidal zones in the NETF (Wang JY. et al., 2022; Chi et al., 2023; Li et al., 2024b). Original intertidal habitats may be destroyed and restoring biodiversity and siltation will necessitate prolonged biogeochemical processes. Furthermore, sediment dynamics and size affect the spatial distribution of *U. prolifera* (Park and Hwang, 2011). Park and Hwang (2011) identified a clear relationship between the density of *U. prolifera* and the ratio of sand to silt in the intertidal flats. Laboratory experiments also demonstrated a significant association between micropropagule survival and sandy sediment particle size.

The sediments of the NETF are primarily sourced from the Yangtze River, consisting mainly of silty sediment with a minor presence of clay. The clay minerals include illite, chlorite, and kaolinite (Yan et al., 2011; Xia et al., 2022b). Further investigation is needed to understand the specific factors influencing the distribution of *U. prolifera* on silty sediment. The construction of dykes and concrete breakwaters in the NETF has a wave-abatement effect, creating relatively calm seawater along the shoreline that provides a suitable habitat for *U. prolifera* and facilitates attachment and germination of its micropropagules. In addition to physical factors, it was observed that *U. prolifera* can persist and grow on decaying higher plants and their seedling roots (Figure 3C). Interestingly, *U. prolifera* exhibited limited distribution in the intertidal zone, characterized by dense growth of higher plants, indicating that the distribution of higher intertidal vegetation influences the spatial pattern of *U. prolifera*. This may be attributed to ecological niche differentiation resulting from interspecific competition, and further investigation into the distribution relationships and mechanisms between intertidal macroalgae and higher vegetation is warranted.

Eutrophication and global warming are significant factors influencing the distribution of macroalgae (Liu et al., 2021b; Qi et al., 2022). The East China Sea has been profoundly impacted by global climate change (Zhang WX. et al., 2022), particularly through an increasing trend in SST, which has implications for the stability of

the marine ecosystem. The increasing SST in China is mainly due to the change in the ocean circulation over the continental shelf caused by local atmospheric forcing (Sasaki and Umeda, 2021). Currently, the response of SST to global warming in China's offshore waters exceeds the global average increase in SST. Moreover, there has been a recent acceleration in the rate of warming over the past decade (Tang et al., 2020). Eutrophication is prevalent in the NETF sea area with heavy or moderate eutrophication observed (Figures 9, 10), and runoff from the Yangtze River significantly contributes to nutrient fluxes within both estuarine and offshore areas (Sun et al., 2023). Within the study area, numerous rivers flow into the East China Sea, discharging nutrient-rich water and creating favorable conditions for the growth and reproduction of macroalgae (*U. prolifera*) in the estuarine intertidal zone. The suitable marine climatic conditions in the mid-latitude region are the "cradle" and "hotbed" for the growth of *U. prolifera*, and environmental factors such as SST (Figure 8A), SSS (Figure 8B), and pH (Figure 9A) in the NETF satisfy the growth conditions of *U. prolifera* (Lin et al., 2011; Ichihara et al., 2013; Cui et al., 2015; Xiao et al., 2016; Rybak, 2018; Zhao et al., 2021). Therefore, the biomass of *U. prolifera* in the NETF has begun to take shape, as indicated by Figures 2, 3, 7. Gradually forming small-scale algal mats have been observed in the intertidal zone (Figures 2, 3).

Reclamation activities in Shanghai since 1953 have contributed to a roughly 20% expansion of the urban area (Wei et al., 2015). Over the past century, the NETF has undergone several projects aimed at promoting silt accumulation (Figure 1). For instance, from 2003 to 2006, approximately 133.3 km^2 of land was reclaimed in Shanghai, leading to an expansion of the coastline both eastward and southward through artificial construction (Figure 1), resulting in the destruction and eventual disappearance of the original intertidal habitat (Zhang, 2012). Subsequently, following natural succession and artificial ecological restoration, *P. australis*, *S. alterniflora*, *S. mariqueter* as well as small amounts of *Suaeda salsa* and *Suaeda glauca* were observed on the newly formed tidal flat (Zhao et al., 2024). In conjunction with the establishment of the Lin-gang Special Area of China (Shanghai) Pilot Free Trade Zone in 2019, there has been a significant alteration in the land-use pattern of the NETF and its environs, resulting from substantial anthropogenic disturbances. Commencing from March 2021 to May 2022, a new phase of slope renovation, roughening, and beach preservation activities was initiated on the outer slopes of the sea ponds at the NETF (Figure 11). Subsequently, in July 2022, the Shanghai Lin-gang Coastal Marine Ecological Protection and Restoration Project was officially inaugurated (Figure 11). Since 2021, researchers have encountered challenges conducting cyclical marine scientific research within the NETF due to ongoing engineering construction projects within this area. In particular, since June of 2021, the habitats in the sample area have been impacted by coastal engineering construction (Figure 11). Although there is still sporadic distribution of attached *U. prolifera* in the vicinity of the sample area, conducting standardized scientific research has become challenging. Once the marine ecological protection and restoration project (artificial modification of the intertidal zone) is completed and the NETF habitat has stabilized, it will be feasible to study *Ulva* spp. distribution in the NETF as well as species succession, aligning with natural evolutionary patterns. It is foreseeable that alterations to the shoreline may lead to changes in waves, currents, and a variety of environmental factors on the tidal flats, including sediment levels, nutrient concentrations, tidal heights, and salinity. Additionally, the ecological restoration project has the potential to artificially drive the succession of plant and animal communities in the NETF. These large-scale coastal projects have the capacity to artificially modify coastal habitats and promote biotic succession; therefore, further investigation into their potential effects on macroalgal distribution in the NETF is warranted.

4.3 The developmental history and ecological risks of *Ulva* in the NEFT

The invasion of green seaweed in intertidal salt marsh areas seems to have become a common phenomenon in recent years (Grimes et al., 2018; Nelson et al., 2021; Woodhouse and Zuccarello, 2023; Xia et al., 2023a, b). Similar to other relevant studies, the process of "establishment of micropropagules → establishment of *Ulva* populations → succession of *Ulva* species → localized outbreak of dominant species" by macroalgae in the intertidal zone is frequently overlooked. It is only when *Ulva* reaches a certain threshold of ecological risk (Lu et al., 2022; Hu et al., 2022) that it attracts significant attention from local residents, tourists, researchers, and governmental institutions.

Reflecting on the historical progression of green macroalgae occurrence and development in the NETF, we can delineate the following events: In March 2015, researchers cultivating intertidal vascular plants at the NETF observed a limited presence of green macroalgae in the intertidal zone. Subsequent identification revealed these attached green algae to be *Ulva flexuosa*, as described by Professor Peimin He from the College of Oceanography and Ecological Science at Shanghai Ocean University. In March 2019, during a study on *S. mariqueter* meadows coverage, researchers noted distinct changes in the morphology of attached green algae at the NETF and an expanded distribution range of these macroalgae. The green macroalgae attached to the detrital matrix of intertidal withered plants were discovered by Dr. Mingxuan Wu from the Royal Netherlands Institute for Sea Research (NIOZ). Upon identification, it was found that all the attached green algae present that year were *U. prolifera*, with no trace of *U. flexuosa*. It was not until 2021 that a localized outbreak of attached algal mats emerged in the intertidal zone of the NETF (Figures 2, 3). This outbreak featured *U. prolifera* (Figures 4-6), capturing our attention and concern. Sample collection was temporarily suspended from the second half of 2021 to the first half of 2024, as a result of beach closures and the impact of the COVID-19 pandemic. Nevertheless, this study provides background data before the green tide outbreak, which is often lacking in other sea areas where basic investigations are only carried out after such an event occurs. This offers a new perspective on the emergence and progression of green tide, as well as the critical considerations in implementing artificial construction projects in the intertidal zone.

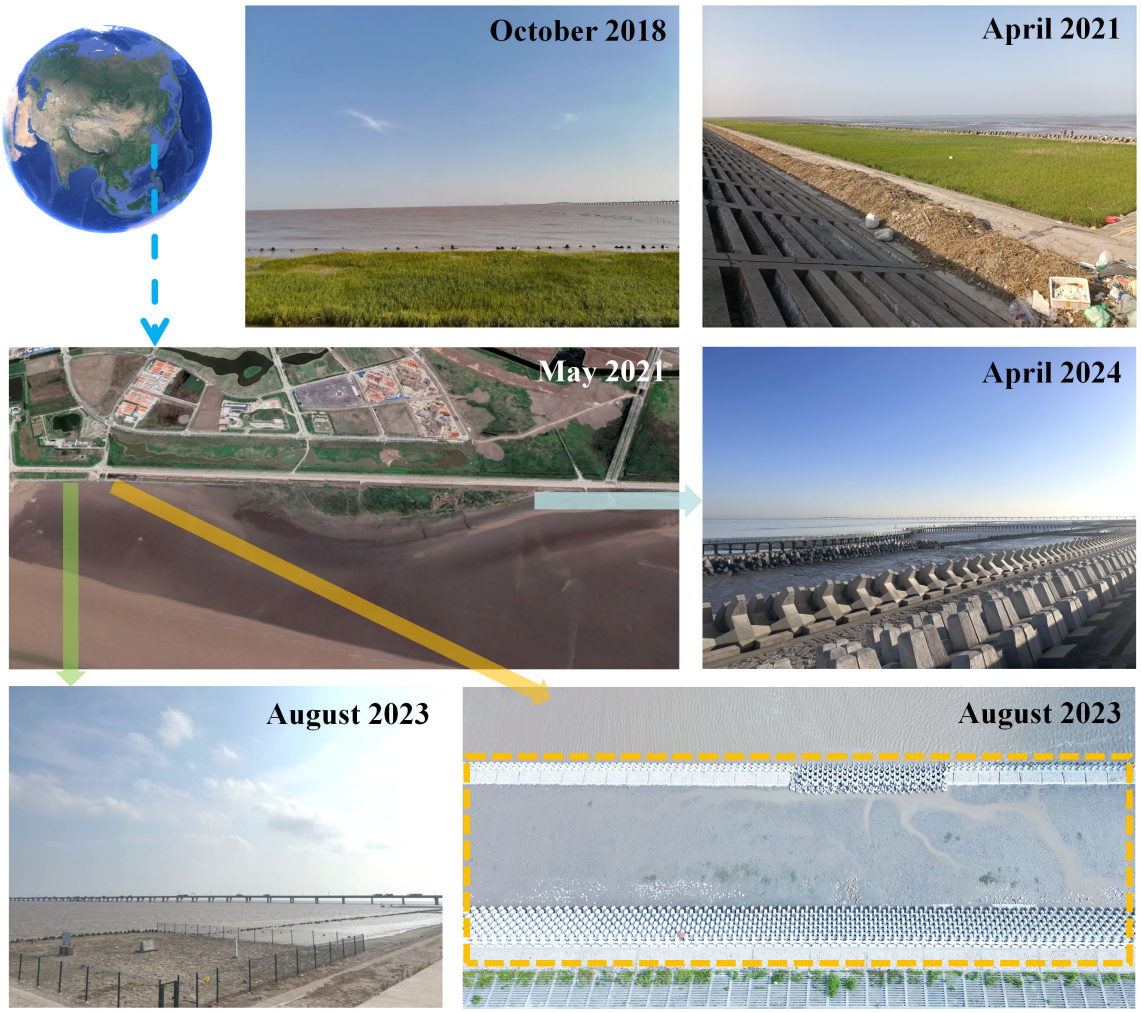

FIGURE 11
Schematic illustration of a section of the Nanhui-east-tidal-flat depicting the destruction of intertidal habitat before and after June 2021. Before June 2021, the yellow dashed area was rich in *Phragmites australis*, *Spartina alterniflora*, *Scirpus mariqueter*, and *Ulva prolifera* (also visible in Figure 2). Subsequent to the commencement of the Shanghai Lin-gang Coastal Ecological Protection and Restoration Project, the original intertidal vegetation in the yellow dashed area was significantly diminished, with only a small amount of *U. prolifera* remaining attached in certain regions.

Six potential sources of *Ulva* macroalgae or micropropagules in the intertidal zone of the NETF are proposed. Firstly, micropropagules may be released by attached *Ulva* macroalgae in the seaward channels of Shanghai. Secondly, from 2010 to 2013, researchers cultivated *Porphyra haitanensis* in the NETF (Huang et al., 2022). Meanwhile, filamentous thallus seedlings of *P. haitanensis* were cultivated in Xiangshan County, Ningbo City, Zhejiang Province. During the cultivation of filamentous thallus seedlings and net attachment stages of *Porphyra* cultivation, micropropagules of *Ulva* (Liu et al., 2013b) present in the local seawater of Xiangshan Bay often co-attached to the net curtains as harmful species. Subsequently, *Porphyra* net curtains were transported to the NETF for cultivation where *Ulva* micropropagules promptly developed into *Ulva* macroalgae. Thirdly, coastal areas of the Yellow Sea and East China Sea have long been impacted by large-scale green tide events (Hu et al., 2010; Xing and Hu, 2016; Min et al., 2019; Li et al., 2022; Cao et al., 2023; Luo et al., 2023; Qu et al., 2023; Xu et al., 2023; Feng et al., 2024). *Ulva* algae, which enters the East China Sea beyond the Yangtze River Estuary, releases micropropagules (Zhang et al., 2015). These micropropagules, along with *Ulva* macroalgae, may be transported into the NETF area by ocean currents and establish attachment. Fourthly, the natural distribution of *Ulva* macroalgae and micropropagules occurs in bays and islands of the East China Sea (Liu et al., 2013b; Tong et al., 2022), and these micropropagules may enter the NETF area via ocean currents. Fifthly, algae attached to floating marine debris and other carriers (Turner and Williams, 2021) may also enter the area and eventually establish attachment. Sixthly, Yangshan Port, the world's largest container port by throughput, is located approximately 15 nautical miles from the NETF. The vicinity of the NETF often witnesses the anchoring of ocean-going vessels, and the likelihood is high that ocean-going vessels' ballast water and sediments carry *Ulva* micropropagules (Flagella et al., 2007, 2010).

In any case, *Ulva* has already established attachment and formed localized algal mats in the NETF area. When *Ulva*

becomes the dominant species in the intertidal zone, it often indicates severe eutrophication and deteriorating ecological conditions in the local marine environment. The preliminary survey in 2024 found that algal mats were still present in the NETF (station F-H in this study). With the Shanghai Lin-gang Coastal Marine Ecological Conservation and Restoration Project nearing completion, following restoration and stabilization of the habitat in the NETF area, *Ulva* and its micropropagules will firmly attach, germinate, and continue to form extensive algal mats, and this phenomenon warrants attention from researchers. Research suggests that phenomena similar to large-scale harmful algal blooms in the Yellow Sea are unlikely to decrease in the short term and are expected to intensify in the future (Qi et al., 2022). As an "opportunistic" algal species (Xu et al., 2012; Zhao et al., 2018), the dominance of *Ulva* as a single species often signals the beginning of a localized and large-scale algal bloom outbreak. These blooms can exert profound adverse impacts on sandy or muddy intertidal habitats (Lyons et al., 2014), potentially influencing their biodiversity and ecosystem stability.

4.4 Current monitoring of green tide macroalgae in the NETF area primarily relies on field surveys

Concerns regarding the potential for a large-scale green tide in the NETF were not unfounded. These concerns materialized in mid-July 2023 when a small-scale green tide was detected near the East Sea Bridge (Figure 12). The emergency was confirmed by releasing a drone to patrol the area of floating macroalgae covering approximately 1 km^2 on July 13, 2023. However, the scale was relatively minor, with the floating macroalgae exhibiting a scattered distribution, and the algal coverage was low, being less than 0.01%. The biomass of these macroalgae, characterized by their small-scale and sporadic distribution, poses a challenge for conventional satellite remote sensing techniques to effectively monitor. Furthermore, this small-scale green tide did not continue to expand, and its impact on the local waters was relatively small, but it is worth raising the attention of researchers. The blooming macroalgae collected in the field (Figure 12) were identified morphologically and molecularly, and the only dominant species in the green tide was found to be *U. prolifera*. The researchers discovered the green tide outbreak approximately 5 nautical miles from NETF, situated in Hangzhou Bay, East China Sea. The sea area is under the jurisdiction of Shanghai Pudong New Area and is adjacent to the sea area of Shengsi County, Zhoushan City, Zhejiang Province. The available evidence is not sufficient to confirm that the small-scale floating *U. prolifera* in the Shanghai coastal area in mid-July 2023 was from the NETF, which will require a future long-period survey of green macroalgal distribution and shedding throughout Hangzhou Bay. It is hypothesized that it may be that the construction of the NETF Coastal Marine Ecological Conservation and Restoration Project in late June to early July 2023 resulted in releasing of attached *U. prolifera* and the formation of a small-scale green tide, or it may have been formed by natural shedding of sporadically distributed macroalgae in this area, which will require large-scale monitoring and traceability analyses for an extended period.

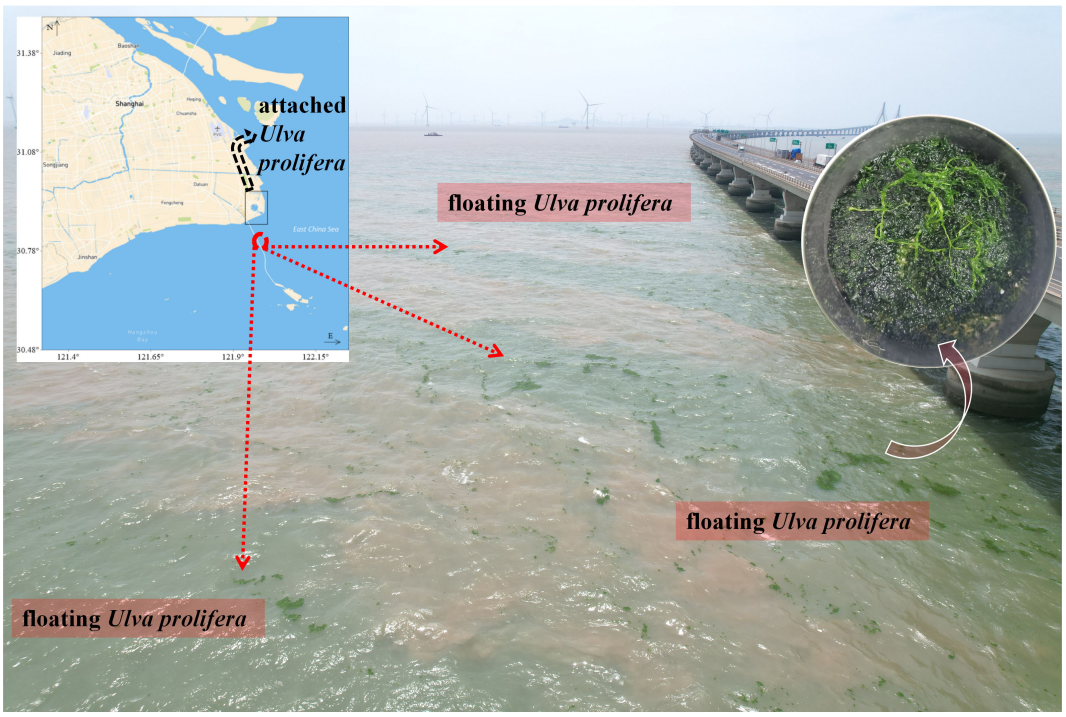

FIGURE 12
A small-scale green tide disaster occurred for the first time in the sea area near the Nanhui-east-tidal-flat in mid-July 2023.

Regarding the monitoring of algal distribution, the current mainstream methods include field surveys (on-site monitoring and drone patrol monitoring) and satellite remote sensing monitoring (Xia et al., 2024a). Among them, satellite remote sensing monitoring technology has a very broad application space during the outbreak of green tides (An et al., 2022; Zhang S. et al., 2022; Hu et al., 2023; Hu, 2024; Qi et al., 2023; Xing et al., 2023; Yu et al., 2023). The specific principle is based on the atmospherically corrected satellite surface reflectance signals, analyzing the spectral characteristics of green tide macroalgae and background water bodies, and using different remote sensing index algorithms (common remote sensing indices include Normalized Difference Vegetation Index, Phytoplankton Floating Algae Index, Difference Vegetation Index, Normalized Difference Algae Index, etc.) to carry out the identification of green tide macroalgae. However, it must be considered that satellite remote sensing monitoring technology is not always fully effective. On the one hand, the performance of different algorithms is easily affected by various observational conditions, including seawater background (turbid and clear seawater) and external observational conditions (such as cloud cover, solar flares, and observational geometry) (Hu et al., 2023). On the other hand, existing research and experience have found that satellite remote sensing monitoring technology is more suitable for monitoring large-scale harmful algal bloom phenomena, such as large-scale outbreaks of golden tides and green tides (Smetacek and Zingone, 2013; Xing and Hu, 2016; Wang et al., 2019; Liu et al., 2021b; Hu et al., 2023). Taking green tides as an example, the annual maximum coverage area of green tides in the Yellow Sea is tens to thousands of square kilometers (Sun et al., 2022a), and conventional satellite remote sensing monitoring technology typically can easily detect the presence of green tide macroalgae only in the middle and late stages of the outbreak (when the distribution area of algae is slightly larger and the coverage is higher); however, in the early and terminal stages of the outbreak, often due to the small distribution area of algae (or even though the distribution area is large, but the algae distribution is discontinuous) and low coverage, conventional satellite remote sensing monitoring technology often fails to detect the distribution of green tide macroalgae in a timely manner; this also leads to the fact that under current technological conditions, field surveys can effectively make up for the shortcomings of conventional satellite remote sensing monitoring technology (Song et al., 2022; Wang et al., 2023; Xia et al., 2024a), and can provide real-time information on algal species and the distribution status of algae, aiding in the early prevention and control of green tides (Sun et al., 2022a; Xia et al., 2024a).

Another case in point is the continuous outbreak of green tides in Qinhuangdao since 2015, which has also attracted the attention of researchers. Conventional satellite remote sensing monitoring technology also finds it difficult to detect green tide macroalgae in the floating stage in the Qinhuangdao Sea area; it is often only when a large amount of algal biomass is driven by wind and ocean currents and accumulates over a large area on the beach that visually striking algal mats (Xiao et al., 2021) are formed, with the scale of the floating green tide macroalgae being relatively limited before accumulating in the intertidal flats. Subsequent researchers mainly used field surveys and other methods to gradually determine that the main source of Qinhuangdao green tide macroalgae comes from the local sea area's subtidal seaweed fields (Han et al., 2019; Song et al., 2019a, b; Han et al., 2022a, b). The small-scale floating green tide macroalgae discovered by this study in mid-July 2023 is far smaller than the scale of the Yellow Sea green tide outbreak and the Qinhuangdao green tide outbreak; the Ministry of Natural Resources attempted to use conventional satellite data (such as MODIS series satellites, Landsat series satellites, Haiyang series satellites, etc.) to detect the small-scale green tide in the NETF sea area, but due to the small distribution area of algae, extremely low coverage, and the limited resolution of conventional satellite remote sensing monitoring technology, the small-scale green tide outbreak event was not successfully detected. Utilizing advanced ultra-high-resolution satellite remote sensing monitoring technology could potentially reveal extremely small-scale floating macroalgae. For instance, Zhang S. et al. (2022) successfully identified small-scale *Sargassum* mats accumulating on Miami Beach and Cancun Beach using 3-m resolution PlanetScope/Dove data. Nevertheless, this approach is limited by user access permissions, and the procurement cost of ultra-high-resolution satellite remote sensing imagery is often prohibitively expensive. When contemplating the initiation of regular monitoring and species diversity research at a low cost, field surveys constitute a significant approach for the early monitoring and warning of green tides.

At the same time, the conventional satellite remote sensing identification of intertidal attached green tide macroalgae has always been a challenge, and few studies have been able to successfully apply satellite remote sensing monitoring technology to identify small-scale attached algal mats in intertidal areas. Xing et al. (2023) applied satellite remote sensing and deep learning technology to identify large-scale attached green tide macroalgae in intertidal areas, and the successful conduct of this study benefited from three important conditions: first, Xing et al. (2023)' study area 2.07 km^2, the length, and width of the area are far greater than the resolution requirements of conventional satellite remote sensing monitoring technology; second, the area routinely experiences large-scale green tide outbreaks (the continuous coverage area of green tide algae is greater than 1 km^2), and there is an early research foundation on the main outbreak species and the preliminary distribution of algae; third, the intertidal area is dominated by the single dominant species *U. pertusa*, with no other higher plants, and only similar species distribution is conducive to satellite remote sensing monitoring. In this study, *U. prolifera* is distributed in the intertidal artificial habitat with a narrow strip feature (Figures 2B, C, 3B, 11), but the width of the habitat where *U. prolifera* is concentrated is about 28-31 meters; and within the area, green tide macroalgae and other higher plants are interwoven, with some higher plants are covered with *U. prolifera* (Figures 2B, 3C, D), the image resolution and species discrimination of existing conventional satellite remote sensing monitoring technology is difficult to effectively apply in this area. Unless advanced ultra-high-resolution satellite remote sensing monitoring technology is utilized (Zhang S. et al., 2022), it is unlikely to detect the small-scale algal mats present in the intertidal zone; considering the limited access to ultra-high-resolution satellite remote sensing imagery, the costly purchase of images, and the interference caused by the

numerous higher plants in the NETF area to the identification of algal distribution, the monitoring of green tide macroalgae in the NETF area currently relies on field surveys, as is the case with studies on other species in the NETF area (Wu et al., 2020, 2021; Wang MQ. et al., 2022; Gao et al., 2024; Li et al., 2024b; Zhao et al., 2024). Field surveys are a basic scientific research method based on on-site research (Song et al., 2019a, b; Liu et al., 2022; Li et al., 2023b; Xia et al., 2023b, c), which are suitable for the analysis of outbreak dominant species in the early stages of attached green tide macroalgae and biomass monitoring.

5 Conclusion

Based on morphological and molecular biological identification, researchers have confirmed that the green macroalgae along the coastline of the NETF from March 2021 to May were *U. prolifera*, characterized by wide blades, the ability to colonize a wide range of substrates in the intertidal zone, and obvious air bladders. The attached *U. prolifera* continued to grow, with the average biomass showing an increasing trend and reaching its peak on May 1st (within the accessible sampling period). Furthermore, environmental investigations suggested that high levels of eutrophication in the sea area as well as favorable environmental conditions contributed to the rapid proliferation of "opportunistic" *Ulva* in the NETF. Existing studies also demonstrate that the implementation of reclamation projects tends to exacerbate the outbreak of green tides (Kuang et al., 2024). In summary, anthropogenic disturbances, particularly continued reclamation activities, severely impact the NETF. It is crucial to maintain a balance between coastal resource development and marine ecological management given the high likelihood of future large-scale algal blooms in NETF; indeed, signs and preludes of a small-scale green tide were observed in July 2023, which requires further long-term monitoring and a set of disaster emergency management measures suitable for the local sea.

The difficulty in conducting large-scale monitoring lies in the substantial consumption of human, material, and financial resources, thus necessitating a case-by-case analysis. When studying attached green tide macroalgae and small-scale floating green tide macroalgae, field surveys are generally employed (Song et al., 2019a, b; Liu et al., 2022; Li et al., 2023b; Xia et al., 2023b, c); when the coverage area of attached green tide macroalgae is large and there are no higher plants or other growths in the habitat, satellite remote sensing monitoring technology can be attempted to confirm the distribution and coverage area of the attached green tide macroalgae (Xing et al., 2023); when tracing the origins or impact areas of large-scale floating green tide macroalgae, a combination of field surveys, micropropagules abundance studies, drift path numerical simulations, and satellite remote sensing monitoring are generally used (Huo et al., 2014; Zhang et al., 2015; Qi et al., 2016; Xing et al., 2019; Han et al., 2022a, b; Tong et al., 2022; Zhang S. et al., 2022; Hu et al., 2023; Xia et al., 2024b); when it comes to early warning and forecasting of large-scale green tide macroalgae floating paths, satellite remote sensing monitoring combined with field surveys is generally used (Sun et al., 2022a; Li et al., 2023c). This study focuses on the early distribution of attached green tide macroalgae in the NETF area, thus primarily conducting related research based on field survey methods; should the NETF area experience large-scale floating green tide macroalgae in the future (where the continuous coverage area of green tide macroalgae needs to be at least greater than 1 km^2), and if this leads to a significant marine ecological disaster, it would be very necessary to combine satellite remote sensing monitoring and other technologies to support the implementation of related early warning and prevention and control efforts.

Overall, the proliferation of extensive algal mats in the NETF area is a natural feedback mechanism in response to an imbalanced ecosystem. Similar to occurrences of *Ulva* outbreaks in other countries (Guidone and Thornber, 2013; Chavez-Sanchez et al., 2018), the growth and outbreak of *Ulva* demonstrate both periodicity and inevitability. The rapid expansion and outbreak of *Ulva* in China can be attributed to a favorable combination of factors, and it is not attributable to the species itself. The primary concern that needs to be addressed is the mitigation of nutrient enrichment in the marine environment (Liu et al., 2013a; Chavez-Sanchez et al., 2017; Lapointe et al., 2023). With China's rapid industrialization, future efforts to promote industrial modernization must be harmonized with ecological conservation. Effective management of pollution sources, including industrial, agricultural, and domestic wastewater discharge into rivers and seas, is essential, as well as initiatives for intensive phosphorus and nitrogen removal from sewage (Lapointe et al., 2023). Developed capitalist nations have dedicated decades to controlling algal blooms (He et al., 2019) and reducing nutrient enrichment in marine environments. Similarly, China faces a lengthy and challenging journey towards these objectives.

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 in the article/supplementary material.

Author contributions

JL: Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. ZX: Conceptualization, Resources, Writing – original draft. YZ: Conceptualization, Resources, Writing – original draft. JX: Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Writing – original draft. PH: Funding acquisition, Project administration, Supervision, Writing – review & editing.

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Conflict of interest

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

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A systematic review of fishing impacts on the trophic level of fish populations and assemblages in the Mediterranean Sea

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Fishing activities alter food web diversity and functioning. Trophic level (TL) has been used as an indicator to assess such impacts on populations and assemblages. We reviewed the scientific literature that examined the relationship between fishing and the trophic aspects of fish species and communities, by focussing on TL. We narrowed the research to the Mediterranean Sea, where fishing is an important economic income for some coastal human populations and might be jeopardised by overfishing and climate change. We collected information on the (i) geographical location; (ii) type of fisheries and (iii) the methodological approach. The 68 collected studies were geographically skewed towards the Western Mediterranean, Adriatic Sea and around Greece. Among the 45 modelling studies, 41 reported TLs for communities or catches. For the field studies, only 6 estimated TLs of species and used stable isotope analysis. Most modelling studies used data from other models, online databases or large-scale monitoring of commercial catches and research surveys, whereas the field studies collected fish locally. Only 6 field and 5 modelling studies used fishing bans or the fully protected zone of marine protected areas as no-fishing control. In these studies, TL values showed different patterns of response to fishing, probably because of differences in environmental factors. Interestingly, recent modelling studies used predictions from the model to explore the impact of different fishing pressure within global change scenarios. The use of trophodynamic modelling is powerful to describe large scale impacts and infer future scenarios, but the *in situ* approach, the use of stable isotopes and spatial comparisons among areas of different fishing pressure, such as no-take zones in MPA could add insights into local variations of fish TLs in response to perturbations, which might be important to refine the outcomes of the models.

KEYWORDS

trophic position, trophic interactions, trophic cascade, fishery, foodweb, Mediterranean Sea

1 Introduction

The impact of fishing activities on marine communities, food webs and seafood supply has been of increasing concern for the last 3 decades (Pauly et al., 1998; Corrales et al., 2015). Fishing may often target large, slow-growing adult fishes that occupy high trophic levels (Farrugio et al., 1993; Watson et al., 2013). When these species become less available and overfished, fishing intensifies the capturing of fishes occupying lower trophic levels; i.e. the so-called 'fishing down food webs' (Pauly et al., 1998; Andersen and Pedersen, 2010; Tremblay-Boyer et al., 2011). At an ecosystem level, the removal of high-level predators triggers trophic cascades, affects the biomass, feeding behaviour and diet of intermediate consumers (Guest et al., 2004), thereby altering the structure of the food web (e.g. Libralato et al., 2010; Fry and Davis, 2015; Cardona et al., 2022). This may lead to potential regime shifts (Möllmann et al., 2008; Rocha et al., 2015) and ultimately to the loss of ecosystem functions (Lotze et al., 2006, 2011; Longo et al., 2015). In the Mediterranean Sea, fishing often targets intermediate consumers, which may still impact the low levels of the food web through trophic cascades. For instance, the fishing of the Sparidae *Diplodus* spp. led to the dramatic increase of sea urchins and the loss of macroalgal cover, causing the shift of subtidal rocky reefs from macroalgal-dominated substrates to coralline barrens (Sala et al., 1998; Guidetti, 2006). These effects may be exacerbated in the proximity of coastal marine areas, where human activities and human-driven climate change strongly impacts biodiversity and impairs important ecosystem services (Giakoumi et al., 2015; Halpern et al., 2019; Zhang et al., 2019; Simeoni et al., 2023).

Elton (1927) provided the fundamental concepts of food chains, trophic pyramids, and trophic levels to define food webs. Since then, estimating the trophic level (TL) occupied by populations and the overall community has become a fundamental component for understanding trophic structure. The TL of populations and of the overall community has been used for indicating the health of food webs affected by human activities (Stergiou and Karpouzi, 2001; Post, 2002; Karachle and Stergiou, 2017; Davis et al., 2019), including the impact of fishing (Shannon et al., 2014; Kytinou et al., 2020) and the status of fisheries (Colloca et al., 2017). At a population level, the TL can allow exploring changes in the diet of the target consumers and thus their role in energy transfer (Cardona et al., 2023), whereas at community level TL may indicate the reduction in biomass of predators and the shift of the food web to a dominance of low trophic level consumers (Pauly et al., 1998; Pauly and Palomares, 2005). The TL definition follows an energy-flow approach and it is based on discrete numbers identifying the place of an organism within a linear food chain (e.g. herbivore, omnivore or predator; Lindeman, 1942; Shannon et al., 2014). This place can be estimated by observing the feeding behaviour and analysing morphological traits related to feeding. However, in nature, what is empirically observed is continuous rather than discrete changes in TL, sometimes called trophic position (TP, Thompson et al., 2012).These changes in TL (or TP) can be estimated by analysing what an organism has ingested (e.g. stomach content analysis, SCA, Hyslop, 1980) or what has been assimilated over time, often using stable isotope analysis (SIA). In this case, SIA is based on the idea that the isotopic ratio of a consumer reflects that of its prey, by taking into account the known isotopic enrichment from the prey to the predator (e.g. fractionation; Post, 2002).

Despite the great progress achieved through the development of new tools and techniques, food web analysis still suffers from important knowledge gaps and limitations of the methodological approaches (Kytinou et al., 2020). Moreover, although fishing exploitation is considered a primary driver to affect food webs, important information such as diet, trophic level estimation, especially for omnivorous species, can be scant (Colloca et al., 2017; Kytinou et al., 2020).

This paper presents a systematic review of studies investigating the relationship between fishing activities and the trophic structure of fish populations and assemblages. It specifically focus on the use of trophic level (TL) as a tool to indicate both the state of fisheries and the healthy status of the fish community. Particular attention is given to the research conducted in the Mediterranean Sea, where fishing activities near the shore account for a large proportion of landings (Lloret et al., 2020, FAO, 2022) and fishing management needs to be improved for a long-term sustainability (Colloca et al., 2017). Understanding the trophic impacts of fishing might provide fundamental information to ecosystem-based management. Our review builds upon previous syntheses of food web dynamics and the impacts of fishing in the Mediterranean (Colloca et al., 2017; Kytinou et al., 2020), by integrating data on Mediterranean fisheries with ecological approaches that assess trophic interactions within coastal fish communities. In details, this systematic review aims to:

(1) Provide a synthesis of the geographical distribution of studies, the types of fishing practices, and the methodological approaches used to estimate TL or trophic position (TP)—which here are considered as an interchangeable terms (Ishikawa et al., 2024).

(2) Identify studies considering different levels of fishing pressure and compare the variations of trophic level or positions in relation to the fishing pressure.

2 Materials and methods

A systematic literature review was conducted following the PRISMA methodology (Moher et al., 2010). The research of relevant articles was performed using the ISI Web of Science core collection database on the 15th of December 2023. Web of Science allows for refined and reproducible searches using detailed filters (e.g., topic, journal, author). This database is also widely used in systematic reviews, making the search strategy reproducible and the methodology consistent with established review standards. We then used Google Scholar as a supplementary quality control to ensure that no relevant studies were missed in the primary search. We first used the string: "(fishing OR fishery OR fisheries) AND (Mediterranean) AND (foodweb OR "food web" OR "food-web" OR "trophic level" OR "trophic interaction" OR "trophic cascade" OR "trophic guild" OR "trophic group" OR "trophic position" OR

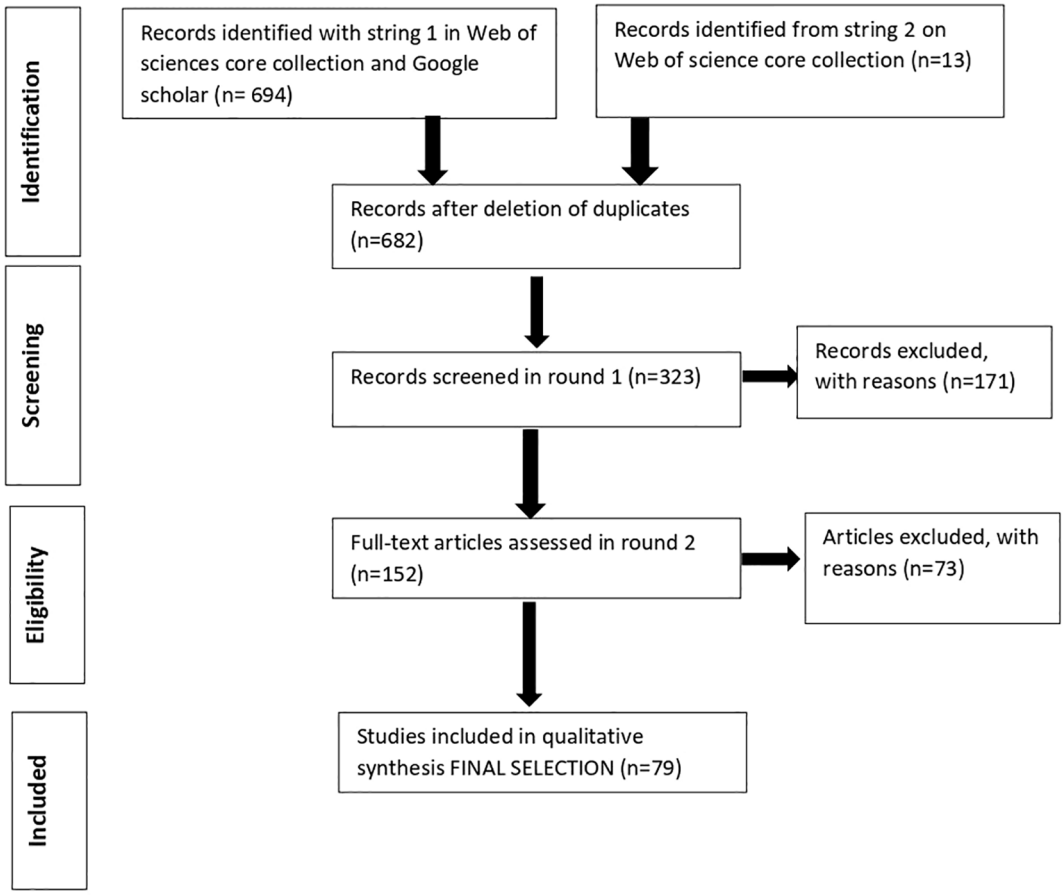

FIGURE 1
Flow diagram of the selection process used in this review (PRISMA methodology, modified from Moher et al., 2010).

"trophic length" OR "gut content") NOT (freshwater OR lake)", with no restriction on publication year.

Then, by performing the quality control on google scholar we found that the string had left uncovered articles concerning the evaluation of fishing impact on food webs in Marine Protected Areas, considered as no-fishing ground (fully protected zone). We thus added this part to the search, by completing with the following string: "(MPA" OR "marine reserve" OR "marine national park" OR "marine protected area")". To ensure scientific rigour and comparability across studies, we restricted our selection to peer-reviewed articles, thereby excluding grey literature. It was indeed difficult not only to access grey literature in an exhaustive manner but also to determine if the found papers could be representative of the study area.

We collected 682 papers, which were first screened through the title and then through the abstract (rounds 1 and 2 in Figure 1). We excluded reviews and research papers that focussed on bioaccumulation or targeted exclusively the pelagic food webs without considering the coastal environment. Specifically, for modelling studies, we selected articles mentioning at least one functional group described as coastal by the authors.

The 152 remaining papers were searched through Introduction, Materials and Methods and Results and retained if they explicitly considered the impacts of fishing activities on trophic aspects of coastal fish populations and assemblages, including trophic interactions, feeding and, of course, trophic level (Figure 1). The final dataset included 68 papers. We recorded: (i) the publication year, (ii) the geographical locations where the study was done (countries, geographical sub-area (GSA; FAO, 2022), (iii) the type of fisheries (trawl and purse seine fisheries, grouped under the label "industrial", small-scale fisheries (SSFs), and recreational fisheries), (iv) the methodological approach. We focussed on the type of study (Modelling, Field study), how trophic aspects were taken into account and how TL was estimated, including the biological scale of interest (population, community). We also reported the studies directly comparing areas that differed in fishing pressures; e.g. studies that included both areas under the impact of fishing and control areas such as Marine protected areas (MPA) or Fisheries restricted areas (FRA), where fishing activities were excluded or reduced. Of these, 9 studies that specifically evaluated trophic level (TL) were retained to assess how TL values vary between fished and non-fished areas. From those studies comparing fishing and no fishing areas, we extracted the TL values reported in the papers; e.g.

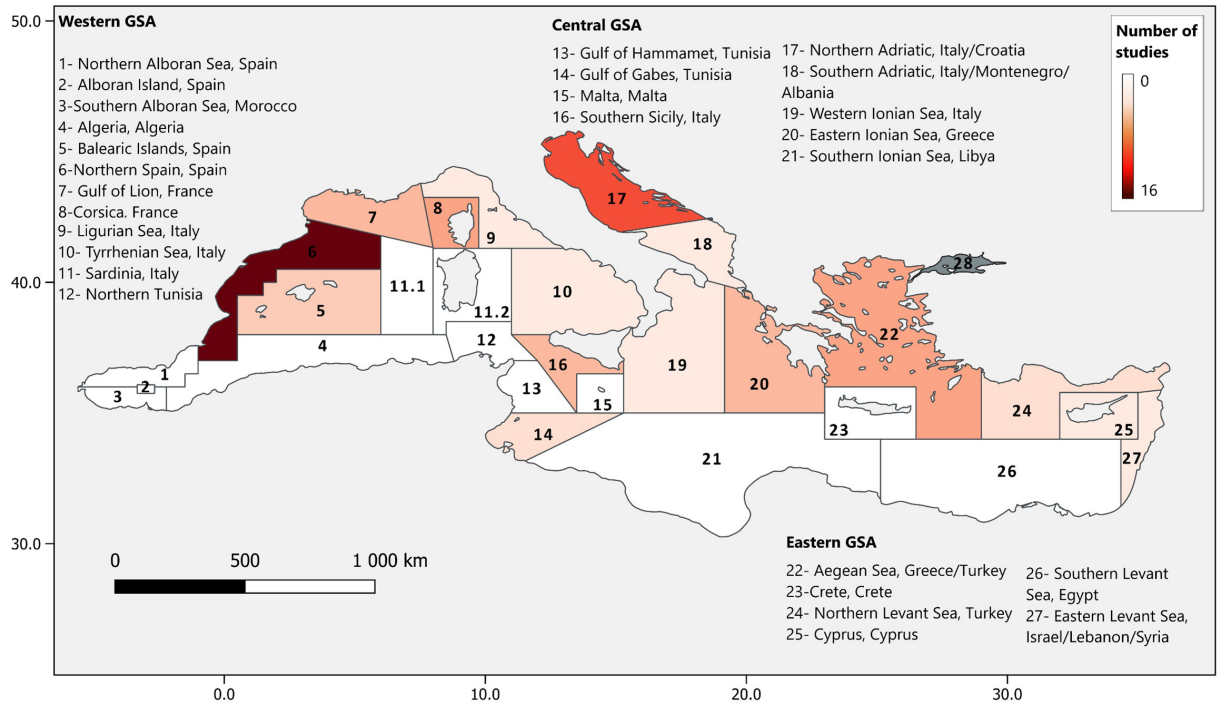

FIGURE 2
Distribution of the studies across the Mediterranean per GSA.

population-level TL, mean TL for catches and communities (mTLc and mTLco, respectively).

3 Results and discussion

The 68 collected publications spanned between 2000 and 2023. There was an increasing number of papers through the years and a remarkable inter-annual variability, with a maximum of 8 studies in 2009 and 2021 (Supplementary Figure S1).

3.1 Geographical areas

The Mediterranean Sea, excluding the Black Sea, is divided into 27 fishing areas referred to as Geographical sub-areas (GSAs) and sometimes studies referred to the GSA as the study location. The collected publications referred to 16 GSAs, mostly those situated in the northern Catalan (Spain), the Adriatic Sea (Italy and Croatia), the Ionian and Aegean Sea (Italy, Greece) or the Sicilian Channel (Figure 2; Supplementary Table S1 and Supplementary Reference list). Most studies conducted research in Italy, Spain, and around Greece (Figure 3A). Except for Tunisia, where 2 studies were found, our research did not identify any published paper considering the southern Mediterranean countries outside Europe (e.g. Algeria, Egypt, Libya and Morocco), despite their high biomass of landings (Figure 3B). The lack of information observed in the southern Mediterranean could be explained by the weak institutional capacity to collect and publish fisheries data. However, there could be data available in the grey literature, which we did not consider as explained in the previous section (FAO 2020). Nonetheless, it is necessary to fill in this gap because these regions possess important artisanal fleets and trawlers, comparable to the most studied GSAs. The largest artisanal fleets occur in Greece (Aegean Sea) and Tunisia, while trawlers are mainly concentrated in Egypt, Spain together with the Adriatic Sea (Croatia, Italy) and Algeria (Figure 3B; Colloca et al., 2017; FAO, 2022). They are also countries where artisanal fishing is not only a source of food, but also an important cultural heritage, where landings represent more than a quarter of the total landings of the Mediterranean (Black Sea excluded, FAO, 2022).

There is growing concern about the sustainability of the current level of fishing exploitation in relation to the unbalanced and unregulated fishing in several areas of the Mediterranean, and a call for ecosystem-based management of fisheries within the context of future scenarios of global change (Colloca et al., 2017). These scenarios include the increasing presence of alien species, warming, and changes in fishing pressure (Michailidis et al., 2019).

Southern Mediterranean countries are considered hot spots for climate change or invasions and their impacts on fisheries and coastal ecosystems (Farahmand et al., 2023). The understanding of fishing impact in southern countries is thus necessary and it could be improved by collecting well-sounded scientific data and refining existing models of fishing impacts at the scale of the Mediterranean or specifically built for the social and ecological conditions of these countries. This is also important to assist the management of fisheries in rural areas and their evolution in terms of fishing capacity (Maynou, 2020).

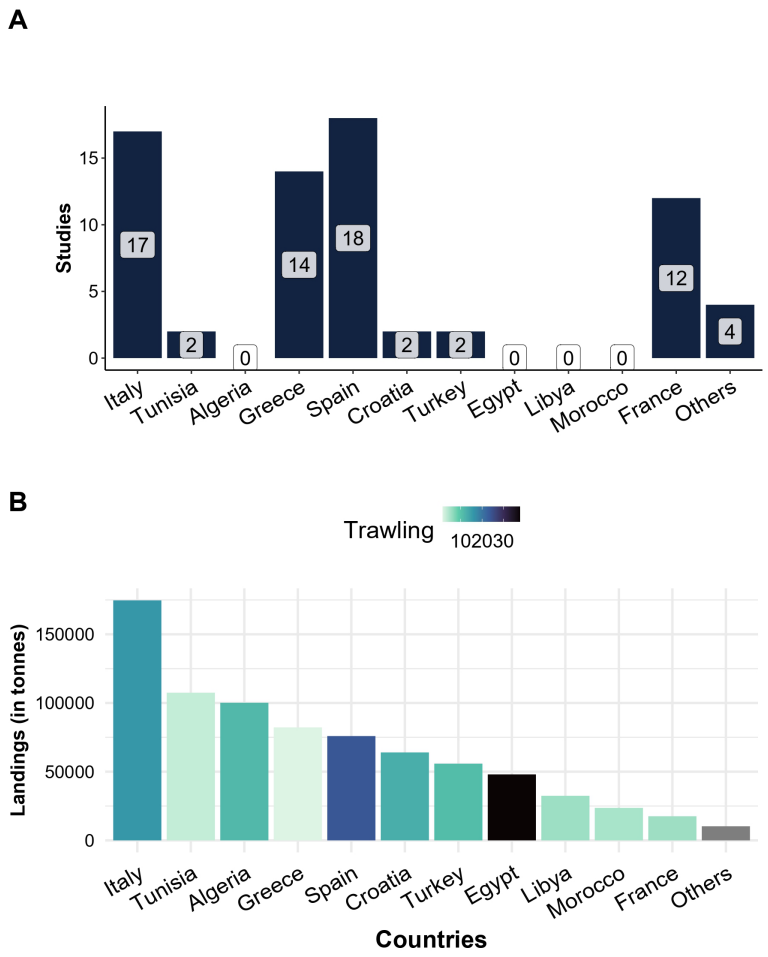

FIGURE 3
(A) Number of studies per country and **(B)** Biomass of landings per country and trawlers percentage among the fishing fleet based on Colloca et al. (2017), grey= non-available values.

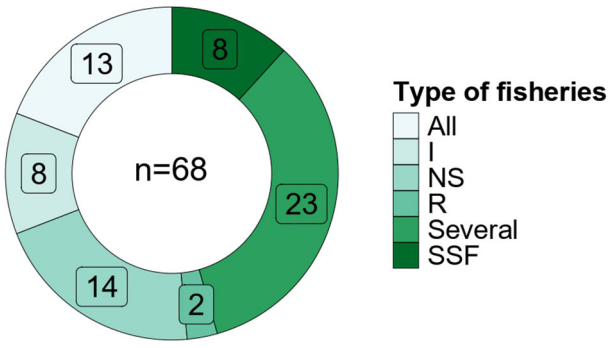

FIGURE 4
Repartition of the fisheries type among the collected studies. All= Industrial, Small scale and recreational; I= Industrial; NS= Not specified; R= Recreational; Several=Combination of 2 fisheries (e.g. SSF+R or SSF+I or R+I); SSF= Small Scale fishery; More details are in the text and in Supplementary Table S1.

3.2 Types of fisheries

Among the reviewed studies, 36 considered a combination of different types of fisheries, 14 did not specify the type of fisheries and only 17 reported to focus exclusively on one type of fisheries; e.g. 8 on industrial, 8 on small-scale fisheries (SSF) and only 2 on recreational fisheries (Figure 4, Supplementary Table S1). SSF in the Mediterranean is multispecies, multigear, and very complex to evaluate in a simple manner. Yet, information on the distinct impacts of SSF, industrial and recreational fishing is needed to implement more effective management in the Mediterranean and worldwide (Goñi et al., 2008; Calò et al., 2022). The different gear types used in SSF are generally considered less destructive to coastal ecosystems than industrial fishing gears (Crowder et al., 2008), but they can have potential ecosystem-wide effects (Stergiou et al., 2007; Crowder et al., 2008). As expected, the papers we collected that reported on the impact of industrial fisheries, particularly trawling, showed a strong decrease in the health of the whole food web (e.g.

Coll et al., 2008a; Libralato et al., 2010). They also showed how increasing the selectivity of trawls could mitigate effects on TLs and other trophic indicators (Coll et al., 2008a; Saygu et al., 2020b). These authors showed that using a large mesh size could have a positive effect on the biomass of both commercial and non-commercial species, thereby improving the TL of the community (TLco; Coll et al., 2008a) or the TL of catches (TLc, Saygu et al., 2020b).

Nevertheless, the authors also emphasise the need of reducing fishing effort in heavily exploited or overexploited fisheries.

The two papers on the impact of SSF in the Corsica island considered fish net, spiny lobster and small trawling. They found SSF to have a very low impact, probably because of the very low level of exploitation of the system. Indeed, evaluation of TL indicators showed small changes in time or considering different fishing pressure scenarios. Nonetheless, they highlighted the negative impact of SSF on functional groups with the highest TLs; e.g. rays and sharks and also on non-targeted groups (Vanalderweireldt et al., 2022; Marengo et al., 2023). The effects of SSF were also variable among geographical areas and strongest in the Ionian and Eastern Mediterranean Sea, probably because of the environmental characteristics of the areas, such as low productivity but also because of the highest number of SSF vessels (Corrales et al., 2018). Similar impacts were reported for recreational fisheries (Lloret et al., 2008). However, recreational fishery was found severely under-represented in the published literature, even if this type of fisheries has been described as important in the Mediterranean Sea (Figure 4; Lloret et al., 2020). This may pose a serious bias in estimating fishing impact on food webs.

While some studies focussed specifically on a single fishery type, others took a gear-based approach to infer fishery impacts.—information that can help infer the type of fishery involved (Smith and Basurto, 2019). These studies consistently found that bottom trawling—commonly used in industrial and semi-industrial fisheries—was the main driver of negative impacts on most exploited functional groups. For example, several regional studies assessed the effects of trawling in the southern Catalan Sea (Coll et al., 2008a, 2008b), the Gulf of Gabès (Hattab et al., 2013), and the Eastern Mediterranean Sea (Corrales et al., 2018), all highlighting its impact on demersal community species. A broader study across the entire Mediterranean basin reported similar findings (Piroddi et al., 2015). Additionally, Corrales et al. (2018) also documented a clear increase in community-level trophic indicators (TLc and TLco) after a cessation of trawling.

In contrast, small-scale fisheries (SSF) generally exert a lower ecological impact than trawling (e.g., Bănaru et al., 2013) or recreational fishing (Prato et al., 2016). However, some research highlights that SSF can negatively affect species at the highest trophic levels, particularly non-targeted species such as dolphins, seabirds, and sea turtles (e.g., Michailidis et al., 2019; Keramidas et al., 2022; Sánchez-Zulueta et al., 2023). Similarly, recreational fishing has been shown to impact top predators, including dolphinfish (Sánchez-Zulueta et al., 2023) and sharks (Michailidis et al., 2019). These impacts on upper trophic levels may trigger top-down effects. For instance, Prato et al. (2016) suggest that recreational fishing, which often targets species with a trophic level above 3, could initiate trophic cascades. Additionally, Albouy et al. (2010) emphasise the combined effects of artisanal and recreational fishing fleets, reporting an increase in benthic mollusc feeders biomass, likely linked to intensified fishing pressure on higher trophic levels.

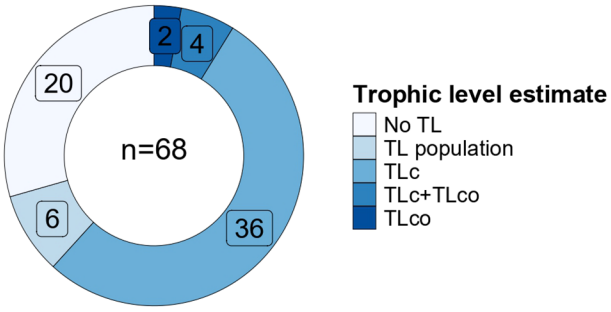

FIGURE 5
Repartition of the estimate of trophic level (TL) among the different types of TL for the collected studies. TL population= estimate for each fish species calculated using $\delta^{15}N$, see Table 1); TLc = estimates for catches done in modelling studies and in 1 field study (Marengo et al., 2023); TLco= estimates for the whole assemblage of consumers. More details are in the text and in Tables 1 and S1.

3.3 Methodological approach

In agreement with other reviews on fisheries (Coll and Libralato, 2012; Colloca et al., 2017) and food webs (Kytinou et al., 2020), we found more studies using a modelling than a field approach (45 and 23, respectively). Among these, 16 field and 4 modelling studies did not report any estimates of TLs, while evaluating other aspects of the food web (Supplementary Table S1, Figure 5).

The 23 field studies reported results on trophic aspects of target fishes using various methods for *in-situ* data collection. The most widely used method was underwater visual census (UVC; 9 out of 23 studies) to quantify fish abundance and biomass per trophic group (fishes occupying similar TL, Supplementary Table S1). Other studies (3) used bioassays to estimate the strength of trophic interactions, e.g. predation on intermediate consumers (e.g. Guidetti, 2006; Vergés et al., 2012; Seytre et al., 2013). Ten studies targeted wild fish populations, not necessarily of commercial value, captured with experimental fishing and used either stomach content analysis (2 studies, Bautista-Vega et al., 2008; Zorica et al., 2021), morphological traits (1 study, Alós et al., 2014) or stable isotope analysis (SIA; 6 studies; Supplementary Table S1). Remaining 2 studies took advantage of landings, by interviewing what fishers had captured (Lloret et al., 2008) or using research survey that were independent from fishery data or sampled catches on fish vessels (Marengo et al., 2023). The use of SIA in only 6 out of 23 studies was surprising since SIA is currently the most extensively used method for the identification of trophic levels within foodwebs (Kytinou et al., 2020). These 6 studies using SIA (Supplementary

TABLE 1 TL estimates for population using stable isotopes as defined by Post et al. (2002); communities of catches (TLc), as suggested by Pauly et al. (1998) and communities of consumers (TLco; Shannon et al., 2014).

Indicators	Full name	Definition	References
TL population	Trophic level of a population	$TL_i = \left[\frac{(\delta^{15}N_i - \delta^{15}N_{ref})}{\Delta\delta^{15}N_i}\right] + TL_{ref}$ TL measured using stable isotope values of δ^{15}N of a species i, based on Post et al., 2002. TL_i and TL_{ref} are the trophic level of group i and a reference baseline material (usually phytoplankton or bivalves)	Post, 2002
TLc	Trophic level of landed catches	$TL_c = \sum_{i=1}^{n} Y_i \cdot \frac{TL_i}{Y_L}$ where YL is total landings, Yi is the landing of species i, and TLi is the trophic level of species i	Pauly et al., 1998; Shannon et al., 2014
TLco	TL of the modelled community (from a specific ecosystem excluding primary producers)	$TL_{co} = \sum_{i=1}^{n} B_{Mi} \cdot \frac{TL_i}{B_{MT}}$ where B_{MT} is total biomass of the modelled ecosystem, B_{Mi} is the biomass of each species i in the model, and TLi is the trophic level of species i as an output of the model	Shannon et al., 2014

Table S1; Figure 5) estimated TL values for fish population using the δ15N of fish muscles against a trophic baseline (Table 1). The δ15N baseline for estimating TL was usually measured from secondary consumers (Badalamenti et al., 2002, 2008; Deudero et al., 2004; Moranta et al., 2020; Zorica et al., 2021) or derived from the literature (Vizzini and Mazzola, 2009). Instead, Marengo et al. (2023) used the data collected on fish species and the available online database (FishBase) for attributing TL values to each captured species and estimating mean catch TL.

All modelling studies were based on trophodynamic models. Input data of biomass of fishes were derived from other published studies or online databases (Supplementary Table S1). Twenty-one studies used data from research survey which were fishery-independent, such as the MEDITS program (Mediterranean International bottom Trawl Surveys) (Bertrand et al., 2002) and a few studies used fishery-dependent data collected aboard vessels. Other fishery-dependent data were collected using fishers' logbooks or (inter)national monitoring. Data on TLs of functional groups were in general derived from existing databases or calculated based on literature information on main prey, as described in Stergiou and Karpouzi (2001). The model then combined biomass with TL and produced values relative to a part of the community or to catches. Most modelling studies evaluated the average TL value of catches (TLc or mTLc), while others evaluated community TLs of whole consumers including non-targeted species (TLco in Table 1 or mTLco or TLco>1). Very few model studies evaluated both catch and community TLs (4 out of 45; Tsagarakis et al., 2010; Corrales et al., 2018; García-Rodríguez et al., 2020; Papantoniou et al., 2021, Figure 5).

The population and community TLs as derived from field and modelling studies provides complementary information (McCormack et al., 2019). Field studies are often snapshots of a short-term situation, but those evaluating TL with stable isotopes can determine the trophic position of local fish populations, which can change, in response to perturbations and fishing pressure (Olson et al., 2020). This can become particularly important when evaluating ecosystem-based fisheries impacts, because the response of fish species to environmental changes may reflect a change in their trophic position, particularly important when generalist and omnivore fishes, prone to diet changes, are the most abundant taxa within the food webs and within catches.

In the modelling studies, the use of data considering large temporal and spatial scales, although necessary for covering large-scale food webs over time, does not take into account local variations of trophic position within the same species. In addition, when data comes from landings, there can be a non-negligible source of uncertainty and imprecision (Shannon et al., 2014). Specifically, landings data are not necessarily representative of actual catches, which also include illegal, unregulated and unreported fishing (IUUF) activities as well as discards (Garibaldi, 2012). The IUFF is a serious issue in the Mediterranean Sea (Piroddi et al., 2015) and little progress has been made in the Mediterranean to combat the phenomenon (Srour et al., 2020).

3.4 Trophic level comparison between fishing and non-fishing areas

Evaluating variation of TLs in relation to fishing activities might be difficult because it requires somehow similar ecological conditions but a different fishing pressure. Among the 21 studies —that considered no-take zones of Marine Protected Areas (MPAs) or Fisheries Restricted Areas (FRAs) as the no-fishing conditions—we found only 5 field studies and 4 modelling studies that compared trophic level (TL) values between fishing and no-fishing areas (Supplementary Table S1). The average (± SD or SE, when available) TL values of those studies are reported in Figure 6). The field studies focussing on population-level TLs showed different patterns of variability in response to protection (Figure 6A). Moranta et al. (2020) showed a positive effect of fishing ban on the rainbow wrasse *Coris julis* related to its ontogenetic development, when changes in competition and predation occur and might be affected by the level of protection. Vizzini and Mazzola (2009) found a decrease in TL values under full protection for 2 out of the nine species. Since these fishes were invertivores (*C. julis* and *Diplodus annularis*), they suggested a possible increase in their predators causing a shift in diet of these species. Badalamenti et al. (2002; 2008), instead, claimed that changes in biomass due to fishing ban were not followed by substantial size-related trophodynamic shifts, which might depend

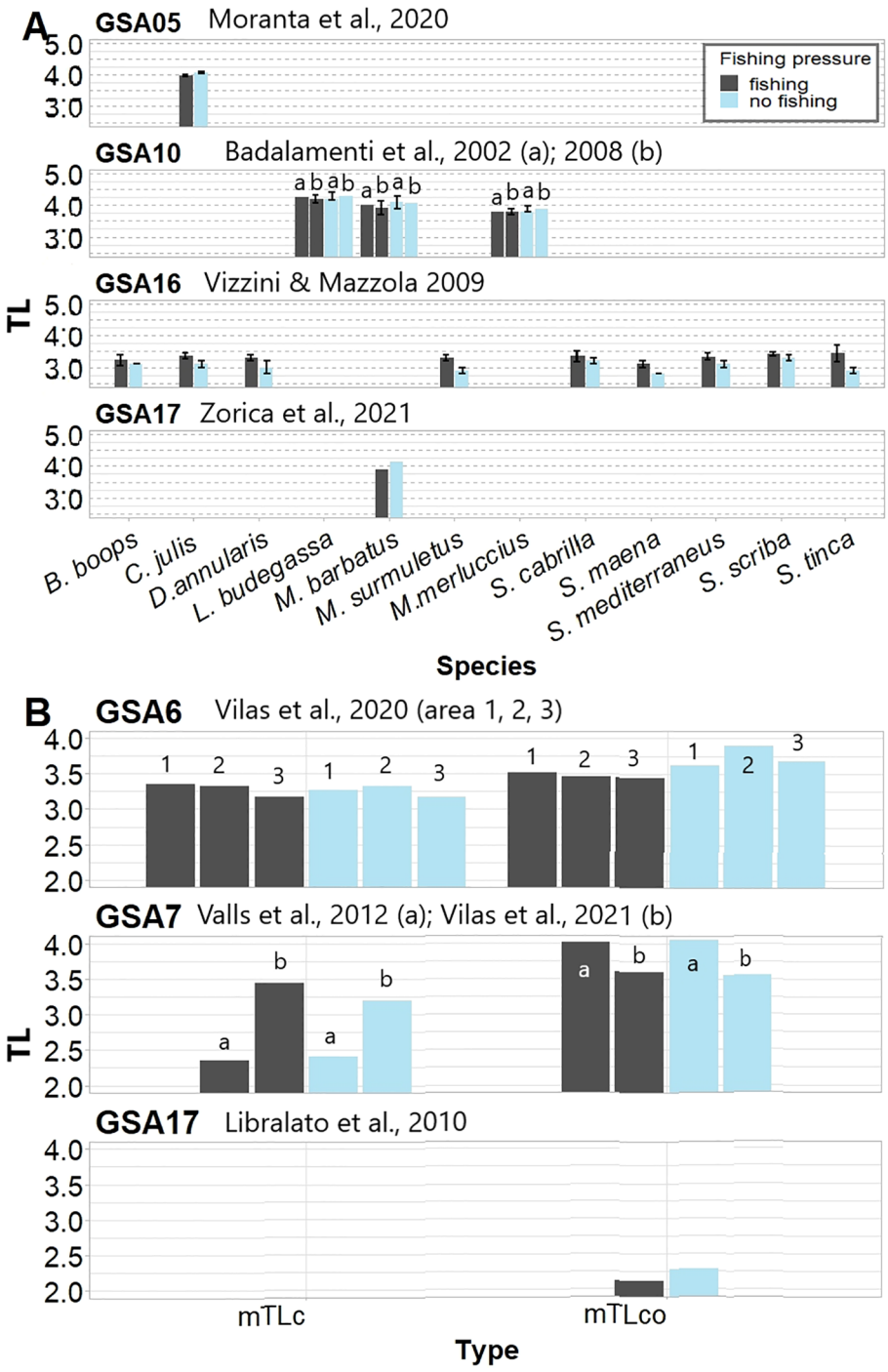

FIGURE 6
Values of trophic levels as reported in the revised papers (cited within the figure) that compared fishing vs. no-fishing areas. Plots are organised by GSA (as in Figure 2b). **(A)** Trophic levels (TL) of fish population (mean ± SD or SE, as reported in field studies) based on stable isotopes analysis (SIA) and, **(B)** TL of catches and community (mTLc and mTLco, respectively) with TL consumers >2 extracted from trophodynamic model studies.

on the availability of food in the area or on the fact that the target species do not shift diet. All these studies were focussed on single species and did not investigate changes at the community level. In the modelling studies focussing on community level, 2 studies found higher TL of catches (TLc) in no-fishing than fishing area (Figure 6B; Valls et al., 2012; Vilas et al., 2020), but the remaining one showed values slightly higher before than after the establishment of a fishery restricted area (2.59 vs 2.50, respectively; Vilas et al., 2021). TLco was similar or slightly higher in no-fishing than fishing areas for the 4 studies reporting it (Libralato et al., 2010; Valls et al., 2012; Vilas et al., 2020, 2021). These variations in the TL response to a fishing ban at both species and community level require further studies in order to gain a better understanding of the pattern of response of TL values under different fishing pressure. While, there is solid evidence of how

the removal of human activities, including fishing, may increase diversity and biomass of fishes within food webs (e.g. Stobart et al., 2009; Seytre and Francour, 2014), it is possible that changes in fish trophic ecology and the resulting community shifts could be more related to environmental differences in the study area or to the species composition of the community and those more affected by protection. In particular, fishes occupying high trophic levels are more abundant and show larger sizes in no-take than other zones within MPAs (Micheli et al., 2005; Consoli et al., 2013; Guidetti et al., 2014; Viladrich et al., 2016; Rojo et al., 2021), thereby increasing predation pressure on low-level consumers and variably affecting other species, depending on the trophic level they occupy (Guidetti, 2006; Vergés et al., 2012; Seytre et al., 2013). These effects can also vary with local physical conditions and diversity (Micheli et al., 2005) or geographical scales (Villamor and Becerro, 2012). The papers we found were done in areas characterised by differences in seabed complexity and a different regime of oligotrophy (Supplementary Table S1), which might have affected the results. Studying changes in population and community levels across MPAs with different species composition and environmental attributes could thus represent an important step for testing how changes in fishing activities may modify population and community TLs, within different environmental contexts.

In addition, it should be noted that 20 modelling studies showed how TLs values of community or catches decreased in time by analysing time series (Coll et al., 2008a; Coll et al., 2009a; Fortibuoni et al., 2017; Marengo et al., 2023; Piroddi et al., 2016) or by testing for scenarios of different fishing pressures (e.g. Vanalderweireldt et al., 2022; Papantoniou et al., 2023; Moutopoulos et al., 2018). Some papers also included changes in fishing pressure within global change scenarios by evaluating future catches of alien species (Saygu et al., 2020a, Michailidis et al., 2019) and/or the impact of warming (Corrales et al., 2018). These latter papers showed how changes in environmental conditions could drive impacts of fisheries.

In summary, our review on the literature explicitly dealing with the fishing impact on the trophic level (TL) of Mediterranean fish populations and assemblages highlights not only the geographical skewness of published studies, but also that more studies should focus on comparisons of population and community TL values between different levels of fishing pressure and under different regimes of environmental conditions, including geographical differences. This information would allow us to better understand how TL could be used as an indicator of fishing impact on food webs and to refine predictions on how changes in environmental conditions as those related to warming or invasions could modify fisheries. This is particularly important for food webs occupying the coastal shelf that are supported by a variety of autochtonous sources and under the influence of several human-induced drivers. No-take zones of marine protected areas or temporal fishing bans may offer good opportunities to quantify the impacts of fishing and the changes in TLs, using both field and modelling studies across the Mediterranean (Pinnegar et al., 2000; Grorud-Colvert et al., 2021). A better prediction of fisheries impacts on fish resources is of fundamental value in order to develop more effective conservation and ecosystem-based management measures in light of ongoing climate change and the importance of fishing activities in the Mediterranean Sea.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

AM: Conceptualization, Data curation, Writing – original draft, Writing – review & editing, Methodology. SB: Writing – review & editing. PG: Writing – review & editing. FR: Conceptualization, Data curation, Methodology, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1489965/full#supplementary-material

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Evaluating the unexplored recreational fishing in the Turkish Black Sea: socio-economic significance and environmental impact

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Marine recreational fishing, a globally popular outdoor activity, has deep cultural roots and ecological implications. This study, conducted between 2021-2022, explores marine recreational fishing practices along the Turkish Black Sea coast. It analyzes fisher numbers and demographics, fishing effort, fishing methods, and species caught and released. Furthermore, the research sheds light on the economic dimensions, emphasizing the substantial contributions of recreational fishing to local economies. Notably, responsible practices, such as catch-and-release initiatives, demonstrate anglers' awareness of conservation efforts. Within the Turkish Black Sea region, an observed 18.5% participation rate among a population of 24.5 million implies the presence of approximately 4.5 million marine recreational fishers. Annually, this translates to nearly 30 million fishing days, accompanied by a total expenditure of 400 million Euros. However, it's imperative to handle these figures cautiously as the timing of the screening survey during the COVID-19 pandemic may have influenced the high participation rate, introducing a potential bias. A detailed examination of a Turkish marine recreational fisher engaged in Black Sea fishing reveals an average annual catch of 16.5 kg of retained fish and 1.2 kg of released fish biomass. When extrapolated to the larger population of 4.5 million fishers, this culminates in a noteworthy landing biomass approaching 74,000 tons. The study unveils that marine recreational fishers in the Turkish Black Sea predominantly target commercially important species, resulting in a retained biomass surpassing commercial landings in 2021. This prompts concerns about potential impacts on crucial commercial fish stocks, underscoring the imperative inclusion of recreational fisheries in stock assessments. The research, providing essential insights into the intricate dynamics of recreational fishing, lays a foundation for well-informed policies and practices that concurrently promote environmental conservation and the continuation of this valued leisure activity.

KEYWORDS

marine recreational fishing, Turkish Black Sea, sustainability, catch-and-release, socio-economic impact, environmental impact, telephone screening survey, recall survey

1 Introduction

Marine recreational fishing (MRF) is a widespread and highly popular outdoor activity that has deep historical and cultural roots across the globe. Engaging in this recreational activity, often seen as a harmonious fusion of art and science, revolves around the pursuit and capture of diverse aquatic organisms. Enthusiasts partake in this endeavor purely for the delight and excitement it brings, relishing the challenge it presents (Cowx and Arlinghaus, 2008; Cooke et al., 2018). MRF represents a multifaceted pastime encompassing a wide range of techniques, equipment, and settings, and it holds a unique place within the broader context of environmental conservation, natural resource management, and socio-economic impact (Tweedley et al., 2023). Beyond its cultural significance, MRF has profound ecological implications. Its close relationship with the well-being of aquatic ecosystems is underscored by its reliance on the existence of diverse and healthy fish populations (Pouso et al., 2018). The impact of MRF on marine ecosystems, however, is not limited to the catch itself; it also encompasses habitat degradation, invasive species introductions, and the potential disruption of natural predator-prey dynamics. Consequently, understanding its ecological consequences is crucial for sustainable resource management and biodiversity conservation (Arlinghaus and Cowx, 2008; Butler et al., 2020; Schafft et al., 2021).

From an economic perspective, MRF has emerged as a significant industry, generating substantial revenues worldwide. Anglers contribute to the economy through the purchase of fishing gear, licenses, and permits, as well as by participating in guided fishing tours and travel (Øystein, 2008; Potts et al., 2022). Additionally, this activity supports various ancillary businesses, including tackle shops, boat rentals, and hospitality services in areas frequented by fishers. These economic dimensions underscore the importance of MRF in regional and national economies and highlight the need for responsible management to ensure long-term sustainability (Tsafoutis and Metaxas, 2021).

In contemporary society, MRF is undergoing a transformation in response to evolving environmental concerns and changing demographics. Conservation-oriented practices, catch-and-release initiatives, and sustainable fishing practices have gained prominence among anglers, reflecting a growing awareness of the need to protect aquatic ecosystems (Drymon and Scyphers, 2017). Furthermore, this activity is evolving to embrace a more diverse and inclusive audience, welcoming women, children, and individuals with disabilities. This shift promotes a wider understanding and admiration for the natural world (Ojea et al., 2020).

Fisheries management is a complex and dynamic field that seeks to balance the extraction of aquatic resources with the need to maintain healthy ecosystems and safeguard the interests of various stakeholders (Bastardie et al., 2021; Shen and Song, 2023). Characterized by its diverse techniques and motivations, MRF represents a unique and significant component of contemporary fisheries. This activity can exert substantial pressure on specific fish species, particularly those highly coveted by anglers (Kadagi et al., 2021). Overfishing of popular game fish worldwide (e.g., salmon, sea trout, and seabass) can lead to declines in their populations, potentially disrupting local ecosystems. Fisheries managers must carefully monitor and regulate recreational harvest to prevent unsustainable exploitation. In addition to the target species, MRF can inadvertently capture non-target species (bycatch), including endangered or protected species. Moreover, the use of impacting fishing techniques can harm fragile aquatic habitats, such as coral reefs or seagrass beds, with cascading ecological effects. Effective fisheries management must consider these collateral impacts and implement measures to minimize harm (Grip and Blomqvist, 2020; Cooke et al., 2023).

Given this background, Mediterranean and Black Sea fisheries face serious challenges, with approximately 58 percent of the scientifically assessed stocks considered to be fished outside safe biological limits (FAO, 2023). In the period 2017-2020, the General Fisheries Commission for the Mediterranean (GFCM) developed a programmatic and multiannual mid-term strategy focused on enhancing the sustainability of Mediterranean and Black Sea fisheries. Pertaining to MRF, Output 2.1 of Target 2 within the mid-term strategy outlined the need for "Robust and timely information on the impacts of small-scale fisheries and recreational fisheries on living marine resources and on their interactions with other human activities in coastal communities." This initiative anticipated the formation of a permanent working group on MRF within the GFCM and the assessment of MRF impacts. It's important to note that the collection of MRF data was a recent development in many countries, and until recently, there was no clear framework for utilizing this data for stock assessment or fishery management.

The aim of this research was to investigate the recreational fishing activity in the Turkish Black Sea coastal provinces. The research, carried out from 2021 to 2022, adhered to the methodology outlined in the "Handbook for Recreational Fisheries Data Collection in the Mediterranean and Black Sea" (Grati et al., 2021). The study comprised two key phases: first, establishing a statistical framework encompassing marine recreational fishers along the Turkish Black Sea coasts, and second, gathering data to evaluate the effects of recreational fishing activities.

2 Materials and methods

2.1 Study area

The Black Sea occupies a low-lying region running from east to west, nestled between two mountainous ranges: the Pontic Mountains to the south and the Caucasus Mountains to the northeast. This sea connects to the Atlantic Ocean via the Mediterranean and Aegean seas, as well as through the "Turkish Strait System" comprising the Istanbul Strait, Sea of Marmara, and Çanakkale Strait. Additionally, the Kerch Strait links it to the Azov Sea.

Türkiye's Black Sea coastline stretches approximately 1,600 km, touching 16 provinces. Eight of these provinces have city centers in close proximity to the coast, while the others are situated farther inland (Figure 1). The combined population of these provinces is approximately 26 million. Notably, the western shores of the Black Sea, particularly Istanbul, boast higher population densities, with Istanbul alone housing 15.8 million people.

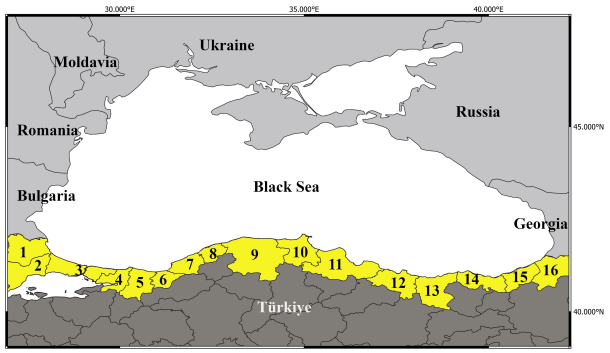

FIGURE 1
Map showing the 16 provinces along the Turkish Black Sea shoreline. 1 Kirklareli; 2 Tekirdağ; 3 İstanbul; 4 Kocaeli; 5 Sakarya; 6 Düzce; 7 Zonguldak; 8 Bartin; 9 Kastamonu; 10 Sinop; 11 Samsun; 12 Ordu; 13 Giresun; 14 Trabzon; 15 Rize; 16 Artvin.

2.2 Data collection

2.2.1 Telephone screening survey (phase 1)

To estimate the population of marine recreational fishers residing in the 16 districts along the Turkish Black Sea shoreline, a comprehensive survey was conducted in 2021 on a complete roster of resident households. The survey, carried out by the company Survey ARAŞTIRMA, utilized a sample of 3,055 landline phone numbers which were randomly extracted from the Turkish directory for fixed telephones (Table 1). The interviewers underwent training provided by the survey company to familiarize themselves with the purpose and content of the interviews. The sample size was identified in order to have an error of <5%. This selection adhered to a stratified sampling scheme, where design weights were applied to both coastal and non-coastal districts (with a distribution of 70 percent coastal and 30 percent non-coastal) (Table 1). The purpose of this approach was to overrepresent coastal municipalities, where a higher concentration of marine recreational fishers was anticipated (see Bolognini et al., 2022). The primary objective was to identify households with individuals participating in MRF, gather their contact details, and enlist them for a more in-depth follow-up survey (Phase 2).

The initial respondent was queried on several aspects, including their gender, age, participation in marine recreational fishing, the number of fishing days undertaken in 2020 (avidity) using different fishing methods (such as shore fishing, boat fishing, and underwater fishing), and their willingness to participate in a subsequent follow-up survey panel. Respondents below the age of 16 were excluded from the survey.

2.2.2 Recall survey (phase 2)

Data on catches, effort and expenditures were collected through a recall survey, which relies on contacting, via telephone, the marine

TABLE 1 Number of interviewed individuals (INT) in coastal and inland districts of Turkish provinces bordering the Black Sea during the telephone screening survey.

Provinces	Coastal districts			Inland districts			Total		
	INT	MRF	PR%	INT	MRF	PR%	INT	MRF	PR%
Artvin	78	34	43.6	31	10	32.3	109	44	40.4
Bartin	70	17	24.3	30	2	6.7	100	19	19.0
Düzce	70	22	31.4	30	3	10.0	100	25	25.0
Giresun	71	12	16.9	38	8	21.1	109	20	18.3
İstanbul	895	151	16.9	385	46	11.9	1280	197	15.4
Kastamonu	72	23	31.9	35	5	14.3	107	28	26.2
Kirklareli	70	12	17.1	30	4	13.3	100	16	16.0
Kocaeli	163	41	25.2	75	13	17.3	238	54	22.7
Ordu	75	21	28.0	31	3	9.7	106	24	22.6
Rize	69	17	24.6	31	11	35.5	100	28	28.0
Sakarya	87	15	17.2	40	3	7.5	127	18	14.2
Samsun	118	14	11.9	50	10	20.0	168	24	14.3
Sinop	72	16	22.2	30	8	26.7	102	24	23.5
Tekirdağ	71	10	14.1	31	2	6.5	102	12	11.8
Trabzon	76	10	13.2	30	8	26.7	106	18	17.0
Zonguldak	71	11	15.5	30	4	13.3	101	15	14.9
Total	**2128**	**426**	**20.0**	**927**	**140**	**15.1**	**3055**	**566**	**18.5**

MRF are individuals identifying as marine recreational fishers and PR% is the corresponding participation rate percentage.

recreational fishers identified during the screening survey who agreed to participate in a subsequent follow-up survey panel.

To mitigate potential recall errors, we chose to limit the recall period to one month, as research has shown that longer recall timeframes can introduce bias into survey results (Grati et al., 2021).

We followed the approach outlined by Grati et al. (2021) to gather data on the fishing activities conducted in the preceding month. This included details about the number of fishing trips undertaken using different methods (such as boat, shore, and underwater fishing), the quantity and weight of species caught and released, the Total Length (TL) of each retained and released specimen, and all related expenditures incurred during that period (including equipment, bait, travel, etc.).

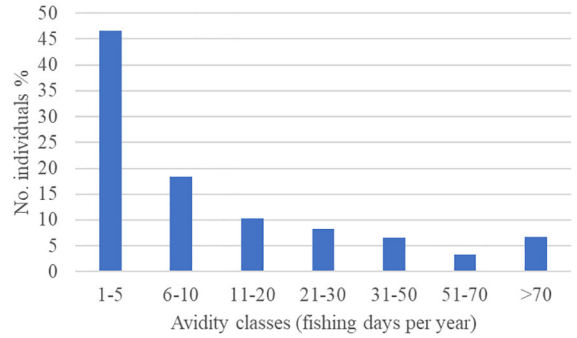

FIGURE 3
Distribution of days spent fishing at sea during 2020 categorized into different classes of avidity.

3 Results

3.1 Telephone screening survey

Among the 3,055 individuals interviewed, 566 identified themselves as marine recreational fishers, constituting a participation rate of 18.5% (Table 1). The participation rate in coastal districts (20.0%) exceeded that in inland districts (15.1%). In total, 291 recreational fishers agreed to be recontacted for a follow-up panel survey.

The majority of respondents were males (70%), with the most common age group being 36-40 years old (Figure 2).

The age groups among respondents who identified as marine recreational fishers mirrored those of the overall respondents, but the proportion of males significantly rose to 92% (Figure 2).

In 2020, the majority of fishers (47%) reported engaging in sea fishing a few times, typically ranging from 1 to 5 days (Figure 3). During that year, Turkish recreational fishermen spent an average of 28.4 days fishing in the Black Sea. Nevertheless, this number might be highly inflated because of potential outliers, like those who reported fishing 200-300 times. Therefore, we consider the median value (10.0 days/year) to be a more realistic, and we utilized this figure for subsequent calculations. However, the restricted frequency of fishing trips can be mainly attributed to limitations in available time, adverse weather conditions, particularly prevalent during the winter months, and economic considerations.

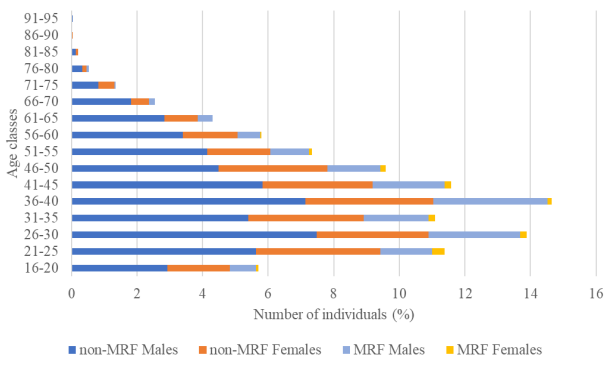

FIGURE 2
Distribution of age groups among respondents, categorized by gender and individuals identifying as marine recreational fishers (MRF) and non-marine recreational fishers (non-MRF).

3.2 Recall survey

Initially, 291 marine recreational fishers agreed to participate in the recall survey. However, this number gradually decreased to 285 within a few months due to factors such as discontinuation of the activity, relocation to another region, lack of time to participate in the survey, and other reasons.

3.2.1 Fishing effort

Recreational fishers in the Turkish Black Sea region displayed a monthly median fishing activity ranging from 0.0 days in September 2022 to 3.0 days in May and June 2022, indicating a clear seasonality (Figure 4). In total, we calculated an average annual value of 6.85 (± 1.3 SD) fishing days during the survey period. This value partially confirms what was already observed in the screening survey, where the majority of respondents (65%) reported going fishing at sea for up to 10 days in 2020 (Figure 3).

The predominant fishing method utilized was shore fishing (80.8%), succeeded by boat fishing (19.0%) and underwater fishing (0.2%). In terms of fishing gear, hook- and- line were the most commonly used (97.5%), trailed by cast nets and seines (0.9%) and longlines (0.6%) (Figure 5).

3.2.2 Catches

Turkish recreational fishers participating in the recall panel captured a total of 24 fish species in the Black Sea from October 2021 to September 2022 (Table 2). Mediterranean horse mackerel was the most commonly caught species in terms of both number and weight, followed by red mullet and bluefish (Table 2). Approximately 25% of Mediterranean horse mackerel and bluefish caught were released at sea, whereas this percentage decreased to 13% for red mullet.

Fishers retained an average of 16.5 kg of fish in the survey year and released an average of 1.2 kg of fish. When extrapolated to the

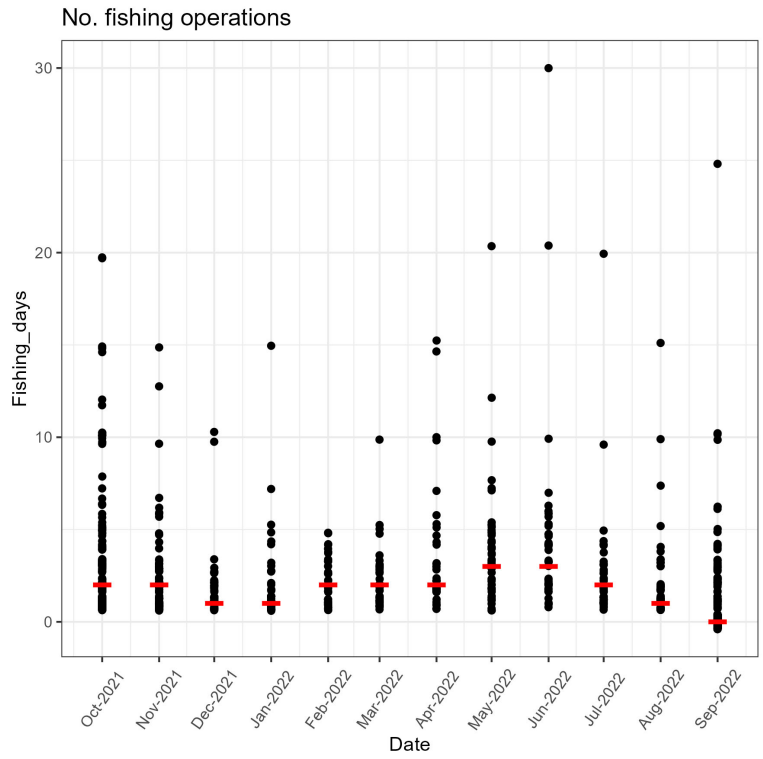

FIGURE 4
Strip chart showing the monthly fishing days spent by Turkish recreational fishers in the Black Sea from October 2021 to September 2022. The red lines indicate the median values.

4.5 million fishers active in the Turkish Black Sea, these figures might contribute to an overall remarkable landing biomass of nearly 74,000 tons. These figures should be validated through future studies, specifically through screening surveys that verify the observed participation rate.

Various fish species were caught throughout the year, with different species available seasonally (Mater and Meriç, 1996; Öztürk, 1999; Bilecenoglu et al., 2002; Lütfiye and Nurettin, 2005; Çetin, 2010). Mediterranean horse mackerel, for instance, can be found in the Black Sea year-round, making it accessible at any time in Türkiye. Bluefish was available between October and December as it migrated along the Black Sea coast from west to east. Atlantic bonito could be found between August and October, while demersal species like red mullet and whiting were available in the summer when the seawater warmed up. Grey mullet migrated close to the Black Sea shore between January and April and was accessible during those months. Garfish could be found between August and December, mainly caught from the boat in the open sea. Black scorpionfish becomes more active when the seawater warms up and can be easily caught by hand line from rocky areas. Seabass and brown meagre are typically found in rocky locations throughout the year.

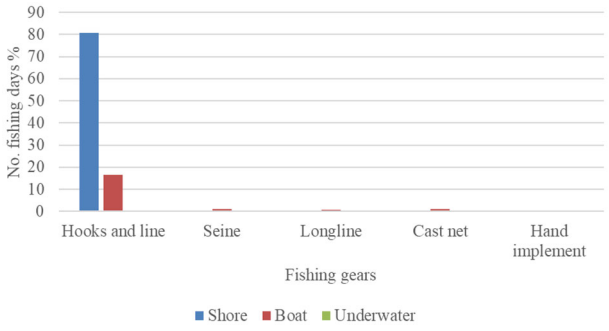

FIGURE 5
The histogram displays the percentage distribution of fishing days by Turkish recreational fishers in the Black Sea from October 2021 to September 2022, segmented by fishing modality and gear.

The length frequency distributions of the three primary species clearly showed that specimens released were predominantly small individuals (Figure 6). In general, recreational fishers typically adhere to the minimum landing sizes of 13 cm Total Length (TL) for Mediterranean horse mackerel and 18 cm TL for bluefish.

3.2.3 Expenditures

Turkish marine recreational fishers operating in the Black Sea spent an average of 87.70 Euro during the year of data collection, with 36.24 Euro specifically related to the use of a boat, covering expenses for fuel, maintenance, rental, and charter. Food and travel costs were comparable, ranging from 16.23 to 18.76 Euro per year, respectively. Expenditures related to equipment (such as hooks, lines, rods) and baits were relatively minor.

The expenditure pattern aligns with the overall trend of fishing effort, showing a consistent increase from November 2021 to June 2022 (Figure 7).

TABLE 2 List of species captured in the Black Sea by Turkish recreational fishers involved in the recall panel (October 2021 - September 2022), including the number of individuals and the weight of specimens retained and released.

Species		Retained		Released	
		No	W (kg)	No	W (kg)
Mediterranean horse mackerel	*Trachurus mediterraneus* (Steindachner, 1868)	138,571	2,770.45	44,328	248.35
Red mullet	*Mullus barbatus* Linnaeus, 1758	7,622	191.03	1,116	8.37
Bluefish	*Pomatomus saltatrix* (Linnaeus, 1766)	5,531	634.88	1,952	54.66
European anchovy	*Engraulis encrasicolus* (Linnaeus, 1758)	2,465	24.60	15	0.08
Whiting	*Merlangius merlangus* (Linnaeus, 1758)	1,652	87.55	613	3.71
Black scorpionfish	*Scorpaena porcus* Linnaeus, 1758	1,108	246.13	55	3.77
Atlantic bonito	*Sarda sarda* (Bloch, 1793)	824	426.57	213	10.12
Garfish	*Belone belone* (Linnaeus, 1761)	656	108.01	277	1.83
Flathead grey mullet	*Mugil cephalus* Linnaeus, 1758	627	87.55	43	1.12
European pilchard	*Sardina pilchardus* (Walbaum, 1792)	220	11.00	800	16.00
European seabass	*Dicentrarchus labrax* (Linnaeus, 1758)	156	42.90	11	0.35
Twaite shad	*Alosa fallax* (Lacepède, 1803)	136	14.00	0	0.00
Blotched picarel	*Spicara maena* (Linnaeus, 1758)	120	11.57	61	1.04
Common two-banded seabream	*Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817)	115	6.30	0	0.00
Round goby	*Neogobius melanostomus* (Pallas, 1814)	50	2.00	65	0.33
Brown meagre	*Sciaena umbra* Linnaeus, 1758	45	13.98	3	0.15
Tub gurnard	*Chelidonichthys lucerna* (Linnaeus, 1758)	24	7.67	119	2.14
Atlantic mackerel	*Scomber scombrus* Linnaeus, 1758	20	4.00	0	0.00
Turbot	*Scophthalmus maximus* (Linnaeus, 1758)	12	11.16	13	1.86
Annular seabream	*Diplodus annularis* (Linnaeus, 1758)	5	0.50	5	0.50
Sand steenbras	*Lithognathus mormyrus* (Linnaeus, 1758)	5	0.50	3	0.02
Gilthead seabream	*Sparus aurata* Linnaeus, 1758	3	0.12	0	0.00
Red porgy	*Pagrus pagrus* (Linnaeus, 1758)	2	0.10	0	0.00
Big-scale sand smelt	*Atherina boyeri* Risso, 1810	0	0.00	2	0.05

4 Discussion

The study provides for the first time a comprehensive overview of marine recreational fishing (MRF) practices along the Turkish Black Sea coast, shedding light on participant demographics, participation rates, fishing effort, fishing methods, species diversity, and economic contributions. The findings highlight the deep-rooted passion for MRF among coastal communities, emphasizing the importance of sustainable fishing practices to preserve biodiversity and marine ecosystems. The Black Sea has encountered various ecological challenges such as overfishing, habitat degradation, and pollution, as highlighted by Bat et al. (2005). Irresponsible practices in recreational fishing have the potential to exacerbate these problems. The participation rate observed in this study (18%) significantly surpasses the one computed by Hyder et al. (2017) for all of Europe (1.6%), affirming the substantial social significance of this activity for individuals residing in the Black Sea coastal areas of Türkiye. However, Hyder et al. (2017) found high variability in participation rates across European countries, with figures ranging from 0.2% in Belgium to 33.0% in Norway. Nevertheless, relying on our expert judgement, we believe that the participation rate in the studied area appears very high and warrants reevaluation for confirmation. This is especially pertinent when calculating the comprehensive effort, expenses, and catches, resulting in total figures that significantly surpass our initial expectations. Indeed, the participation rate significantly influences all subsequent estimations and thus warrants careful consideration.

The timing of the screening survey during the COVID-19 pandemic may have contributed to the high participation rate. Pita et al. (2021) found that engaging in marine recreational fishing boosted individuals' perceived health and well-being during the crisis. Access to marine recreational activities helped mitigate socioeconomic impacts, especially among vulnerable groups.

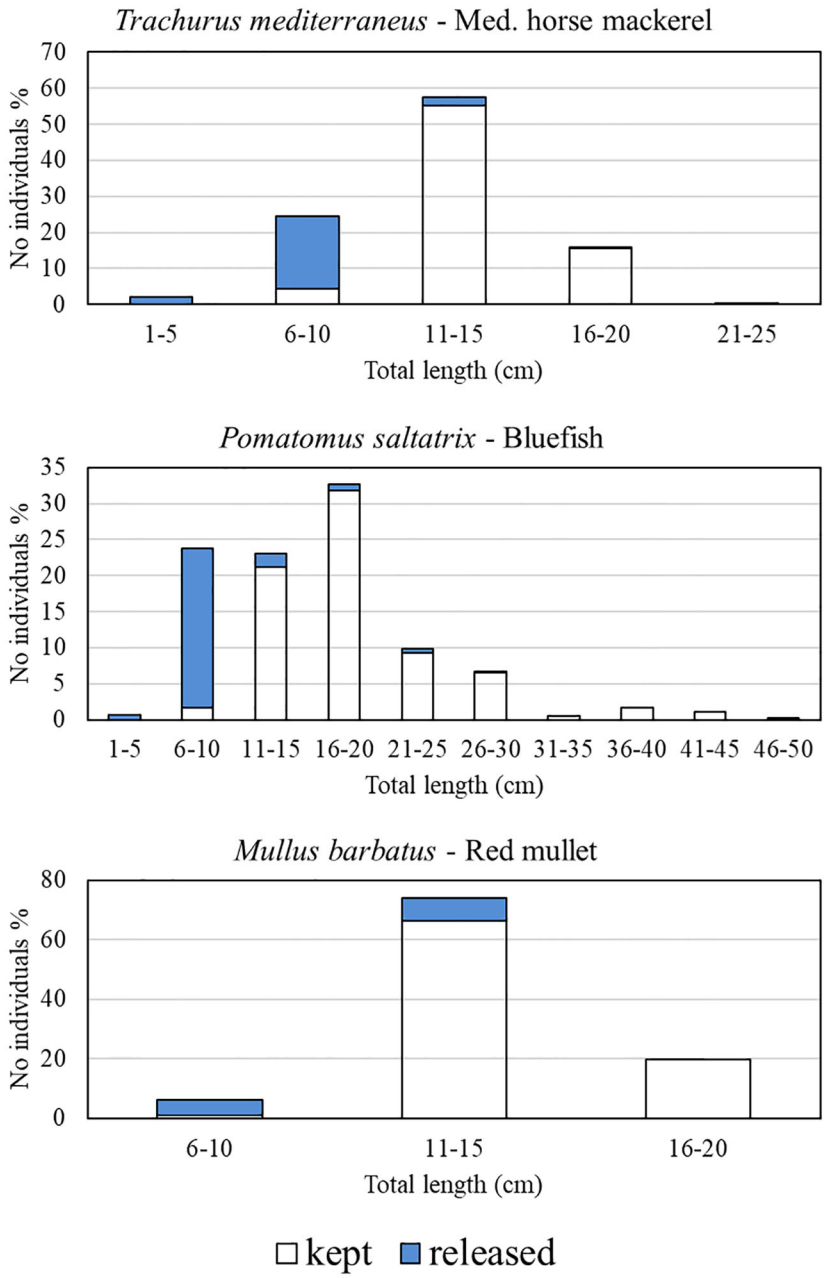

FIGURE 6
Length frequency distributions of Mediterranean horse mackerel, bluefish and red mullet caught in the Black Sea by Turkish recreational fishers involved in the recall panel (October 2021 - September 2022).

Social restrictions globally increased the demand for outdoor activities, and outdoor leisure pursuits aided social distancing and indirectly reduced the spread of COVID-19, especially in natural environments.

Hence, it's possible that the number of individuals engaging in recreational fishing surged notably during the survey period, potentially leading to an overestimation of the overall number of people fishing in the Turkish Black Sea (4.5 million). A reassessment would be necessary in the future to validate these figures, particularly when calculating comprehensive efforts, expenses, and catches, which might exceed initial projections significantly. Indeed, the participation rate profoundly impacts all subsequent estimations and, therefore, demands meticulous attention.

In our study, the frequency of fishing trips was predominantly ascribed to a combination of factors, notably the constraints imposed by limited available time, adverse weather conditions, particularly prevalent during the winter months, and economic considerations. These constraints collectively contribute to a reduced opportunity for individuals to engage in recreational fishing. It is noteworthy, however, that amidst these challenges, the fishing activity exhibited a surprising resilience during the COVID-19 pandemic. Contrary to expectations, the impact on

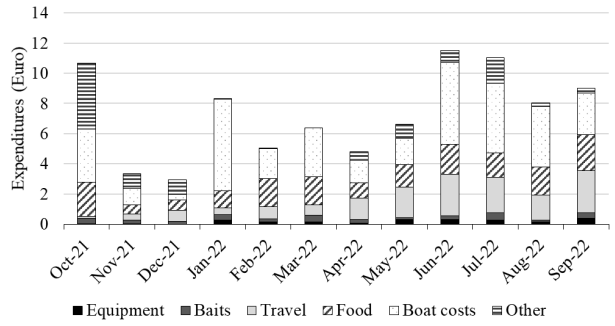

FIGURE 7
Monthly average expenditures (in Euro) of Turkish marine recreational fishers in the Black Sea, categorized into equipment, baits, travel, food, boat costs, and other expenses.

recreational fishing appeared to be relatively minimal. This unexpected trend could potentially be attributed to the conscientious adherence to stringent safety protocols by fishing enthusiasts. The commitment to measures such as wearing masks and practicing physical distancing likely played a pivotal role in maintaining a semblance of normalcy in fishing activities despite the disruptions caused by the pandemic. This observation underscores the adaptability and dedication of the recreational fishing community, highlighting the significance of prioritizing safety measures to sustain and safeguard the pursuit of this outdoor activity, even in the face of external challenges.

From an economic standpoint, even when acknowledging the potential bias in the participation rate mentioned earlier, the considerable projected total expenditure of 400 million Euros by marine recreational fishers in the Turkish Black Sea highlights the significant economic influence of this activity on the region. This financial contribution plays a vital role in supporting local economies and businesses, such as fishing gear retailers, hospitality services, and boat rentals. The infusion of such substantial funds not only enhances the economic fabric of the Turkish Black Sea coastal areas but also fosters job creation and sustains livelihoods within these communities. In comparison to the broader context presented by Hyder et al. (2017), where the cumulative expenditure for all EU countries bordering the Mediterranean amounted to 920 million Euros, the Turkish Black Sea's share could be indeed noteworthy. This contrast may reflect both the scale of marine recreational fishing activities in the Turkish Black Sea and the economic significance of the region's coastal tourism. Moreover, the economic impact extends beyond direct spending on fishing-related activities. The ripple effect encompasses indirect benefits to various sectors, such as local tourism, restaurants, and associated businesses that cater to the needs and preferences of recreational fishers. This economic symbiosis emphasizes the interdependence between marine recreational fishing and the broader local economy.

Turkish marine recreational fishers (MRF) displayed a distinct focus on specific species, namely Mediterranean horse mackerel, red mullet, and bluefish, resulting in a potential retained biomass of 43,700 tons, 3,000 tons, and 10,000 tons, respectively. Notably, these figures might surpass the commercial landings recorded in 2021, which were 18,053 tons for Mediterranean horse mackerel, 454 tons for red mullet, and 5,612 tons for bluefish, as reported by fao.org/fishery/statistics-query.

The significant disparity between the quantities retained by recreational fishers and those landed commercially might raise concerns about the potential impact of recreational fisheries on crucial commercial fish stocks in the Turkish Black Sea. These observations prompt the consideration of recreational fisheries in stock assessments, as the substantial biomass retained by recreational fishers may have noteworthy implications for the overall health and sustainability of the targeted fish populations.

This study represents the first attempt of estimating the impact of marine recreational fisheries in the Turkish Black Sea. As previously emphasized, the overarching estimate derived from a notably high participation rate indicates a population of fishers nearing 4.5 million individuals, a figure requiring validation through subsequent research.

However, as the data indicates, the impact of recreational fisheries on important commercial fish stocks should be regarded as a critical factor. The considerable quantities caught, especially when compared to commercial landings, underscore the necessity of integrating recreational fisheries data into broader stock assessments. This holistic approach is essential for achieving a comprehensive understanding of the dynamics and sustainability of fish stocks in the Turkish Black Sea. Recognizing the significance of recreational fisheries in stock assessments is a crucial step toward implementing effective management strategies that balance the interests of both recreational and commercial sectors while ensuring the long-term health of marine ecosystems.

One of the key highlights of the study is the anglers' awareness of conservation efforts, demonstrated through responsible practices such as catch-and-release initiatives. The conscious decision to release a significant portion of caught specimens, especially small individuals, indicates a keen understanding of the need to preserve fish populations for future generations. This conservation-oriented approach aligns with global efforts to mitigate the impact of recreational fishing on marine ecosystems (Arlinghaus and Cowx, 2008) and underscore the vital role anglers play in contributing to the preservation of aquatic biodiversity. Another possible explanation for this enthusiastic behavior might be that the individuals who have agreed to take part in the data collection panel generally possess a deeper understanding of the importance of data collection and are also more sensitive to fisheries conservation issues.

Sustainable fisheries management is essential to balance the enjoyment of recreational fishing with the preservation of marine ecosystems. Therefore, it is crucial to monitor and regulate recreational harvest, especially for popular game fish, to prevent unsustainable exploitation and population declines. Furthermore, collateral impacts such as bycatch and harm to fragile aquatic habitats must be minimized through effective management measures (Cooke and Cowx, 2004).

Furthermore, the study emphasizes the inclusive nature of MRF, as it embraces a diverse range of participants, including women, children, and individuals with disabilities. This inclusivity goes beyond mere participation figures, serving as a testament to the accessibility and adaptability of the activity to people from various backgrounds and abilities. Beyond the individual benefits, the

inclusivity of MRF strengthens the societal connection with marine environments. It promotes a shared sense of responsibility for the well-being of aquatic ecosystems and encourages a collective commitment to sustainable practices. The diverse perspectives brought forth by participants of all backgrounds enrich the collective understanding of marine environments, fostering a community-driven approach to conservation.

Data availability statement

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

Author contributions

ME: Data curation, Formal analysis, Funding acquisition, Investigation, Writing – original draft. AC: Conceptualization, Methodology, Project administration, Resources, Supervision, Writing – review & editing. FG: Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

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

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Status and long-term changes of coral reefs around Zanzibar

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Introduction: Coral reefs as key ecosystems in Zanzibar are exposed to several anthropogenic and natural stressors.

Methods: The benthic composition and coverage of coral reefs were investigated on three data sets involving ten coral reefs monitored from 1992 to 2016. Firstly, we investigated differences in the reef composition using data from seven reefs in 2015. Secondly, we analyzed communities on three distinctive reefs (2010 to 2012) to understand the importance of seasons and reef zones (slope, crest and flat) on species abundance. Finally, we investigated long-term changes (1992 to 2016) of five reefs.

Results: Branching *Porites* and *Acropora*, and soft coral order Corallimorpharia, characterized sheltered reef communities. Soft corals and algal species characterized the reef communities exposed to strong hydrodynamic conditions, which also displayed greater cover of rocks and rubbles. The average dissimilarity between reefs ranged between 60% and 75%. The seasonal changes in community structure for reefs near Stone Town were mostly associated with soft coral Corallimorpharia. Indeed, the bare rock and algae distinguished the northern exposed reef from more sheltered reefs. *Acropora* was a key genus for the sheltered Chumbe reef, which explained between 14% and 18% of the dissimilarities among the three reefs. Hard corals covered between 40% and 70% in most years, with severe declines following El Niño events in 1998 and 2016. The dominating genus *Acropora* showed a strong decline from the late 1990s' with signs of recovery at remote reefs compared to reefs closer to human residence.

Discussion: Our results highlight the importance of seasonality and spatial differences, reflecting differences in human impact and physical exposure and significant long-term changes in coral communities. Continued monitoring of reef health is essential to evaluate the success of ongoing management to sustain the reef services.

KEYWORDS

coral reef, community structure, zonation, seasonality, long-term changes, Zanzibar

1 Introduction

Coral reefs are among the most valuable coastal ecosystems in Zanzibar (Johnstone et al., 1998). The reefs host high biodiversity, are productive (Jiddawi and Öhman, 2002; Lange and Jiddawi, 2009), providing significant support to human livelihoods in the coastal zones, and are a key selling point for the prosperous tourist industry (Muhando and Jiddawi, 1998; Wolanski et al., 2003). The reef ecosystems in the recent decade, however, have been exhibiting signs of increasing degradation (Muhando, 2008; Staehr et al., 2018; Ussi et al., 2019). Very strong El-Niño events occurred in 1998, 2007 and 2016, resulting in massive coral bleaching due to global warming in this region (Wilkinson et al., 1999; McClanahan et al., 2007; Gudka et al., 2018; Ussi et al., 2019). Furthermore, severe outbreaks of the invasive crown-of-thorns starfish destroying corals through predation were observed from 2002 to 2008 (Muhando and Lanshammar, 2008; Ussi, 2009). The ongoing destructive fishing practices such as the use of blast fishing (Chevallier, 2017; Gray et al., 2017; Raycraft, 2018), and drag-net fishing (Wallner-Hahn et al., 2016) continue to affect the reef communities negatively (Wells, 2009; Raycraft, 2018). In addition, declining water quality in the near shore areas due to pollution and poorly managed tourism have been reported to further exacerbate the negative impact on coral reefs off Stone Town (McClanahan et al., 1999; Muhando et al., 2002; Obura, 2002; Wells, 2009; Muzuka et al., 2010). The consistent increase in coral-reef ecosystem degradation, attributed to these threats has resulted in a substantial change in coral reef community structure at different magnitudes among reefs. Coral reef degradation is projected to continue in response to the intensity of existing impacts (Porter et al., 2017). It is therefore important to periodically assess the health status of existing reef communities, and evaluate the impacts of long-term threats at the community level for proper management.

Located in the Inter-Tropical Convergence Zone, Zanzibar experiences seasonality driven mostly by the northeast monsoons (NEM) from October-March and the southeast monsoons (SEM) from April-September. Four seasons can be identified; 1) From December to February, conditions are calm and hot (related to summer); followed by 2) a heavy rain season from March to May (related to spring); 3) a cold windy season from June-August (related to winter) and finally 4) another wet period referred to as the short rainy season from September-November (related to autumn). Given these clear seasonal changes in weather conditions, we expect some seasonal variability in the cover of reef benthic communities as indicated by previous studies in the region (Nzali et al., 1998). The knowledge of this seasonality will be important for planning future monitoring and for setting proper management targets for the coral reefs around Zanzibar.

Coral reef monitoring around Zanzibar started in 1992. However, the regular monitoring was interrupted from 2009 to 2015 due to a lack of financial resources. Fortunately, a series of research studies carried out by postgraduate students ensured data on coral health status during these periods. Together with these resources, this study provides three supplementing analyses of the coral reef health around Zanzibar. Firstly, we gave a systematic description of the reef structure and differences between seven important coral reef sites around Zanzibar islands based on data collected in 2015. Secondly, we explored the extent to which community structure is sensitive to seasonality and or to the reef habitat orientation of the monitored zone using data from three distinct reefs monitored from 2010 to 2012. This information was important for interpreting the existing data collected during different seasons and for future planning of monitoring activities. Finally, we updated previous reports on long-term changes in key biological and physical structures using a unique dataset from 1992 to 2016 on five reefs. This also made it possible to evaluate the importance of the different environmental conditions explaining these changes to guide management efforts.

2 Materials and methods

2.1 Study sites

Ten reef sites with varying amounts of data (year and season) and sampling frequency were studied (Figure 1). To improve the quality of data and meet the statistical validity, data were standardized using the method described by Holmes and Johnstone (2010) (Holmes and Johnstone, 2010). Variations in data quantity among reef sites were mostly an outcome of differences in the monitoring starting at the different periods. For example, four reef sites (Changuu, Chapwani, Bawe and Misali) were monitored from 1992, two reefs (Chumbe and Mnemba) were monitored from 1994, and monitoring of Kwale reef began in 1996.

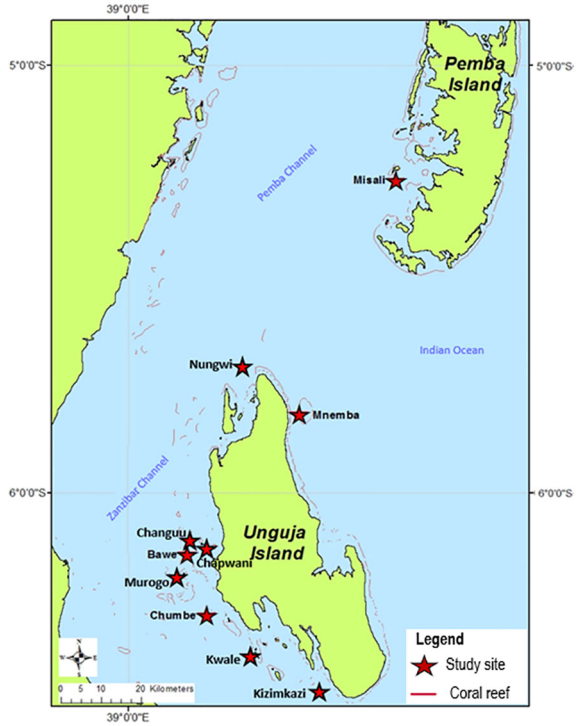

FIGURE 1
Map of Zanzibar showing the locations of 10 reefs sites included in this study.

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All these seven reefs were monitored at different intervals until 2016. Kizimkazi, Murogo and Nungwi reefs were the newest sites with the most recent monitoring data available for 2015-2016. These reef sites were selected based on expected differences related to the human pressure and management regimes. Chapwani, Bawe and Murogo reefs are located at increasing distances (3.8, 6.2 and 7.1 km respectively) from Stone Town, the most populated area of Unguja Island. The reef sites off Stone Town are relatively sheltered from the effects of monsoons (Figure 1). The northern reef sites off Nungwi and Mnemba are particularly exposed to strong wind conditions during the North-East Monsoon (NEM), whereas the reefs off Kizimkazi at the southern tip and Kwale on the southwest of Unguja Island are exposed to the South-East monsoon (SEM). Misali site is located off the west coast of the less populated Pemba Island. Mnemba reef is located on the North-East coast of Unguja (Figure 1, Table 1), and is a national protected area, where fishing restrictions are applied in the core zone of the reef area with permission for selective fishing gear in the

TABLE 1 Overview of the investigated reefs around Unguja and Pemba Island, with information on the number of transects, sampling month and season.

Year	Reef	No. of plots	No. of transects	Month	Season
1992	Chapwani	2	–	November	Short rain
1992	Changuu	2	–	November	Short rain
1992	Bawe	2	–	November	Short rain
1992	Misali	4	–	May	Heavy rain
1994	Mnemba	2	–	November	Short rain
1994	Chumbe	3	–	November	Short rain
1996	Kwale	2	–	November	Short rain
1996	Chapwani	2	–	April	Heavy rain
1996	Chapwani	2	–	December	Calm hot
1996	Changuu	2	–	April	Heavy rain
1996	Changuu	2	–	August	Windy cold
1997	Chapwani	2	–	June	Windy cold
1997	Changuu	2	–	June	Windy cold
1997	Bawe	4	–	June	Windy cold
2008	Misali	2	12	May	Heavy rain
2008	Misali	2	12	November	Short rain
2009	Misali	2	12	May	Heavy rain
2009	Misali	2	12	November	Short rain
2010	Changuu	2	12	October	Short rain
2010	Mnemba	2	12	October	Short rain
2010	Chumbe	2	12	October	Short rain
2011	Changuu	2	12	April	Heavy rain
2011	Mnemba	2	12	April	Heavy rain
2011	Chumbe	2	12	April	Heavy rain
2011	Changuu	2	12	November	Short rain
2011	Mnemba	2	12	November	Short rain
2011	Chumbe	2	12	November	Short rain
2012	Changuu	2	18	May	Heavy rain
2012	Mnemba	2	18	May	Heavy rain

(Continued)

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TABLE 1 Continued

Year	Reef	No. of plots	No. of transects	Month	Season
2012	Chumbe	2	18	May	Heavy rain
2015	Kwale	2	12	June	Windy cold
2015	Chapwani	2	12	September	Short rain
2015	Bawe	2	18	September	Short rain
2015	Mnemba	2	12	July	Windy cold
2015	Nungwi	2	6	December	Calm hot
2015	Kizimkazi	2	12	June	Windy cold
2015	Murogo	2	12	September	Short rain
2016	Misali	2	8	June	Windy cold
2016	Chapwani	2	8	June	Windy cold
2016	Bawe	2	8	June	Windy cold
2016	Chumbe	2	8	June	Windy cold
2016	Mnemba	2	8	June	Windy cold

For the 1992-1997 data, the number of transects could not be accurately registered as data were only stored as percentage average values.

periphery of the reef. Chumbe reef is a private marine protected area with restricted access. Kizimkazi and Kwale reefs are located within marine conservation areas with fishing gear restrictions, whereas reefs off Stone Town (Changuu, Chapwani, Murogo and Bawe reefs) are freely accessible.

2.2 Data sets

At each reef site, two to four permanent monitoring plots were established, each of approximately 75m x 50m. The plots were used for the ongoing monitoring and were separated by approximately 300 m. In each plot, 6 to 12 twenty-meter line-intercept transects (Table 1) were set on the reef flat (1 - 5m deep), the reef crest (3-4m deep) and the reef slope (5 - 15m deep), all parallel to the reef front. The transects within plots were not fixed but established haphazardly during each survey. The benthic assessment was done by taxonomically skilled divers, who measured all benthic categories underlying the 20-m long line-intercept transect (LIT) (English et al., 1997) with modifications. The modifications involved dentification of hard corals at the genus level instead of growth forms only and upgrading the coralline algae and Corallimorpharia from sub-categories into full categories because of their substantially increased dominance in the community. This modification resulted in benthic cover descriptions of nine categories instead of the previous seven Appendixes A, B).

Until 1998, coral reef benthic cover was described using seven categories (Appendix A) (Muhando, 2010); (1) Live hard corals (*Acropora* and non-*Acropora*), (2) Corallimorpharia, (3) Sponges, (4) Algae, (5) Others, (6) Soft non-biotic substrate (SU_1) and (7) Hard non-biotic substrate (SU_2). From 1999, the number of reef benthic cover categories was expanded by including specific species or species groups. In addition, coralline algae and hexacorallian soft corals (the order Corallimorpharia) were changed from sub-categories into full respective categories. This change allowed harmonization with previous categories (Appendix B) (Muhando, 2010). The number of sites, plots and transects investigated over the years and across seasons have changed over time (Table 1). In addition, the original transect data collected from 1992 to 1997 could not be obtainable and only aggregated data representing average values of cover data were available, and hence standardized.

Three data sets were used in our analysis. One dataset collected in 2015 included a more detailed description (Appendix B) of the biological diversity as well as non-biotic benthic elements of seven reefs (Table 1). This dataset was used to provide a detailed and the most recent characterization of the coral reef's health. The second dataset was collected in 2010, 2011 and 2012 and was based on the detailed description (Appendix B), and was used to evaluate the effects of year, season, sampling zone and site on community structure. The third dataset consisted of a long-term time series (1992-2016) used to explore long-term changes in overall reef structure and health. Here we categorized data into nine groups consisting of (1) Live hard corals (*Acropora* species and other non-*Acropora* hard corals), (2) Coralline algae, (3) Soft corals, (4) Sponges, (5) Algae, (6) Others, (7) Corallimorpharia, (8) Hard non-biotic substrate (SUB_1) and (9) Soft non-biotic substrate (SUB_2). The constituent sub-categories for each group are shown in Appendix B.

2.3 Data analysis

A One-way ANOSIM test based on Bray-Curtis similarities (Bray and Curtis, 1957) from non-parametric multivariate statistical software PRIMER (Clarke and Gorley, 2015) was used to detect overall spatial differences in benthic community structure

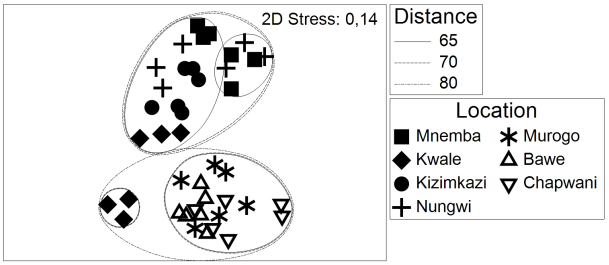

FIGURE 2
MDS plot reflecting key elements on coral reefs collected at seven different sites in 2015 around the Island Unguja. Six transects were monitored on each reef site. Clusters of observations generated by a beta flexible Cluster analysis are shown for three different distances and then overlaid the MDS plot.

between reef sites in the 2015 data subset. Two replicates of each zone per location were considered. Possible seasonal effects were neglected as data from the different reef sites were collected over three seasons.

A Permutational Analysis of Variance (PERMANOVA from the PRIMER add-on package (Anderson, 2008) based on the Bray-Curtis similarity matrix was performed for the matrix of benthic cover studying the effect of location, year, season and zone in the subset of data covering three years (2010, 2011 and 2012), and two seasons. Data were unbalanced as both seasons were only present in 2011 (Table 1). The benthic covers were used without transformation of the data. Location, year, season and reef zone (slope, crest and flat) were included as fixed effects with interactive terms. We ran PERMANOVA using sums of squares (SS) Type III to account for the unbalanced design (Anderson, 2008). Highly insignificant terms (p>50%) were removed from the final model and those terms were pooled with residuals, as they were considered sources of error.

Similarities among sample groups (reefs, seasons, years, zones) are visualized in Multi-Dimensional Scaling plots (MDS-plots) from the PRIMER software package (Clarke et al., 2014; Clarke, 2015). A Beta Flexible Cluster analysis was performed on the nine key biological and structural categories and the results were used as an overlay on one MDS plot to visualize clusters of observation

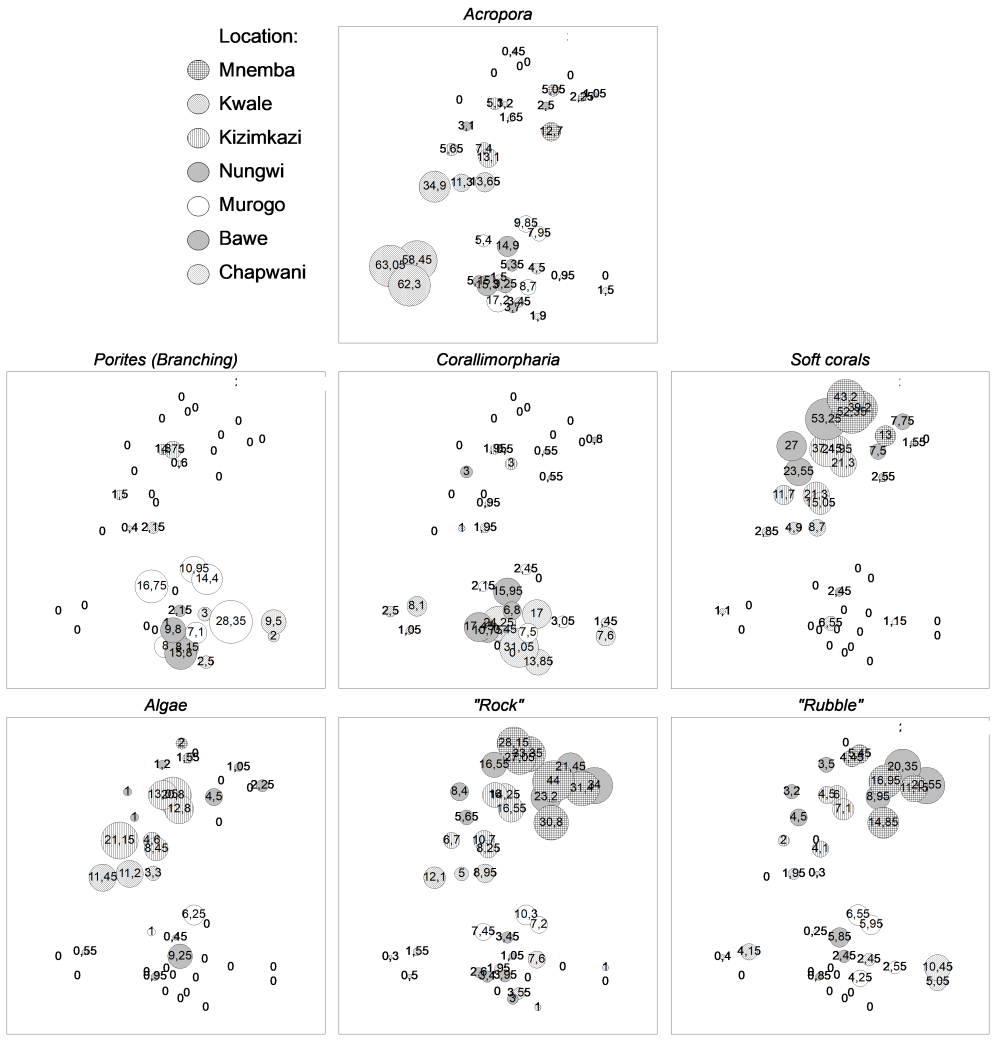

FIGURE 3
MDS plots reflecting similarities in cover of eight key biological and structural elements representing the seven different coral reefs in 2015 around Zanzibar. The size of the bubbles represents the percent cover with the actual value given within bubbles or as zero.

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TABLE 2 PERMANOVA results on benthic community structure on three reefs (Chumbe, Changuu and Mnemba) in 2010, 2011 and 2012.

Source	df	SS	MS	Pseudo-F	P(perm)	% Estimates of Variation
Season	1	5763.4	5763.4	67798	0.0001	1.5
Year	2	10420	5209.8	61286	0.0001	2.7
Site	2	133900	66949	78756	0.0001	35.1
Zone	2	16348	8174.2	96159	0.0001	4.3
Season x Site	2	2338	1169	13751	0.1584	0.6
Season x Zone	2	22982	1149.1	13518	0.1678	6.0
Year x Site*	3	6279.2	2093.1	24622	0.0009	1.6
Year x Zone	4	5971.8	1493	17563	0.013	1.6
Site x Zone	4	16735	4183.9	49217	0.0001	4.4
Pooled**	157	133460	850.08			
Total	179	381410				

* Term has one or more empty cells.
** (Residual + Season x Site x Zone + Year x Site x Zone).

from the different reefs (Clarke et al., 2014). The SIMPER analysis in PRIMER was used to calculate the average similarity within groups of samples and the dissimilarity between groups. This procedure also provided the percentage of each category that contributed to the similarity and dissimilarity, and they were ranked according to their importance. No transformation on data was used as there was no need to down weight any category given the percentage cover scale used.

The long-term development of coral health was investigated for five reef sites; Chapwani, Changuu, Bawe, Chumbe and Misali, with data from the early 1990s. We used the non-parametric Spearman rank correlation analysis to describe changes over the years of five selected key elements; total hard coral cover, dead coral cover, algal cover and the cover of the more sensitive *Acropora* genus of corals compared to the less sensitive "non-*Acropora*" species group.

3 Results

3.1 Differences between coral reefs in 2015

Investigation of differences in the coral community structure on reefs around Zanzibar in 2015 revealed an overall significant distinction between reef sites (One-way ANOSIM test, global R = 0.711, p = 0.001). Only two reef sites Nungwi and Mnemba at the northern tip of Unguja could not be distinguished from each other

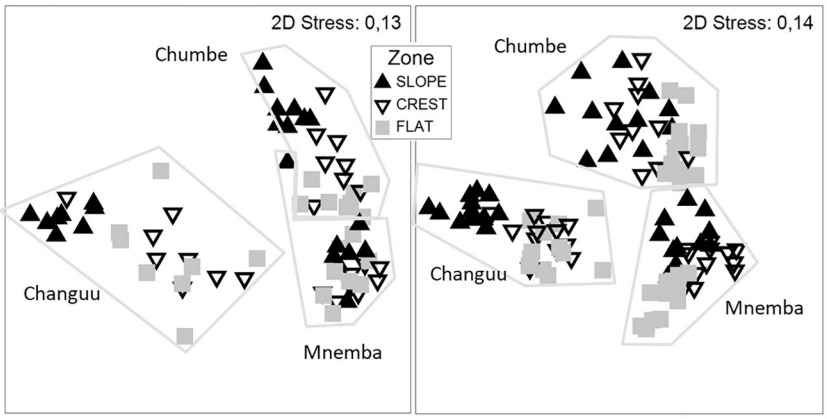

FIGURE 4
MDS plots showing the coral reef community structure of the different locations and sampling zones. This illustrates the importance of location and sampling zones (Flat, Crest and Slope) when considering reef characteristics. he left figure presents data collected in 2010 and 2011 during the short rain autumn season and the right figure data collected in 2011 and 2012 during the heavy rain spring season. Symbols indicate whether observations were made on the slope, crest or top flat part of the reef sites.

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TABLE 3 Mean percentage cover of the most important key elements separating the community on three different reefs at two different seasons.

	Long rain season (Year 2011-2012)			Short rain season (Year 2010-2011)		
	Changuu	Chumbe	Mnemba	Changuu	Chumbe	Mnemba
Porites	***38.4***	3.5	0.3	***37.5***	2.0	0.1
Acropora	2.7	***26.0***	3.7	1.8	***22.2***	4.3
Corallimorpharia	***14.2***	0.5	0.1	***14.7***	0.2	0.1
Algae	12.1	5.9	***22.7***	6.2	4.3	***12.7***
Rock	10.0	11.8	***38.1***	11.6	17.0	***40.3***

Data are averaged percentage cover over transects, reef zones and two years.
The bold values indicate the average cover for the dominating benthic categories within sites.

in the pairwise test (R statistics 0.124 and p = 0.0014). Although all other reef sites differed significantly, the sites near Stone Town (Chapwani, Bawe and Murogo) formed a cluster with pairwise R statistics between 0.232 and 0.409, and this group of reefs differed from the reefs at the northern and southern part of the island (Mnemba, Nungwi and Kizimkazi). Kwale was the only reef found in both of the two major clusters (Figure 2).

To visualize the importance of the key components describing the different reef sites, we provided multidimensional scaling MDS plots where the sizes of the circles represent the cover of the eight most important biological and structural elements (Figure 3). The branching hard coral genus *Porites* and the soft coral Corallimorpharia were present in all transects on three reef sites near Stone Town (Chapwani, Murogo and Bawe). At other reef sites; Mnemba, Kwale, Kizimkazi and Nungwi, the Corallimorpharia cover was very minimal on most transects investigated The hard corals belonging to the genus *Acropora* had considerably higher cover at the offshore Kwale reef on the eastern side compared to all other reef sites. Soft corals, except Corallimorpharians, and algal species were present at all transects investigated at Mnemba, Nungwi and off Kizimkazi and reached a cover of up to 55% and 22% respectively, whereas soft corals other than Corallimorpharia and algae had relatively low coverage at the reef sites off Stone Town. The percentage of "rock" and "rubble" representing solid seabed from old dead coral reefs were considerably higher at the two northern reef sites Nungwi and Mnemba as well as the southern reef off Kizimkazi.

3.2 Effects of site, year, sampling zone and season

The datasets available for investigating differences among years, seasons zones on the reef, and reef sites were collected at Chumbe, Changuu and Mnemba reefs in 2010, 2011 and 2012. All four factors site, year, zone and season differed significantly among themselves and site, zone and year in combination with one another (Table 2). In total 51.2% of the total variation were explained with location being the far most important predictor of benthic habitat structure. Figure 4 illustrates the importance of location and sampling zones for data collected in each of the two seasons.

The SIMPER analysis showed that the most important benthic categories across years, zones and seasons that distinguished the Changuu reef from the other reefs was a substantially higher cover of the hard coral *Porites* and the soft coral Corallimorpharia (Table 3). The presence of a high amount of bare rock together with high algal coverage and almost no hard coral *Porites*, distinguished Mnemba from the other two reefs. There was a negative association between the algal overgrowths and the hard coral coverage at Chumbe. The hard coral *Acropora* was found to be a key genus for Chumbe compared with the other two sites. Altogether, the five key benthic categories (*Porites*, *Acropora*, Corallimorpharia, Algae and Rock) explained 50. 5 to 71.9% of the dissimilarity between the reefs for both seasons.

Data collected in 2011 at Chumbe, Changuu and Mnemba were most suitable to investigate differences between seasons. Algal cover and bare rock were the two most important benthic categories distinguished the two seasons. The average algal cover on the three reef sites was 17.2% in the heavy rainy spring season and only 4.9% in the short rainy autumn season in 2011. The average cover of bare rock shows the opposite pattern with 17.6% in the heavy rain season and 26.4% in the short rain season.

3.3 Long-term changes

In early 1990's, the observed total cover of hard coral species has ranged between 30% and 70% in most years at the four reef sites off Stone Town (Changuu, Chapwani, Bawe and Chumbe), with no significant trend (Figure 5, Table 4). At Misali reef west of Pemba Island, the total cover of hard coral used to be above 70% in the 1990s' but four observations since 2003 were considerably lower at 20 to 30% cover (Figure 5), suggesting a significant decline in hard coral cover (Table 4). Common for all above mentioned five reef sites, except Chapwani, is a significant increase in dead coral over the 25 years of investigation from 1992-2016. The most dramatic increase in dead coral from almost zero to approximately 50% was observed at Misali corresponding to the decrease in total hard coral cover. Changes in algal cover were not significant for any of the

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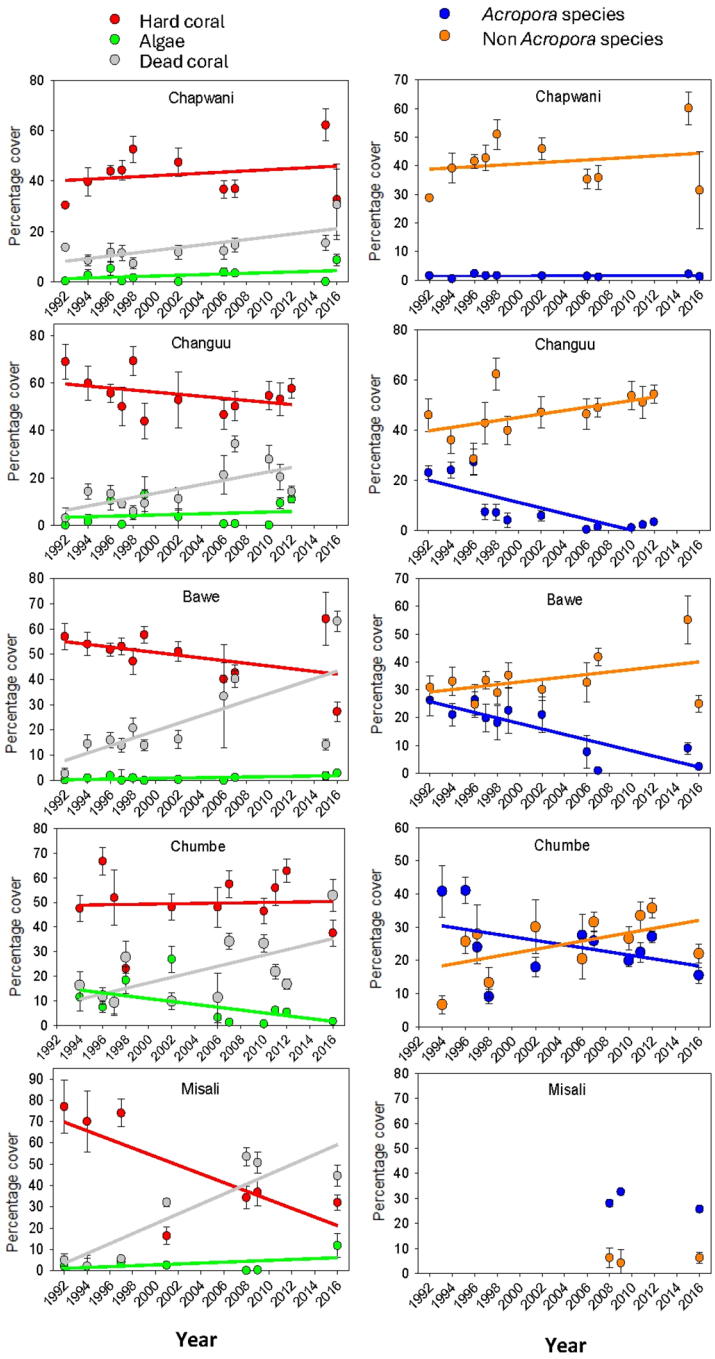

FIGURE 5
Cover of selected key elements (± Standard deviation) from 1992 until 2016 at four reef sites on the sheltered west coast of Unguja Island (Chumbe, Chapwani, Chunguu and Bawe) and one sheltered site (Misali) located off the coast of the northern Island Pemba. Three sites near Stone Town, (Chapwani, Chunguu and Bawe), represent reefs with increasing westward distance from Zanzibar City, with the small island Chumbe south of Stone Town even further away (See Figure 1). The left panel shows the cover of hard corals, dead corals and algae and the right panel shows the overall cover of *Acropora* species and the remaining cover of other hard corals. A full dataset for *Acropora* and non-*Acropora* does not exist for Misali. While the significance of trends is analyzed with Spearman rank correlation analysis (Table 4), linear regression lines are inserted to indicate trends.

reefs, but showed a tendency towards a decrease at the reef site off Chumbe but increased at all other sites (Figure 5, Table 4).

The more sensitive species belonging to the genus *Acropora* have become rare at the three reef sites closest to the Stone Town; Changuu, Chapwani and Bawe (Figure 5). There was a significant decline observed at Changuu and Bawe reefs (Table 4). The coverage of the non-*Acropora* hard coral species have increased significantly at Changuu and Chumbe, and is today dominating the coral community on most reefs around Unguja Island. However, this development is still not observed at Misali reef off Pemba Island.

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TABLE 4 Spearman rank correlation analysis on changes in five selected key elements (*Acropora*, non-*Acropora*, hard coral, dead coral and algae) on five reef sites off the coast of Zanzibar.

Reef site	Variable	r	p-value
Bawe	***Acropora***	**-0.80**	**<0.01**
	Non-*Acropora*	0.23	0.48
	Hard coral	-0.42	0.19
	Dead Coral	**0.65**	**0.03**
	Algae	0.33	0.31
Changuu	***Acropora***	**-0.83**	**<0.01**
	Non-*Acropora*	**0.69**	**0.01**
	Hard coral	-0.30	0.33
	Dead Coral	**0.70**	**0.01**
	Algae	0.23	0.46
Chapwani	*Acropora*	-0.10	0.76
	Non-*Acropora*	0.33	0.33
	Hard coral	0.33	0.33
	Dead Coral	0.46	0.17
	Algae	-0.14	0.68
Misali	Hard coral	-0.60	0.10
	Dead Coral	**0.86**	**<0.01**
	Algae	0.07	0.83
Chumbe	*Acropora*	-0.28	0.36
	Non-*Acropora*	**0.56**	**0.05**
	Hard coral	0.05	0.87
	Dead Coral	**0.57**	**0.05**
	Algae	**-0.63**	**0.03**

The table gives the coefficient of correlation (r) and level of significance (p-value). A negative r indicates a negative change over time and the opposite. Significant changes ($p<0.05$) are highlighted in bold.

4 Discussion

4.1 Differences between coral reefs in 2015

Distinct differences in coral community structures were found among the seven monitored coral reefs in 2015 (Figure 2) and the three studied in 2010-2012. Results from Chumbe, Changuu and Mnemba indicated that some of the deviations identified in the 2015 investigation could be related to comparing different seasons. However, our result supports previous findings (Connell et al., 1997) that composition and coverage of corals and associated flora and fauna could be strongly influenced by physical disturbance and prevailing hydrodynamic regimes. The clear clustering of sites near the main population center, Stone Town, also supports the earlier studies on the importance of human pressure on reef community structure (Johnstone et al., 1998; Staehr et al., 2018). Reef clusters from the northern side of Unguja Island (Nungwi and Mnemba) were very different from the western side (Murogo, Bawe and Chapwani). Even though there were no physical variables measured in this study, which makes it very difficult to draw any conclusions other than based on literature, this finding suggests that protection from strong waves and strong currents (McClanahan et al., 2000) and proximity to human influence such as pollution, fishing pressure and large number of tourists visiting the sites over long time largely defined coral communities near Stone Town. Correspondingly, the similarity of Kwale and Kizimkazi reefs with the reefs from the northern side suggests the resemblances in exposure to physical disturbance and hydrodynamic regimes driven by monsoonal wind patterns, though in an opposite direction. Kizimkazi Reefs were highly exposed to the SE monsoon and were directly affected by strong waves from April to September, and Kwale reef to a lesser degree. Similarly, northern cluster reefs were highly exposed to the NE monsoon and were disturbed mostly from October to March. The partial overlap of the Kwale reef with the western cluster suggested that the southwest orientation provided some protection from the NE monsoon. Similar reef compositions amongst NE and SE monsoon exposed reefs accordingly, indicated the importance of differences in

exposure level more than the location of the reef around the Island in defining the reef communities.

As reef communities develop in response to a combination of environmental, biological, chemical, physical and anthropogenic conditions (Veron and Stafford-Smith, 2000; Bell et al., 2015), it was difficult to relate and isolate the observed differences in 2015 to physical conditions alone. Nevertheless, the observed pattern of key biological and structural elements gave some important insights into the more specific differences in community structure amongst coral reefs (Figure 3). For instance, hard coral species of branching *Porites*, which were predominant in a relatively sheltered cluster of reefs off the Stone Town area, are recognized to thrive best in shallow leeward-sided reefs, as they are sensitive to strong waves and currents (Porter et al., 2017). Likewise, branching hard corals, such as *Acropora* species, are common on sheltered reefs with less wave exposure (Veron and Stafford-Smith, 2000), and indeed Kwale Reefs specifically on the leeward side supported higher cover of this genus. Higher cover of branching *Acropora* was also reported to dominate the sheltered Changuu and Bawe reefs, in particular off Stone Town, until the late 1990s (Obura, 2002; Muhando, 2003) when they were strongly reduced by the El Niño event in 1998 that caused massive coral bleaching. Soft corals and algae are known to thrive best in areas with strong water currents and wave exposure (Fabricius, 2005; Bronstein and Loya, 2014). High contributions from soft corals and algae at exposed reefs of Mnemba, Nungwi and Kizimkazi, along with exposed solid aragonite seabed (rock) and rubbles (Figure 3), were therefore expected. Growth of algae and soft corals such as Corallimorpharia were also expected to flourish in areas with high nutrient levels (McCook, 1999; Miller et al., 1999; Szmant, 2002; Islam and Tanaka, 2004; Fabricius, 2005). While algae did not contribute significantly, the cover of Corallimorpharia was higher on reef clusters near Stone Town (Chapwani, Bawe and Murogo). The findings support the recent observations of elevated levels of nutrients and organic pollution near Stone Town on the west coast of Unguja (Staehr et al., 2018), suggesting that these reefs are more affected by human induced changes compared to more remote reefs.

4.2 Effects of year, season, sites and sampling zone

Differences in the distribution of corals have previously been documented in this region (Mbije et al., 2002). Our detailed sampling from 2010 to 2012 (Changuu, Mnemba and Chumbe reefs) similarly revealed significant differences in coral cover between individual reefs and between reef zones, but also between seasons and years (Figure 4, Table 3). Similar to (Zvuloni et al., 2010), our sampling supports expectations that reefs in well managed marine protected areas such as Chumbe, were in a better state with a higher cover of the sensitive *Acropora* corals, compared to non-protected reefs, such as Changuu or less managed reefs such as Mnemba, that were characterized by a low coral cover (Table 3). Regardless, all three reefs had almost twice as much cover of algae during the heavy rain season compared to other seasons (Table 3). This is because algae proliferate during periods of high sea-surface temperatures and elevated nutrient run-off thus supporting algal growth during the heavy rain season, before being abraded during the cold and windy SE monsoon period in June to August (Shunula, 1988; Ussi, 2014). There was a slight negative association between the algal overgrowths and the hard coral cover at Chumbe, which suggests that seasonal differences in algal overgrowth could have affected estimates of hard coral cover. Although there were significant differences in the cover of algae and hard coral cover between the two main seasons at Chumbe (Table 4), the overall projection revealed a positive trend in hard coral cover over the years and a negative trend in macroalgal cover (Figure 5). The results imply that with our current monitoring approach and the available dataset, we fail to conclude with confidence if this observed algal growth cover seasonality at Chumbe could affect coral cover. This possible bias therefore highlights the necessity of optimizing the coral reef monitoring methodology, which should account more accurately for hard corals and algae, and the relationship/association between these two. Furthermore, a consistent sampling period is highly recommended.

Similar to the 2015 data set, we observed a higher cover of soft coral Corallimorpharia at the Changuu Reef from 2010 to 2012. This reef was very close to the untreated sewage water effluents from Stone Town, indicating that the site was affected by elevated nutrient levels (Muhando et al., 2002; Staehr et al., 2018). In comparison, reefs near Mnemba on the north coast had a higher cover of bare rock and algae but lower cover of soft corals and *Porites*. It seemed likely that this difference resulted from a higher exposure to strong waves and currents (Richmond and Francis, 2001; Mbije et al., 2002; Bronstein and Loya, 2014), and that only the substrate became occupied seasonally by resistant sessile benthic species, like certain macroalgal species.

4.3 Long-term changes

Historically, reef communities close to Stone Town, specifically Changuu and Bawe, were more similar to the remote reefs further away from Stone Town such as Chumbe and Kwale. Being geographically located on the sheltered western side of the major Unguja Island, these reefs were initially dominated by dense populations of branching *Acropora* coral, which develop well in sheltered areas (Muhando, 2003). Our results showed that from 1992 to 2016, the cover of hard corals ranged between 40% and 80% in the five monitored reef sites. There was, however, an overall decline in *Acropora* at four of the reef sites with an annual average loss of 0.5-2.3% since 1997. The loss of *Acropora* was mostly profound at Bawe and Changuu (Figure 5). Devastation by the invasive crown-of-thorns starfish that started in 1997 (Obura, 2002; Ussi, 2009), followed by a massive coral bleaching event in 1998, resulted in a widespread mortality of *Acropora* (Wilkinson, 1998; Obura, 2002). The crown-of-thorns starfish problem reappeared from 2004 to 2009, and resulted in even higher mortality of recovering *Acropora*. A crown-of-thorns starfish removal program was introduced at Chumbe from 2004 (Muhando and Lanshammar, 2008). Interestingly, the cover of *Acropora*, with a persistent crown-of-thorns starfish removal program, increased considerably

compared to other sites like Bawe and Changuu (Muhando and Lanshammar, 2008) until the 2016 El Niño bleaching event (Gudka et al., 2018) (Figure 5). The findings suggest that the establishment of marine protected conservation areas with active management including consistent removal of the reef predator like the invasive crown-of-thorns starfish, together with control of fishing activities (Staehr et al., 2018) could have enhanced the recovery of *Acropora* corals. In a similar way, the coral reef at Misali, Pemba was severely damaged by the El Niño event in 1998, diminishing the hard coral cover by a factor of 4 (Figure 5). Establishment of a non-extraction zone (~protected area) within a Marine Conservation Area Reef helped hard corals recovery (Poonian, 2008). Our data furthermore documented recovery of *Acropora* during the last three investigations in 2008, 2009 and 2016 at Misali reefs. However, prior to 2007, there was no record of *Acropora* in Misali because the benthic cover categories during data collection did not consider specific species or species groups. In comparison, non *Acropora* species had increased on all our reef sites around Unguja Island, although not significantly. The other more remote reef among surveyed sites of Unguja, Kwale, showed some stability in hard coral cover. The observed stability could explain the impact of less exposure to human pressure due to a greater distance from human residence and better exchange of clean waters. In summary, these results highlighted the recovery potential of Zanzibar reefs, given proper management of human related pressures, allowing reefs to remain at proper thriving conditions.

According to (Vytopil and Willis, 2001) the loss in *Acropora* cover could have negative impact on reef communities due to loss of important microhabitats. Branching, bushy and tabulate *Acropora* corals are well known to significantly contribute to reef complexity, which importantly provides microhabitats for juveniles of many fish species and other invertebrates (Stella et al., 2010; Graham and Nash, 2013). Likewise, branching *Acropora* is known to contribute to increased modifications to the local hydrodynamic environment (Holmes and Johnstone, 2010), and increased potential for niche separation (Ricklefs and Schluter, 1993). Hence, the loss of *Acropora* on reefs off Zanzibar has likely caused important negative changes in reef ecosystem functions.

The highest cover of algae was observed on Chumbe reef in the 1990s and early 2000s, with a gradual decrease in recent years where reef management intervention has been in place (Muhando and Lanshammar, 2008). In comparison, algal cover seemed to be gradually increasing at Changuu lately and at Chapwani and Misali in 2016. This change in algal cover could have been influenced by changes in local conditions in terms of water quality (D'Angelo and Wiedenmann, 2014; Risk, 2014; Silbiger et al., 2018). Changuu and Chapwani were prone to nutrient pollution from Stone Town (Staehr et al., 2018). However, the varying sampling season likely played an important role as well, as shown in Table 3. Regardless, the results highlight the necessity of detailed monitoring of water quality along the coast of Zanzibar to strengthen coastal ecosystem management through pollution control.

The global coral reef ecosystems have experienced substantial fluctuations over the past times due to numerous environmental pressures, including climate change, overfishing, and pollution (Hughes et al., 2017). Recent assessments reveal that about half of the world's coral reefs are considered degraded due to these environmental stressors. Live hard coral cover was comparatively stable until the first massive coral bleaching event in 1998. The event led to a substantial 8% loss in global coral cover. Between 2009 and 2018, there was an additional decline of approximately 14% in coral cover, mostly due to recurrent large-scale coral bleaching events exacerbated by deficient recovery periods between events (Souter et al., 2021). The observed trend in coral cover in this study contributes to the reported global decline. However, efforts to improve reef management, increase resilience through reef restoration techniques, and global initiatives to decrease greenhouse gas emissions are critical to reversing some of these trends and safeguarding future coral health. Overall, the health of the world's coral reefs is a combination of challenging declines and hopeful signs of resilience, underscoring the need for continued conservation and intervention efforts to preserve these vital ecosystems.

4.4 Implications for management and monitoring of coral reefs around Zanzibar

In conclusion, we provide the first documentation of long-term degradation of coral reefs in Zanzibarian waters with significant increase of areas with dead corals at the investigated sites. For most reefs, particularly sites off Stone Town, we report a significant decline of *Acropora* species being replaced by non-*Acropora* species and the soft coral Corallimorpharia, which were favored by elevated nutrient concentrations (Muhando et al., 2002). El Nino events and invasion by crown-of-thorn starfish likely also contributed to this decline, with physical disturbance from fisheries and tourism further exacerbated the degradation (Staehr et al., 2018). These findings call for concern and the need for better management of human influence. In particular, attention should be given to control of coastal pollution with nutrients and toxic substances. Attention should also be given to destructive fishing efforts and other physical damage on reef structures, such as underwater tourism. Such management is vital for development of a long-term sustainable local food supply and tourist industry. Promising results were provided from the protected reef site at Chumbe, where enforced restriction of tourists and fishing as well as active efforts to reduce the numbers of invasive crown of thorn starfish have been undertaken. These initiatives showed a strong recovery potential of Zanzibar coral reefs even after severe El Nino events, with regrowth of sensitive *Acropora* species and a flourishing fish community. To better understand the causes and effects of these human mediated pressures, and possible mitigation success, a long-term monitoring program needs to be implemented. To evaluate the success of urgently needed management to ensure continued health function of these highly valuable coastal habitats, it is essential to strengthen the currently fragmented monitoring on reef health around Zanzibar. The monitoring of coral reef communities should apply a methodology that accounts for effects of seasonality by describing algal cover and fauna as an add-on cover on top of the hard substrate of living and dead coral structures and other sessile faunal organisms.

Consistent reef monitoring is important to document the changes of corals and associated communities to climate change, and other anthropogenic and/or natural disturbances. Such knowledge is essential for identifying areas of concern, initiate conservation and restoration actions to protect and restore endangered reef sites.

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 manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

AU: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. MM: Conceptualization, Data curation, Investigation, Methodology, Writing – review & editing. RR: Writing – review & editing. MS: Writing – review & editing. PS: Conceptualization, Data curation, Formal analysis, Methodology, Writing – review & editing. CM: Investigation, Writing – review & editing. SY: Investigation, Writing – review & editing. KD: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing.

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Conflict of interest

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

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Appendix A

Seven key benthic categories (SN 1-7) used for monitoring from 1992 until 1999 including different species, species groups and substrate (benthic objects).

Category number	Benthic category	BENTHIC OBJECTS (OBJECT ID)
1	Live hardcorals (HC)	*Acropora*, branching (ACB) *Acropora*, encrusting (ACE) *Acropora*, submassive (ACS) *Acropora*, digitate (ACD)
		Acropora, tabulate (ACT)
		Coral, branching (CB) Coral, encrusting (CE) Coral, foliose (CF) Coral, massive (CM) Coral, submassive (CS) Coral, mushroom (CMR) Coral, millepora (CME) Coral, heliopora (CHL)
2	Soft corals (SC)	Soft coral (SC)
3	Sponges (SP)	Sponges (SP)
4	Algae (AL)	Coralline algae (CA)
		Algal assemblage (AA) Algae, Halimeda (HA) Algae, Macroalgae (MA) Algae, Turf algae (TA)
5	Others (OT)	Seagrass (SG)
		Zoanthids (ZO)
		Clam (CLAM) Corallimorpharian (RH) Others (OT)
6	Substrate (SU_1)	Sand (S)
		Silt (SI)
7	Substrate (SU_2)	Rock (RCK)
		Rubble (R) Dead coral (DC) Dead coral with algae (DCA)

Appendix B

Nine key benthic categories used for monitoring from 1999 to date including different species, species groups and substrate (benthic objects).

Category number	Benthic category	Benthicobjects	Object ID
1	ACROPORA	Acr-branching	ACB
	ACROPORA	Acr-digitate	ACD
	ACROPORA	Acr-encrusting	ACE
	ACROPORA	Acr-tabulate	ACT
	ACROPORA	Acr-submassive	ACS
	NON-ACROPORA	*Acanthastrea*	Acan
	NON-ACROPORA	*Alveopora*	Alve
	NON-ACROPORA	*Astreopora*	Astr
	NON-ACROPORA	*Blastomussa*	Blas
	NON-ACROPORA	*Caulastrea*	Caul
	NON-ACROPORA	*Coscinarea*	Cosc
	NON-ACROPORA	*Cyphastrea*	Cyph
	NON-ACROPORA	*Diploastrea*	Dilp
	NON-ACROPORA	*Echinophyllia*	Echph
	NON-ACROPORA	*Echinopora*	Echpo
	NON-ACROPORA	*Euphyllia*	Euph
	NON-ACROPORA	*Favia*	Favia
	NON-ACROPORA	*Favites*	Favit
	NON-ACROPORA	*Fungia*	Fung
	NON-ACROPORA	*Galaxea*	Gala
	NON-ACROPORA	*Gardinoseris*	Gard
	NON-ACROPORA	*Goniastrea*	Gonia
	NON-ACROPORA	*Goniopora*	Gonio
	NON-ACROPORA	*Halomitra*	Halo
	NON-ACROPORA	*Herpolitha*	Herp
	NON-ACROPORA	*Hydnophora*	Hydn
	NON-ACROPORA	*Leptastrea*	Lepta
	NON-ACROPORA	*Leptoria*	Lepto
	NON-ACROPORA	*Lobopyllia*	Lobo
	NON-ACROPORA	*Merulina*	Meru
	NON-ACROPORA	*Millepora*	Mill
	NON-ACROPORA	*Montipora*	Monti
	NON-ACROPORA	*Montastrea*	Monta
	NON-ACROPORA	*Mycedium*	Myce
	NON-ACROPORA	*Oulastrea*	Oula
	NON-ACROPORA	*Oulophyllia*	Oulo
	NON-ACROPORA	*Oxypora*	Oxyp
	NON-ACROPORA	*Pavona*	Pavo
	NON-ACROPORA	*Physogyra*	Physo
	NON-ACROPORA	*Platygyra*	Platy

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Continued

Category number	Benthic category	Benthicobjects	Object ID
	NON-ACROPORA	*Plerogyra*	Plero
	NON-ACROPORA	*Pleiastrea*	Plei
	NON-ACROPORA	*Pocillopora*	Poci
	NON-ACROPORA	*Podabacia*	Poda
	NON-ACROPORA	*Porites* branching	Pobr
	NON-ACROPORA	*Porites* massive	Poma
	NON-ACROPORA	*Psammacora*	Psam
	NON-ACROPORA	*Seriatopora*	Seri
	NON-ACROPORA	*Stylophora*	Styl
	NON-ACROPORA	*Symphyllia*	Symp
	NON-ACROPORA	*Turbinaria*	Turb
	NON-ACROPORA	Unid-Corals	Co-ot
2	CO-ALGAE	Coralline algae	CA
3	S-CORAL	Soft corals	SC
4	SPONGES	Sponges	SP
5	ALGAE	Algal Assemblage	AA
	ALGAE	Halimeda	HA
	ALGAE	Macroalgae	MA
	ALGAE	Turf algae	TA
6	OTHERS	Seagrass	SG
	OTHERS	Zoanthids	ZO
	OTHERS	Clams	CLAM
	OTHERS	Others	OT
7	CO-MORPH	Corallimorpharia	RH
8	SUB_1	Dead coral	DC
	SUB_1	Rock	RCK
	SUB_1	Dead coral with algae	DCA
	SUB_1	Rubble	R
9	SUB_2	Sand	S
	SUB_2	Silt	SI
	SUB_2	Water	WA

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Environmental impact on marginal coastal benthic communities within the Jeju Island, South Korea temperate transition zone

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Aim of study: Marine climatic transition zones are boundary areas of major climate zones, here the boundary between the subtropical and temperate zones. They present areas containing high abundance of organisms living at the limit of their physiological tolerance. These marginal populations are particularly sensitive to changes in their environment. As such, marine climatic transition zones are excellent natural playgrounds for climate change-related hypothesis testing, especially with respect to marine habitat response to ocean warming. The marginal biogenic habitats around Jeju Island, South Korea, which lies within the temperate transition zone, have gradually changed from macroalgal-dominated to hard coral-dominated habitats. Understanding the specific abiotic environmental factors that influence the distribution of the marginal populations in temperate transition zones (i.e., species at their occurrence limit) is crucial to predicting and managing temperate zone habitat changes caused by climate change. This study aims to identify the specific abiotic environmental factors that contribute to explaining the current spatial distribution of the declining temperate and expanding subtropical foundation species in Jeju waters.

Methods: Coverage and composition of sessile benthic communities were determined by photo-quadrat analysis at two depths (10 m and 15 m) at three sites along the island's south, east, and north coasts in May and November 2022. Divergences in community composition between sites were characterized in light of ten quantitative environmental parameters.

Results: Our results show that sessile foundation communities vary significantly at different sites around the island. While the south is defined by high-latitude hard corals, predominately *Alveopora japonica*, the east is defined by the temperate canopy-forming macroalga *Ecklonia cava*, and the north is characterized by coralline algae. Winter sea surface temperature, water transparency, nutrient concentration, and water movement were statistically the most impactful environmental factors determining which foundation species constitute each distinct benthic community.

Conclusion: This study provides valuable baseline information on the impacts of abiotic environmental factors on marine sessile communities in a temperate transition zone.

KEYWORDS

barren grounds, climatic transition area, environmental control, foundation species, high-latitude hard corals, kelp forest, marginal populations, ocean warming

1 Introduction

Marine climatic transition areas are geographically located between two separated climate zones, but they display a combination of characteristics from both. This leads to a high environmental variability that promotes the co-occurrence of different marine communities (Ferro and Morrone, 2014; Shimabukuro et al., 2023). These communities are considered marginal communities, describing the fact that they experience environmental conditions near their physiological limit, which makes them particularly vulnerable to changes in environmental conditions, biotic interactions, and local extinctions (Kawecki, 2008; Wernberg et al., 2016; Agostini et al., 2018; Soares, 2020). Jeju Island, the southernmost region of South Korea (33°23.75' N, 126° 33.42' E), is a temperate transition zone, as it is part of the Temperate Northern Pacific ecoregion, but exhibits subtropical characteristics due to the Kuroshio Current, a massive, subtropical current that brings warm, oligotrophic waters to the region (Sakamoto et al., 2005; Spalding et al., 2007; Wu et al., 2012). In fact, Jeju Island lies between two climatic zones with alternating influence depending on the season: the "polar dry" in winter and "tropical/subtropical moist" (due to a short monsoon) in summer (Shimabukuro et al., 2023). Additionally, Jeju Island is frequently affected by typhoons (Park et al., 2006; Lee K.-T. et al., 2023). Over the past half a century, the coastal waters of Jeju, and the Korean mainland in general, have recorded a rise in annual sea surface temperature (SST) by +1.23°C, 2.5 times the global average (Belkin, 2009; Wu et al., 2012; Hobday and Pecl, 2014 ; Han and Lee, 2020; Tang et al., 2020). Takatsuki et al. (2007) reported an increase in Jeju winter SST by 2.1°C per century from the early 20th century until 2007, while Kim T. et al. (2022) reported a rise in Jeju winter SST of 3.6°C over the last 36 years (compared to just 0.7°C in summer). This trend is associated with an increase in heat wave- and typhoon-frequency and -intensity (Oouchi et al., 2006; Park et al., 2006; Lee S. et al., 2023), highlighting Jeju Island's significant position as a climate change hotspot (Hobday and Pecl, 2014). All these circumstances lead to a large portion of Jeju's marine life being highly susceptible to environmental changes, especially benthos with limited mobility and dispersal abilities, such as sessile species.

Although biotic interactions, anthropogenic pressures, and general environmental conditions all determine benthic marine community composition, including species distribution and diversity dynamics (Sousa, 1984; Hillebrand, 2004; Campbell et al., 2014; Pinsky et al., 2020), water temperature is largely accepted as a primary factor in structuring species distribution (Sunday et al., 2012; Tanaka et al., 2012; Ribas-Deulofeu et al., 2023). Therefore, marine climatic transition zones are expected to undergo severe changes in their biogenic habitats as a consequence of global ocean warming. Changes in marine community composition, detrimental to native temperate species, such as increasing numbers of species with tropical affinities and species of turf-forming algae, have already been observed in high-latitude areas worldwide, for example, in the Atlantic Ocean along the Portuguese continental coast (de Azevedo et al., 2023), the west Pacific Ocean and East China Sea along the Japanese coast (Yamano et al., 2011), and the Indian Ocean along the western Australian coast (Wernberg et al., 2016). This settlement of subtropical and tropical species in temperate ecosystems also raises concerns about the management of marine systems, as it may be too difficult to return to previous states (Hobbs et al., 2006; Beger et al., 2014; Makino et al., 2014; Pecl et al., 2017). Moreover, prominent changes in foundation species, such as a kelp species, can have cascading consequences for the entire community (Vergés et al., 2014) by altering biotic interactions and modifying the habitat, hence the goods and services the ecosystem provides (Kang, 2010; Pecl et al., 2017; Aguilar et al., 2022). Until the late 1980s, Jeju Island's benthic ecosystem was dominated by temperate kelp forests, especially the native species *Ecklonia cava* (Kang, 2010). This foundation species plays a critical role for associated organisms, providing shelter, food, and nursery grounds (Steneck et al., 2002; Filbee-Dexter and Wernberg, 2018). The fishing industry in South Korea, especially on Jeju Island, relies heavily on kelp forest habitats to sustain economically valuable species (Kang, 2010, 2011; Hwang et al., 2013). Previous changes in canopy-forming algae coverage have reportedly decreased commercial animal species catches (Serisawa et al., 2004; Kang, 2010). Currently, the *E. cava* population around Jeju Island is declining and being replaced by a variety of species, especially crustose coralline algae (CCA), leading to the formation of a habitat type known as "barren grounds" (Kim, 2006; Kang, 2010). This phenomenon, called "*getnoguem*" in Korea, is similar to "*isoyake*" in Japan (Fujita, 2010; Lee et al., 2022). Barren grounds are characterized by large areas of bare rock, extensively covered by CCA, and exhibiting low biodiversity (Serisawa et al., 2004; Kang, 2010; Uribe et al., 2015). Around Jeju Island, barren ground

coverage has increased by nearly 11% over a 5-year period between 1998 and 2003, at which point it was covering 4541 hectares of coastal seafloor (Kim, 2006).

This study aims to investigate the distribution of marine benthic communities in Jeju waters with regard to local environmental conditions. As such, focus was laid on dominant sessile macro-foundation species, such as canopy-forming algae (characterizing kelp forests), coralline and turf-forming algae (characterizing barren grounds), hard corals (characterizing high-latitude coral habitats), soft corals (characterizing soft coral beds), and sponges and bryozoans (characterizing sessile invertebrate macrofauna habitats). To determine how site-specific local stressors and hydrographic parameters may influence marginal marine communities, three sites from different parts of the island were chosen to ensure an extensive range of biotic and abiotic data. At each site, sessile communities at two specific water depths were analyzed to determine potential depth-related changes in species coverage and composition, as depth is directly correlated with light and nutrient availability and, as such, impacts the vertical zonation of many marine benthic species, especially photosynthetic organisms and organisms sensitive to nutrient flux and chlorophyll content, respectively (Kang and Kim, 2012; Muir et al., 2015). This study provides valuable insights into the primary abiotic environmental factors that can structure coastal benthic communities on an annual scale in a marine climatic transition zone.

2 Materials and methods

2.1 Study site

This study was conducted at three sites around Jeju Island: Sinheung (SH) in the northeast (33°33.5173' N, 126°39.1891' E), Seongsan (SS) in the east (33°27.2356' N, 126°56.5033' E), and Bomok (BM) in the south (33°14.2995' N, 126°35.3935' E) (Figure 1B). Globally, Jeju Island is surrounded by the Yellow Sea in the east, the East/Japan Sea in the west, and the East China Sea in the south (Figure 1). Jeju Island's marine environment is strongly influenced by the Kuroshio Current (Figure 1A), which is characterized by high temperature, high salinity, and low dissolved oxygen values (Park, 1986; Choe, 1988). Specifically, the Tsushima Warm Current (TWC; Figure 1A), a warm and saline surface branch of the Kuroshio Current, which originates at 31°N and flows northward reaching the southern coast of Jeju Island, has a strong influence during summer (Lie et al., 1998; Hur et al., 1999; Cha and Moon, 2020). The majority of the TWC passes southeast of the island, flowing eastward up to the Tsushima Strait, while a minor branch flows westward and turns clockwise in the Jeju Strait as Jeju Warm Current (Teague et al., 2003; Cha and Moon, 2020) (Figure 1A). However, coastal circulation is primarily driven by tidal currents, particularly in the Jeju Strait, north of the island (Cha and Moon, 2020). These regional impacts are measurable, leading to distinct environmental conditions between the north and the south of the island, with a conspicuous thermal north/south gradient expressed by average annual water temperatures of 18.8 ± 4.5°C and 20.0 ± 4.6°C, respectively (average SST from 2004 to 2022; Korea Marine Environment Management Corporation, http://data.kma.go.kr/, accessed on 08 March 2023). Despite these local differences, environmental conditions present a strong seasonality. In winter, the coastal waters are mainly influenced by strong and cold Siberian winds, cooling down the water column (Hur et al., 1999). In summer, the fresh discharge of the China-based Changjiang River combined with the summer monsoon accentuates the stratification of Jeju waters by reducing sea surface salinity (Park, 1986; Hur et al., 1999) (Figure 1A). Despite the natural differences in water mass-driven conditions, each site is, in varying degrees, affected by locality-specific anthropogenic stressors. The northern SH site is located within proximity of three fish farms (distance of 890 m to 1331 m), while the eastern SS site is far from any obvious artificial effluents. The southern BM site is just 350 m from a sewage treatment plant.

2.2 Environmental variables

All abiotic environmental variables applied in this study were extracted from publicly available websites. Hydrographic variables are available from the Korea Marine Environment Management Corporation website (KOEM, n.d.) , while meteorological variables are available from the website of the Korean Meteorological Administration (KMA, n.d.). Data from 2004 (beginning of systematic record at the sites) to 2022 were used. Hydrographic variables (KOEM data) were collected quarterly (i.e., February, May, August, November; one data point each) by boat survey from coastal surface waters at each site (1.5–2.5 km from the coastline) (Figure 1B). KOEM parameters were measured using a CTD-rosette sampler followed by laboratory analyses (Korea Marine Environment Management Corporation, 2019). KMA variables were recorded hourly at each site from ground atmospheric observatories (Synopsis Weather Observations - ASOS program). Consequently, for meteorological variables, the monthly average for February, May, August, and November, respectively, was computed to also gain one data point for each month. Recording locations closest to the coordinates of our respective sampling site were chosen (indicated by stars on the map; max. distance to study site: 10 km; Figure 1B).

A total of 10 variables were chosen for statistical analyses, 9 hydrographic variables and 1 meteorological variable: Chlorophyll *a* (Chl*a*; µg L^{-1}), Dissolved Inorganic Nitrogen (DIN; µg L^{-1}), Dissolved Inorganic Phosphate (DIP; µg L^{-1}), Dissolved Oxygen (DO; mg L^{-1}), pH, Salinity (PSU), Suspended Organic Matter (SOM; mg L^{-1}), Sea Surface Temperature (SST; °C), Transparency (m) (from KOEM); and Wind Speed (WS; m s^{-1}) (from KMA). An additional 4 variables were considered for discussion purposes: Nitrite (NO_2^-; µg L^{-1}), Nitrate (NO_3^-; µg L^{-1}), Ammonia (NH_4^+; µg L^{-1}) (from KOEM); and Wind Direction (WD; degrees) (from KMA). Nutrient concentration-related variables (DIN, DIP, NO_2^-, NO_3^-, NH_4^+) were converted to µmol L^{-1} based on the corresponding molar masses to facilitate comparisons to the literature. Wind speed and direction were used as proxies for water movement and surface currents (Charlier, 2005; Skirving et al., 2006).

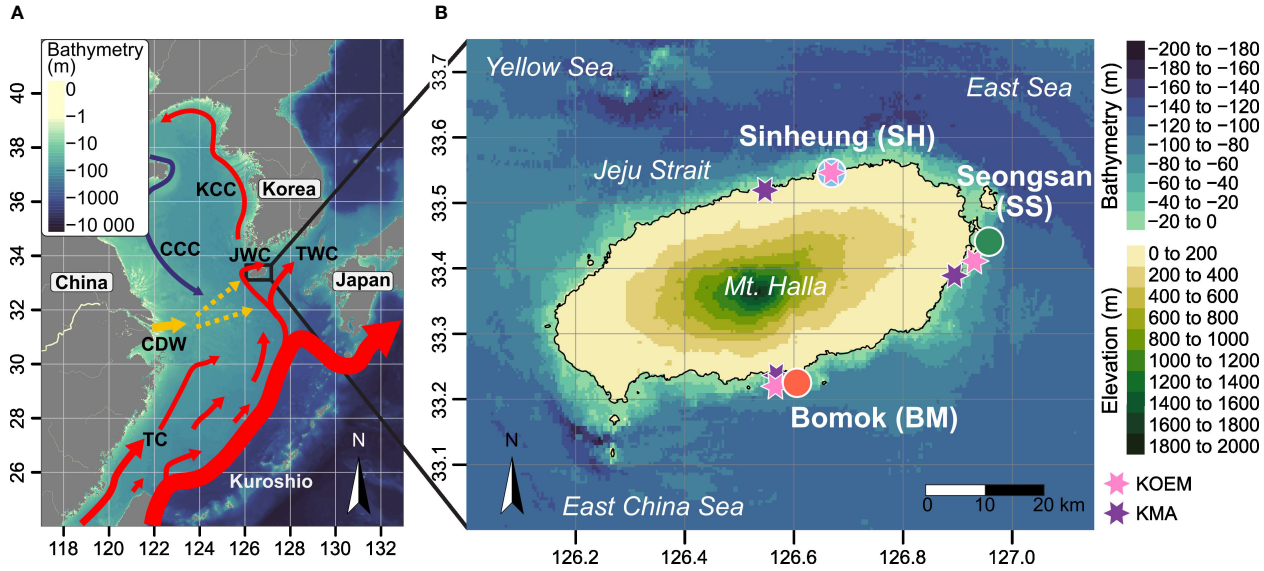

FIGURE 1
(A) Map of the study region and the main currents (based on Park et al., 2017; Figure 4A). CDW, Changjiang Discharge Water; CCC, Chinese Coastal Current; JWC, Jeju Warm Current; KCC, Korean Coastal Current; TC, Taiwan Warm Current; TWC, Tsushima Warm Current. **(B)** Map of study sites on Jeju Island, South Korea. Dots represent sites with permanent 100-m line transects at 10 m and 15 m depth. Purple stars are KMA stations (wind speed and direction data), and pink stars are KOEM stations (all other environmental data). Bathymetry and elevation data are from NOAA. Coastline coordinates are from GADM website (accessed on 17 November 2023).

2.3 Benthic community

Two surveys were carried out by scuba diving in May and November 2022, respectively. These months were chosen to avoid extreme summer and winter environmental values, in order to reduce seasonal variations in the data set and obtain a representative picture of benthic communities by site. Indeed, May and November show temperatures close to the annual average (Supplementary Table 1), and this study focuses on dominant foundation macro-species at each site, all of which have a perennial life cycle and an overall annual stable coverage (Haroun et al., 1989; Vieira et al., 2016). At each site, permanent 100-m line transects were installed at 10 m and 15 m depth, respectively, parallel to the coastline following each isobath. The 10 m and 15 m depths were chosen according to the vertical distribution of dominant benthic species around Jeju Island (Supplementary Table 2) and to avoid intertidal and sand bottom zones, respectively. The transects were installed in a "zigzag" fashion to cover a wider area (Supplementary Figure 1). Along the transects, 100 photos (1 x 1 m) were taken at each site and depth using an underwater camera (Sony ILCE-7RM3A with underwater housing; maximum resolution of 7952 × 5304 pixels). The "zigzag"-scheme ensures that the one photo taken at every meter of the respective permanent transect does not overlap with the next. The camera was mounted on a tetrapod quadrat to maintain a constant distance from the substrate and ensure comparable pictures. At the SH-10m site, data are missing for the November 2022 survey because typhoon Hinnamnor destroyed the permanent line transect at that depth in September 2022.

Dark, blurred, and poorly framed images were excluded from the photo stack (n = 12 in May, and n = 8 in November). From the remaining photos, 30 images (i.e., replicates) were randomly selected using the "base::sample" function in R from each "site-depth-month" group (e.g., BM-10m-May; hereafter called "group") for image annotation. The PhotoQuad® software (version 1.4; Trygonis and Sini, 2012) was used to identify and quantify benthic organisms and bare substrate in each group following our benthic community categories (Supplementary Table 3). The relative percentage cover of the benthic community in each photo-quadrat was estimated using the software's stratified random points count tool (Figure 2). On each image, a point was randomly placed on each of the 100 grid cells (i.e., 100 points), and the underlying benthic organism and substrate type (i.e., sand, gravel and rock) was identified to the lowest possible taxonomic level (Supplementary Table 3; except for coralline and turf algae) based on visual information, such as texture, color, and shape. Taxonomic identification was mainly based on fieldwork taxonomic books of Jeju and Japanese coasts (Masuda et al., 1986; Sugihara et al., 2014; Kim M.-S. et al., 2022). Indeterminate annotations and motile benthic organisms, such as asteroids and other echinoderms, polychaetes, holothurians, bivalves, and gastropods were removed before statistical analyses. Sand, gravel, and rock annotations were grouped in the "Substrate" category, which was included in the analysis as the only non-biological component because of its essential role in habitat characterization. Based on the overall species percentage distribution in our data set, a species or non-biological component was described as "major" when its coverage was greater than 2.5% in a group. "Dominance" was defined as a coverage over 25% by a single species or category in a group (e.g., BM-10m-May), following Reimer et al. (2021). All remaining species (cover < 2.5%) were merged into the "Other" category. Coverages were reduced to 100% at the group level. As the dense

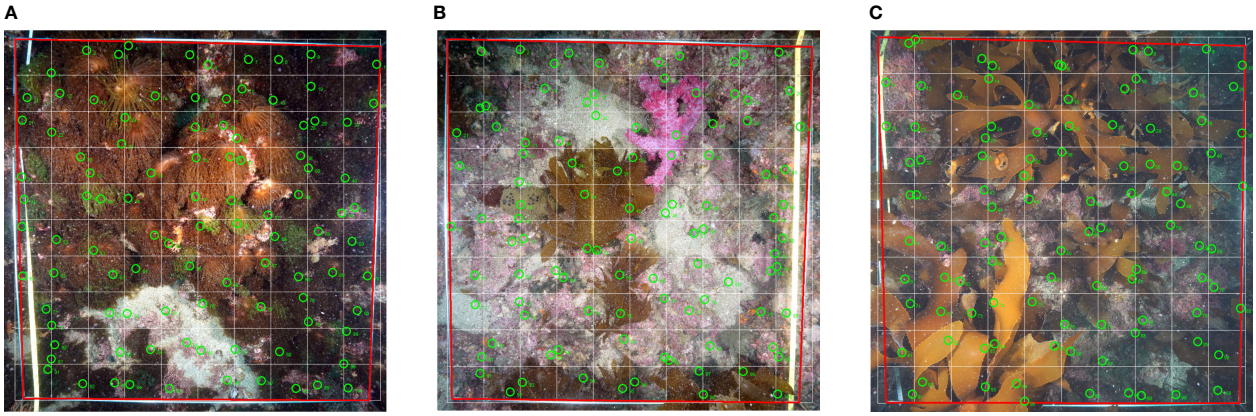

FIGURE 2
Examples of photo-quadrat annotations on PhotoQuad® of **(A)** Bomok site at 15 m, **(B)** Sinheung site at 15 m, and **(C)** Seongsan site at 15 m, in May. The stratified random points count method (100 points per image) was used to assess the relative percentage cover (%) of benthic communities.

kelp cover obstructs the vision of underlying species, this photo-quadrat method cannot be used to study species-specific coverages and biodiversity in the presence of canopy-forming algae, and percentage cover data have been interpreted cautiously. All species categories used to classify benthic communities in the image annotations are listed in Supplementary Table 3.

2.4 Statistical analyses

All statistical analyses were performed using R (version 4.3.0).

2.4.1 Environmental variables

Statistical analyses were carried out for each month independently (i.e., February, May, August, and November, corresponding to four time series of 18 points each) to eliminate seasonal variability in the results. Each monthly time series was then detrended using linear regression to remove the inter-annual trend, thus obtaining each site's "average" environmental conditions and avoiding masking spatial variability. The median of each monthly time series was summed with the regression's residuals (Supplementary Figure 2). The resulting data (hereafter called "environmental data") were used in further statistical analyses.

A Principal Component Analysis (PCA) was performed on the ten standardized abiotic variables selected to assess spatial divergences in environmental conditions. The PCA distance biplot (i.e., scaling 1) was used to visualize the most impactful environmental variables contributing to the spatial data ordination. Furthermore, to test the effect of space (i.e., site) and time (i.e., year) on environmental conditions, a non-parametric Multivariate Analysis of Variance (PERMANOVA; vegan::adonis2) was carried out (Anderson, 2001). A Kruskal-Wallis test (KW) was performed on each variable to specifically determine which environmental parameters vary according to the factor "site" (Kruskal and Wallis, 1952). When the test was significant, a Dunn's post-hoc test with a Bonferroni correction for multiple comparisons was performed (Dunn, 1964).

2.4.2 Benthic community

Multivariate analyses were conducted at the species level. The percentage cover matrix of the benthic community was transformed using Hellinger's method to reduce the weight of rare and absent species (Legendre and Gallagher, 2001).

To investigate which spatiotemporal factor (i.e., "site", "depth", and "month") statistically influences benthic communities the most, partial Redundancy Analysis (pRDA) was carried out (Legendre and Legendre, 2012). The pRDA searches for the variability in the community matrix explained by a single, main explanatory factor (i.e., the constraining factor) by removing the variability induced by additional explanatory variables (i.e., the conditioning factors). In this study, the factors "site" (i.e., BM, SH, SS), "month" (i.e., May, November), and "depth" (i.e., 10 m, 15 m) were each, in turn, considered as the main explanatory factor, resulting in three pRDA models. The RDA*x* axes indicate the proportion of variation explained by the pRDA model, while PC*x* axes indicate the proportion of variation in the residuals (which is not explained by any model). After each pRDA, a permutation test (nperm = 999) was used to test for the analysis' significance and each RDA axis' significance. In addition, the effect of each spatiotemporal factor without interaction (i.e., "site", "depth", and "month", respectively) on the percentage cover of the benthic community was tested using PERMANOVA. The test was performed using the Hellinger distances of the percentage cover matrix, with 9999 permutations. For the factor "site", as it contains three levels, as soon as a significant difference between benthic communities was detected, a post-hoc, pairwise PERMANOVA test (pairwiseAdonis::pairwise.adonis) with Bonferroni significance correction was conducted to identify which site was responsible for the difference. The role of biotic interactions in shaping benthic communities was excluded from the scope of this paper.

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TABLE 1 (A) PERMANOVA test results from Euclidean distance matrix of the 10 standardized environmental data. (B) Pairwise PERMANOVA test results for the factor "site".

(A)	Month	Factors	R^2	F Statistics	P-value
	February	Site	0.140	11.536	**0.0001**
		Year	0.641	5.869	**0.0001**
	May	Site	0.073	5.614	**0.0001**
		Year	0.692	5.904	**0.0001**
	August	Site	0.078	6.209	**0.0001**
		Year	0.697	6.188	**0.0001**
	November	Site	0.214	17.320	**0.0001**
		Year	0.564	5.073	**0.0001**
(B)	**Month**	**Pairs**	**R^2**	**F Statistics**	**Adjusted P-value**
	February	BM vs. SS	0.105	4.214	**0.0003**
		BM vs. SH	0.175	7.647	**0.0003**
		SH vs. SS	0.039	1.471	0.478
	May	BM vs. SS	0.059	2.260	**0.047**
		BM vs. SH	0.075	2.928	**0.002**
		SH vs. SS	0.032	1.207	0.830
	August	BM vs. SS	0.077	2.994	**0.014**
		BM vs. SH	0.065	2.494	**0.034**
		SH vs. SS	0.034	1.265	0.762
	November	BM vs. SS	0.136	5.648	**0.0003**
		BM vs. SH	0.263	12.868	**0.0003**
		SH vs. SS	0.072	2.802	**0.024**

Factor "site": Bomok (BM), Sinheung (SH), Seongsan (SS); factor "year": from 2004 to 2022. The P-values were adjusted using Bonferroni correction for multiple comparisons. Significant P-values ($P \leq 0.05$) are highlighted in boldface type.

3 Results

3.1 Environmental variables

To determine and illustrate the weight of each abiotic variable in setting the environmental conditions around Jeju Island, PERMANOVA, KW tests, and PCA were applied. Environmental variables clearly clustered according to sites, with distinct seasonal differences, largest between November and February (Table 1A; Figure 3). In November, clustering appeared along the primary PCA axis only, while in February, clustering appeared along primary (PC1: 20.9% of the variance) and secondary (PC2: 17.4% of the variance) axes, representing 38.3% of the total February variance (Figures 3A, D). The first principal component in the November graph (PC1: 29.4% of variance) was related to salinity, SST, transparency, DIN, DIP, and WS. In the February graph, the first principal component was related to SST and DIP, and the second principal component was related to WS and transparency. The driving environmental variables of the site variability, therefore, are season-dependent, consisting of temperature (SST), phosphorus levels (DIP), WS, and transparency in February, and salinity, SST, phosphorus and nitrogen levels (DIP and DIN), transparency, and WS in November. Although no distinct site-specific clustering was discernible in May and August in the PCA, the PERMANOVA, KW, and Dunn tests indicated significant differences (Figures 3B, C, 4; Table 1): in August, DO was lower at SH (mean ± SD = 7.3 ± 0.7 mg L^{-1}) than at BM (7.6 ± 0.6 mg L^{-1}) and SS (7.7 ± 0.7 mg L^{-1}), while in May, the DIN concentration was lower at SS (median = 0.7 µM) than at BM (1.1 µM) and SH (1.0 µM) (Supplementary Table 1). WS was always significantly lower at BM, especially in November and February (Figure 4E). The wind directions also differed between sites and months (Supplementary Figure 3). In February and November, strong north-westerly winds dominated at SS and SH (February mean ± SD = 3.5 ± 0.1 m s^{-1} and 3.7 ± 0.1 m s^{-1}, respectively), with maximal gusts of up to 4.2 m s^{-1} and 4.3 m s^{-1}, respectively (Supplementary Figures 3B, C). In contrast, BM was subject to light winds, mainly from the north (max. 3.2 m s^{-1}; mean ± SD = 2.4 ± 0.1 m s^{-1}) (Supplementary Figure 3A). In May and August, the wind regime shifted. BM experienced winds from the southwest and the northeast, while wind directions at SS and SH were similar and highly variable (Supplementary Figure 3).

Regardless of season (i.e., months), BM was consistently distinct from SS and SH (Table 1B). Specifically, November and February DIN and DIP concentrations were significantly lower at BM (November mean ± SD = 1.2 ± 0.8 µM and 0.07 ± 0.06 µM, respectively) than at SH (November mean ± SD = 1.8 ± 0.9 µM and 0.09 ± 0.05 µM, respectively) (see also Figure 4 and Supplementary Table 1). November and February transparency and SST were significantly higher at BM (November mean ± SD = 12.6 ± 2.7 m and 21.5 ± 1.7°C, respectively) than at SS (November mean ± SD = 10.4 ± 2.2 m and 20.5 ± 1.2°C, respectively) and SH (November mean ± SD = 8.8 ± 1.5 m and 19.5 ± 1.3°C, respectively). In contrast, SS and SH exhibited generally similar environmental conditions (Table 1B). However, although no statistically significant trend in nutrient concentration-related measurements (i.e., DIP, DIN, NO_2^-, NO_3^-, and NH_4^+) could be established, it is noteworthy that the mean November concentrations were consistently highest at SH (Supplementary Table 1).

3.2 Benthic community

Forty-six benthic taxa and one non-biological component were identified, 16 of which were considered major (percentage cover > 2.5%) (Supplementary Tables 3, 4). All three sites were dominated (percentage cover > 25%) by a single species or category (Figure 5). Generally, the wide range of species coverage percentages (Supplementary Table 5) combined with very high standard deviations (when compared to the mean percentage cover of each species by group; Supplementary Table 4) mirror a patchy distribution of benthic species. Sixteen species were present at all three sites in variable percentages, including coralline algae, turf-forming algae, and the encrusting rhodophytes *Peyssonnelia* sp. and *Hildenbrandia* sp. that had high coverages at all three sites (Supplementary Tables 4, 6). However, regardless of depth and

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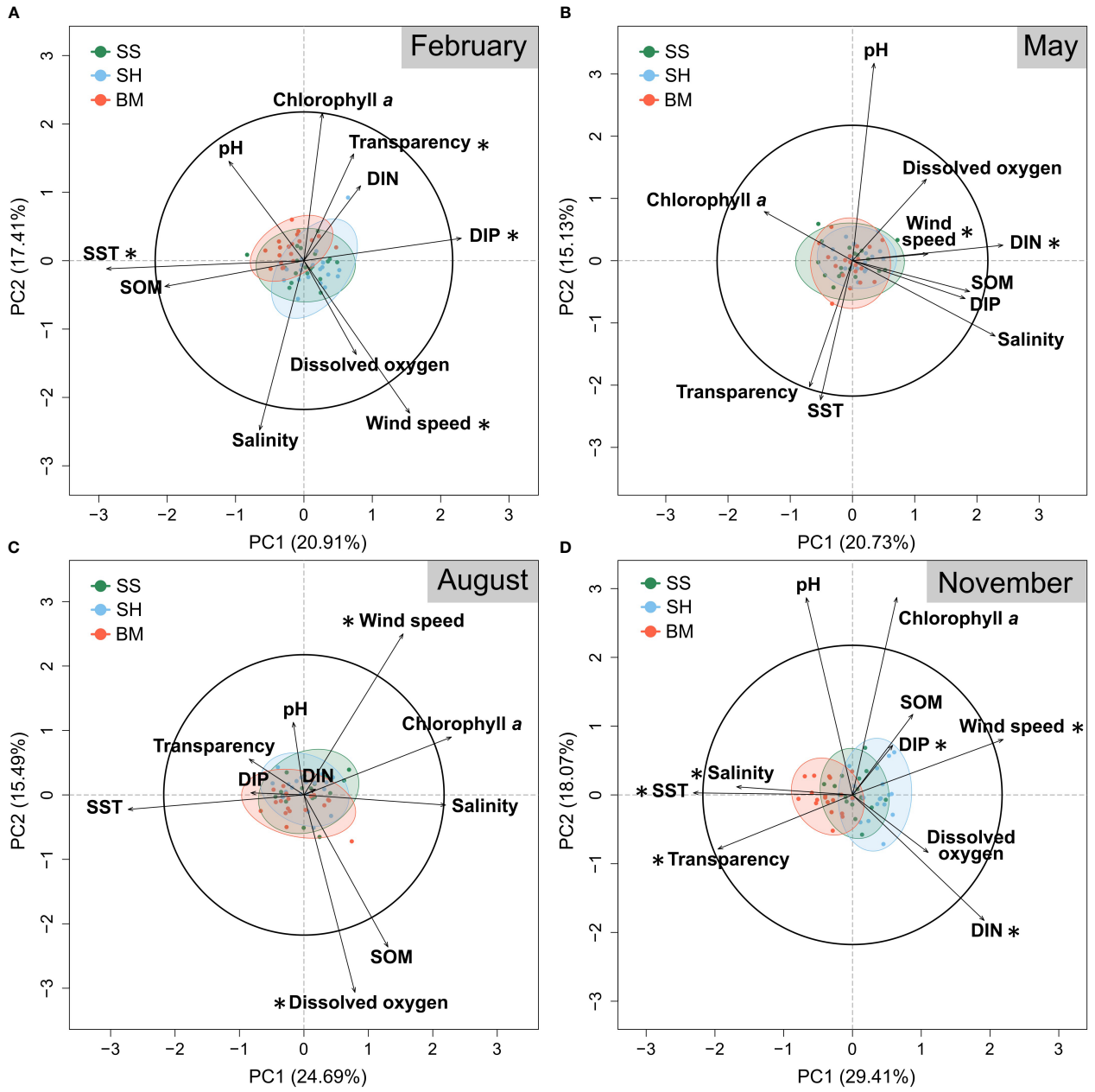

FIGURE 3
Principal Coordinate Analysis (PCA) biplot – scaling 1 – of the standardized environmental data from 2004 to 2022 of **(A)** February, **(B)** May, **(C)** August, and **(D)** November. Each dot represents a year. Red: Bomok (BM); Blue: Sinheung (SH); and Green: Seongsan (SS). The ellipses are the square-root chi-squared density distributions of objects with quantile = 0.95. The black asterisks indicate significantly different variables according to sites using the non-parametric Kruskal-Wallis test. The black circle is the equilibrium circle of descriptors. DIN, Dissolved Inorganic Nitrogen; DIP, Dissolved Inorganic Phosphate; SOM, Suspended Organic Matter; SST, Surface Seawater Temperature.

season, coralline algae species strongly dominated at SH, with CCA showing coverages between 7.5% and 62.0% per image and geniculate coralline algae between 0% and 51.0%. At SS and BM, respectively, CCA coverage ranges of 0–48.3% and 4.0–57.0%, and geniculate coralline algae coverage ranges of 0–35.4% and 0–42.9% were recorded (Supplementary Table 5). Interestingly, SH had the lowest coverage of bare substrate (mean ± SD = 2.5 ± 3.5%) compared to SS and BM (5.6 ± 8.5% and 5.3 ± 7.6%, respectively). SH also showed highest coverage percentages in recorded bryozoans (max. 6.5%) and sponges (max. 12.5%), as well as sponge diversity (7 species) (Supplementary Tables 4, 5). At BM, only 4 Porifera species (max. 1.1%), and at SS, only 3 Porifera species (max. 6.7%) were recorded (Supplementary Tables 4, 5). Additionally, highest diversity in soft and fire corals was recorded from SH, including one species of sea anemone (*Heteractis* sp., max. 2.2%), one species of thick-polyp-bearing soft coral (*Dendronephthya gigantea*, max. 36.1%), and two species of fire corals (*Solanderia* sp., max. 1.1%; *Aglaophenia pluma*, max. 6.7%) (Supplementary Table 5). At SS, although environmentally most similar to SH, no soft corals were recorded. At BM, two species of

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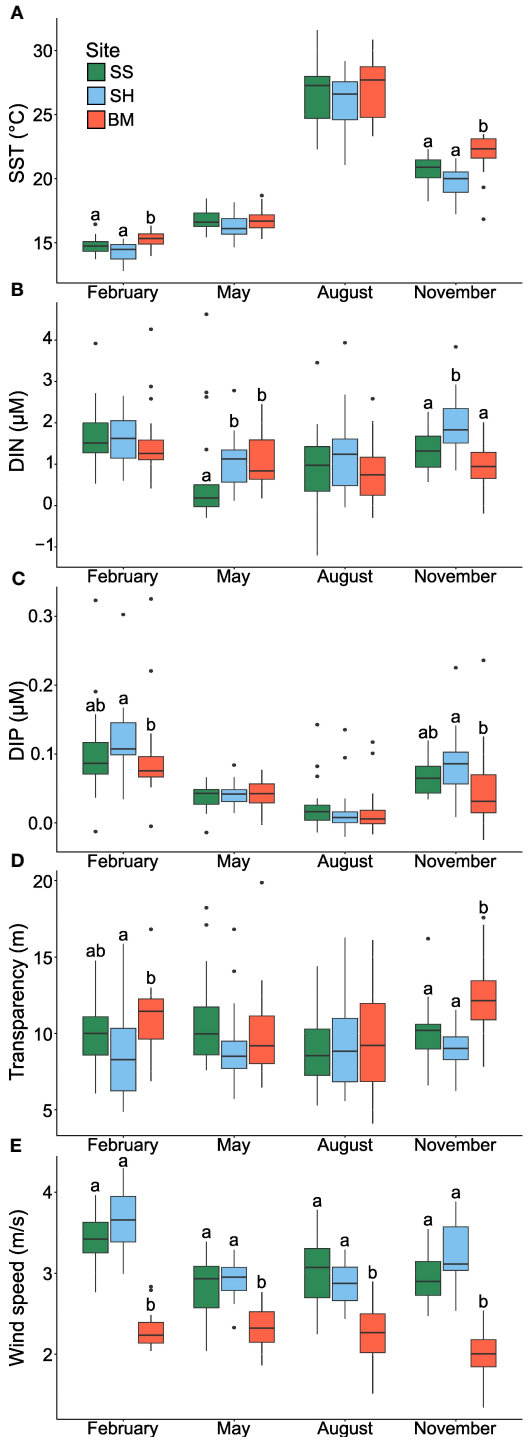

FIGURE 4
Boxplots by month and site of **(A)** Surface Seawater Temperature (SST, °C), **(B)** Dissolved Inorganic Nitrogen (DIN; µM), **(C)** Dissolved Inorganic Phosphate (DIP; µM), **(D)** transparency (m), and **(E)** wind speed (ms^{-1}). Red: Bomok (BM); Blue: Sinheung (SH); and Green: Seongsan (SS). Letters indicate the results of the non-parametric pairwise Dunn test in cases where the Kruskal-Wallis test was significant.

sea anemone were recorded (*Entacmaea* sp., max. 10.3%; *Heteractis* sp., max. 4.1%) (Supplementary Table 5). Scleractinian hard corals were present at all three sites, although the highest diversity (4 species) and, by large, the highest coverage percentage (sum by site = 54.7 ± 25.1%) were recorded from BM, followed by SS (3 species; sum by site = 0.5 ± 1.9%), and SH (2 species; sum by site = 0.06 ± 0.5%) (Supplementary Table 4). At BM at both depths, *Alveopora japonica* dominated by over 60% in May and 30% in November (Figure 5B; Supplementary Table 4). Recently, it has been suggested that there are three cryptic species of *Alveopora japonica* corresponding to their Japanese, Korean and Taiwanese distributions respectively (Kang et al., 2020). At SS at both depths, canopy-forming brown algae (*Ecklonia cava* and *Sargassum* spp.) dominated by over 65% in May and 23% in November. At SH at both depths, coralline algae (geniculate coralline algae and CCA) dominated by over 40% in May and 66% in November (only 15 m depth data available). These differences in dominance are highlighted by multivariate analyses, showing a clear difference in benthic percentage cover between sites (Figure 6A; Tables 2, 3).

The pRDA results showed that the greatest proportion of variance in the benthic community cover was explained by the factor "site" (50.3%), followed by "month" (8.0%) and "depth" (1.3%), while 40.0% of the variance remained unexplained by these factors (Figure 6; Table 2). All three pRDA models were significant (Table 2; p-value = 0.001). However, the variability explained by the pRDA model (RDA axis) was far greater than that of the residuals (PC axis) for "site" only, where the first two canonical axes were significant (Table 2A; RDA1 = 39.6%, RDA2 = 16.1%). The inter-site variability observed in the benthic community was explained primarily by the species *E. cava*, *Plocamium* sp., and *Sargassum* spp. (i.e., macroalgae species) which were representative of SS, opposed on the first axis to *A. japonica* (i.e., scleractinian hard coral) representing BM. *Undaria pinnatifida*, coralline algae, and *D. gigantea* (i.e., macroalgae and soft coral species, respectively) represented SH on the second axis (Figure 6A). The PERMANOVA test showed an F-statistic and R^2 of more than two times higher for sites than for months and depths, although all three factors significantly influenced the benthic community (Table 3A). The benthic communities of BM and SS were the most distinct, followed by BM and SH, then SH and SS (Table 3B; Figure 6A).

The benthic compositions of BM and SS exhibited differences between May and November (Figure 5; Table 3), mainly characterized by a decrease in the percentage cover of the dominant taxa (i.e., *E. cava* and *A. japonica*), an increase in coralline algae, and the emergence of filamentous turf, *Hildenbrandia* sp. and *Peyssonnelia* sp. as major species. At SS, the rhodophytic macroalgae *Grateloupia angusta* and *Plocamium* sp. had higher coverages in November. At SH, the canopy-forming algae *E. cava* and *U. pinnatifida* and the chlorophyte *Codium* sp. were present at non-negligible coverages only in May (mean ± SD between depths = 8.2 ± 12.8%, 27.8 ± 21.4%, and 3.9 ± 6.4%, respectively) (Figure 5B; Supplementary Table 4). At all three sites, the coverage of substrate was constantly higher in November than in May. These observations are supported by the pRDA "month" model (RDA1 = 16.7%; Figure 6B), where *A. japonica*, *E. cava*, *U. pinnatifida*, and *Sargassum* spp. were indicative of May, while substrate, coralline and turf algae, *Hildenbrandia* sp., *Plocamium* sp., and *Peyssonnelia* sp. were linked to November. Note that SH data from November at 10 m depth are missing.

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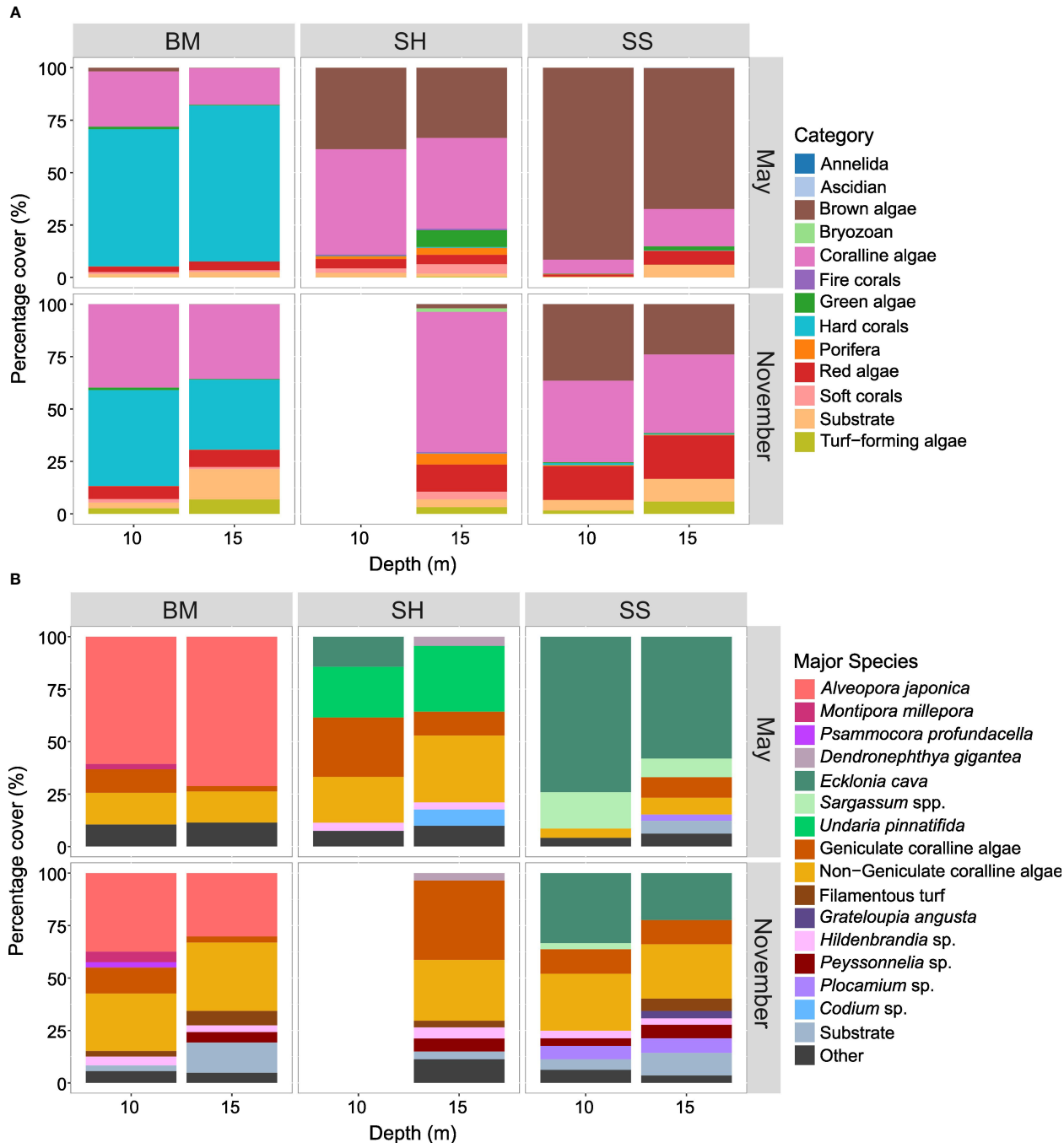

FIGURE 5
Percentage cover (%) of **(A)** categories and **(B)** major species/substrate for each site and depth in May and November 2022. BM, Bomok; SH, Sinheung; SS, Seongsan. In **(B)**, species with a percentage cover < 2.5% in each column are summed in the group "Other". The data are missing at the SH site at 10 m in November.

There were slight differences in benthic percentage cover between depths (Figures 5, 6C; Table 3). Indeed, the variation explained by the factor "depth" was five times lower than the proportion of variance in the residuals (PC1 = 17.9%; RDA1 = 3.1%). Regardless of months and sites, only macroalgae species and substrate were responsible for the variability observed across depths. For instance, *U. pinnatifida*, *Sargassum* spp., *E. cava*, and geniculate coralline algae were representative of the 10 m depth, while *Plocamium* sp., *Peyssonnelia* sp., *Codium* sp., filamentous turf and CCA converged to 15 m depth (Figure 6C). Specifically, at BM, at 10 m, geniculate coralline algae, hard coral species *Montipora millepora* and *Psammocora albopicta*, sea anemone *Entacmeae* sp., and chlorophyte species *Cladophora wrightiana* had higher coverage than at 15 m, contrary to rhodophyte *Peyssonnelia* sp. and sea anemone *Heteractis* sp. (Supplementary Table 4). At SS, the coverages of canopy-forming brown algae were

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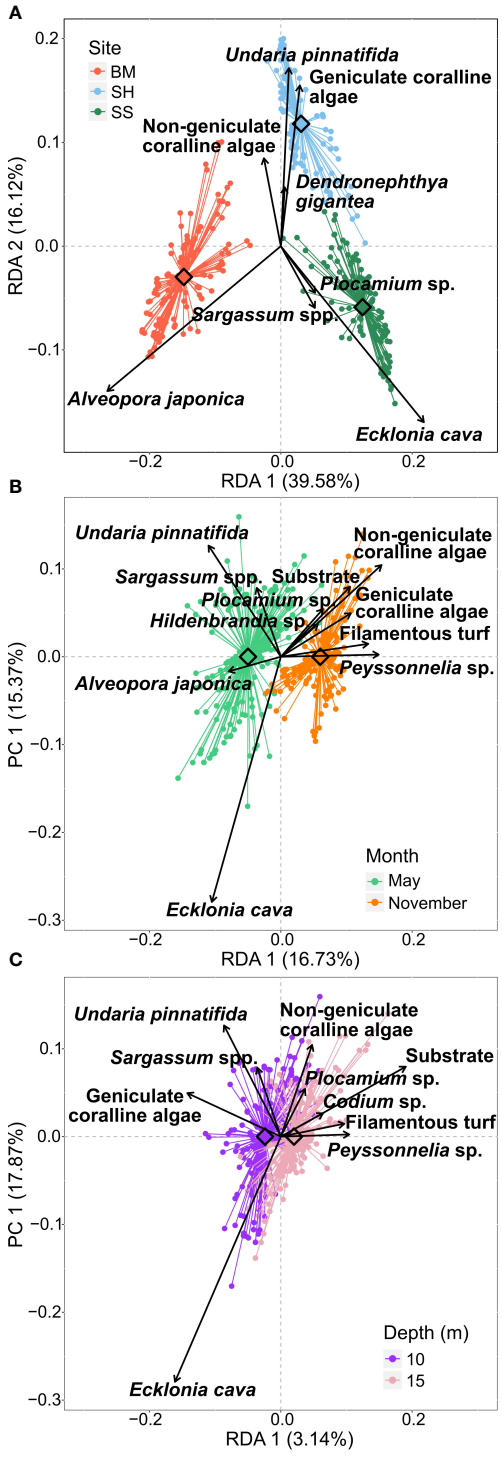

FIGURE 6
Partial Redundancy Analysis (pRDA) of Hellinger transformed percentage cover data. The constraining factor is **(A)** "site", **(B)** "month", and **(C)** "depth". For each graphic, the influence of the two other factors was removed (conditioning factors). The diamond is the centroid of each group. Each dot represents a photo-quadrat. In **(A)** – Red: Bomok (BM); Blue: Sinheung (SH); and Green: Seongsan (SS). In **(B)** – Light green: May 2022; and Orange: November 2022. In **(C)** – Purple: 10 m depth; and Pink: 15 m depth. Table 2 reports the pRDA models' details and the permutation test results.

TABLE 2 Complementary pRDA results of Figure 6.

(A)	Model result	Inertia	Proportion (%)
Figure 6A ("site")	Total	0.497	1.000
	Conditioned	0.048	0.097
	Constrained	0.250	0.503
	Unconstrained	0.199	0.400
	Permutation test	**F Statistics**	**P-value**
Figure 6A ("site")	RDA Model	204.31	**0.001**
	RDA 1	290.36	**0.001**
	RDA 2	118.26	**0.001**
(B)	**Model result**	**Inertia**	**Proportion (%)**
Figure 6B ("month")	Total	0.497	1.000
	Conditioned	0.258	0.519
	Constrained	0.039	0.080
	Unconstrained	0.199	0.400
	Permutation test	**F Statistics**	**P-value**
Figure 6B ("month")	RDA Model	65.319	**0.001**
(C)	**Model result**	**Inertia**	**Proportion (%)**
Figure 6C ("depth")	Total	0.497	1.000
	Conditioned	0.292	0.587
	Constrained	0.006	0.013
	Unconstrained	0.199	0.400
	Permutation test	**F Statistics**	**P-value**
Figure 6C ("depth")	RDA Model	10.533	**0.001**

The constraining factor is **(A)** "site" (i.e., Bomok, Sinheung, Seongsan), **(B)** "month" (i.e., May, November), and **(C)** "depth" (i.e., 10 m, 15 m). The influence of the two other factors was removed (conditioning factors). The first table is the pRDA model result. The second table is the result of the permutation test to test the significance of the pRDA model and each RDA axis. Significant P-values ($P \leq 0.05$) are highlighted in boldface type.

higher at 10 m than at 15 m, contrary to the trends recorded for rhodophytes *G. angusta*, *Peyssonnelia* sp., and *Plocamium* sp., as well as the substrate category. At SH, the soft coral *D. gigantea*, CCA, Porifera, turf-forming algae, and rhodophytes *Peyssonnelia* sp. and *G. angusta* were more abundant at 15 m depth, contrary to kelp species *E. cava*.

4 Discussion

This study quantified abiotic environmental variations at three sites around Jeju Island and investigated accompanying community dynamics of sessile benthos. Hard corals dominated in the TWC-influenced, low-energy (i.e., less windy), southern BM; canopy-forming brown algae dominated in less TWC-influenced, high-

TABLE 3 (A) PERMANOVA test results from Euclidean distance matrix of Hellinger transformed percentage cover data of all species. (B) Pairwise PERMANOVA test results for the factor "site".

(A)	Factors	R^2	F Statistics	P-value
	Site	0.500	203.280	**0.0001**
	Month	0.086	70.156	**0.0001**
	Depth	0.013	10.533	**0.0001**
(B)	**Factors**	**R^2**	**F Statistics**	**Adjusted P-value**
	BM vs. SS	0.508	245.953	**0.0003**
	BM vs. SH	0.425	153.435	**0.0003**
	SH vs. SS	0.314	95.044	**0.0003**

Factor "site": Bomok (BM), Sinheung (SH), Seongsan (SS); factor "month": May, November; and factor "depth": 10 m, 15 m. The P-values were adjusted using Bonferroni correction for multiple comparisons. Significant P-values ($P \leq 0.05$) are highlighted in boldface type.

energy, eastern SS; and coralline algae dominated in shallow, strongly tide-influenced, more eutrophic, northern SH.

First, it was found that the level of environmental distinctness between sites varied with season, being strongest in November and February, respectively, while being weakest in May and August. Consequently, the distinct environmental setting at each site was subject to seasonal variations. The TWC, a branch of the warm, saline, and oligotrophic Kuroshio Current, shows seasonal variability, intensifying in summer (i.e., reaching further north than in winter), with a current velocity that can vary by 20 cm s^{-1} between July and January (Takikawa and Yoon, 2005; Cha and Moon, 2020). Additionally, Changjiang River discharge (termed Changjiang Diluted Water, CDW) from the Chinese mainland arrives at Jeju Island in the southwest. Then, driven by southerly summer winds, the CDW encompasses the whole island, peaking in July and August (Park, 1986; Kim et al., 2009; Park et al., 2011; Kwon et al., 2018). Therefore, during summer, environmental heterogeneity around the island is further reduced as CDW adds fresh, warm, oligotrophic water to the TWC-dominated coastal surface waters. Moreover, increased precipitation during the summer monsoon season further homogenizes surface water properties around the island (Kwon et al., 2020). In winter, however, the weakened TWC only reaches the south of Jeju Island, increasing the SST by up to 2°C at BM compared to SS and SH. Cha and Moon (2020) even reported a winter temperature gradient of 6°C between the northwest (12°C) and the southeast (18°C), compared to just 3°C in summer (25°C and 28°C, respectively). Additionally, in winter, the east and north are subject to strong northerly wind bursts, impacting currents, surface mixing layer, SST, nutrient supply and turbidity, while Mt. Halla, a nearly 2000 m high volcano situated near the center of the island, acts as a wind-breaker, sheltering the south from these strong, northerly winter gusts (Jacobs et al., 2000; Nishihara and Terada, 2010; Cho et al., 2013). Hence, environmental conditions between sites were most similar in summer and most different in winter. Considering that in our benthic community data, the factor "month" explained only a comparably low proportion of variability in sessile community coverages (pRDA = 8.0% between May and November), these environmental winter differences may play a key role in structuring benthic community around the island. However, a more in-depth study, including high time-resolution data to detect seasonal patterns, is necessary to confirm this assumption.

Second, the recorded site-specific sessile benthic compositions around Jeju Island were consistent with the observed local environmental conditions and topography. It was found that all three sites showed a distinct sessile benthic composition. Each site was dominated by one foundation species or category, which reflected local abiotic conditions. While all our study sites showed the presence of hermatypic scleractinian coral species, BM was characterized by highest coverage and species diversity, including *A. japonica*, *M. millepora*, *P. profundacella*, and *P. albopicta*. Generally, the southern coastal marine area is steep and deep, while winds are milder (see Figure 1 bathymetry). In addition, the tidal energy contribution is low (< 30%), while the majority of prevailing environmental conditions are determined by the specific water properties of the TWC (i.e., saline, warm, oligotrophic) passing Jeju Island (Hur et al., 1999; Cha and Moon, 2020). Such hydrographic and topographic features may promote a comparably oligotrophic environment. Although the nutrient concentration at BM may show a localized peak due to the presence of a sewage treatment plant near the sampling site, environmental data from the exact sampling site are currently lacking. In addition, the consistent supply of oligotrophic TWC waters may soften direct impacts of the sewage treatment plant. As high nutrient concentrations can benefit corals' competitors and hinder coral physiological processes (Harriott and Banks, 2002; Manzello et al., 2014; Kwon et al., 2020), more oligotrophic conditions could favor the thriving of hard coral species at BM. Moreover, this low-energy habitat and the influence of the TWC lead to significantly higher winter SST and transparency readings. At BM, the mean SST and transparency in February were over 15°C and 10 m, respectively, contrary to SH and SS. Subtropical hard coral richness and abundance are more sensitive to minimum temperatures and short-term thermal variability (Sommer et al., 2018), which is in line with Jeju's hard coral thermal optimums (see Supplementary Table 2). For instance, temperatures between 10°C and 15°C can induce *A. japonica* bleaching and reduction of its basal metabolism, although without being lethal (Higuchi et al., 2020; Keshavmurthy et al., 2021). Recenthly, it was showed that three cryptic species of Alveopora japonica corresponding to Japonese, Korean and Taiwan distributions existed (Kang et al. 2020). Moreover, McIlroy et al. (2019) reported that 80% of the maximum productivity of five subtropical coral species, including one *Montipora* species, was maintained at temperatures between 15.7°C and 32°C, with their optimal temperatures always being greater than 20°C, which fall within the annual temperature range of BM. Additionally, photosynthetic symbionts-carrying hard corals thrive better in high transparency waters where there is more sunlight (De'ath and Fabricius, 2010; Muir et al., 2015), while the reduction in suspended particles can promote coral recruitment by decreasing the abrasion effect (Gilmour, 1999; Gove et al., 2015). However, habitats dominated by *A. japonica* (percentage cover > 25%) have been identified at Biyangdo, northwest of Jeju Island (Denis et al., 2014). Although the environmental conditions at this site are unknown, they are likely to differ from those at BM, and

additional controlling factors could explain this hard coral outbreak (see Kwon et al., 2020). The low coverage of canopy-forming algae and other non-encrusting macroalgae species at BM (< 2.5%) can favor the growth of hermatypic scleractinian corals by decreasing competition stress, abrasion and dislodgment (Coyer et al., 1993; Miller and Hay, 1996; Tuckett et al., 2017; De Vargas Ribeiro et al., 2022). Interestingly, a few decades ago, the perennial canopy-forming brown alga *E. cava* thrived at BM (Chung et al., 1998; Ribas-Deulofeu et al., 2023). Meanwhile, in our study, *E. cava* was not found at the BM site, while it was present at the SH site and dominated the SS site. Tuckett et al. (2017) reported a shift in ecosystems in Western Australia from temperate canopy-forming algae to hard coral species with warm water affinities. They attributed this shift to a competitive release caused by kelp decline resulting from heatwaves and global warming. Indeed, temperate kelps, such as *E. cava*, are heat-sensitive (Wernberg et al., 2011, 2016) (Supplementary Table 2) and, like hard corals, may be limited by water temperature in winter. The optimal water temperature for *E. cava* growth during winter is 15–18°C, while water temperatures above 20°C in summer can inhibit growth, although promoting reproductive potential (Yokohama et al., 1987; Kim et al., 2016). At SS, mean SST in February and May were nearly 15°C and 17°C, respectively, lying within the range of *E. cava*'s optimal temperature. Moreover, the high-energy environment caused by strong winter winds could contribute to the persistence of kelp forests at SS. Water motion is key in promoting and aiding kelp forest growth by dislodging grazers (Denny and Gaylord, 1996) and increasing nutrient availability and uptake (Hurd et al., 1996; Nishihara and Terada, 2010). *E. cava* is well-equipped to handle these physical disturbances due to its finger-like holdfasts and large thalli, which help to attach itself firmly to the substrate (Kang et al., 2011; Kang and Kim, 2012; Lee K.-T. et al., 2023). Therefore, climate change-related events, such as the intensification of the KWC (i.e., increased SST and oligotrophy) (Wu et al., 2012; Kim et al., 2022a), could promote the expansion of high-latitude hard coral communities along the southern coastline towards east and west, while driving a decline in eastern temperate kelp forests. On the north of the island, the coastal marine area is flat and shallow, the wind speed is high, and tidal energy is prevalent (> 90%) in setting local environmental conditions (Cha and Moon, 2020). Results showed that DIN and DIP concentrations were significantly higher at SH than at BM, and generally, all nutrient concentration-related variables were consistently highest at SH, especially the November measurements. This may be due to a combination of reasons, such as topography hindering quick dilution, increased input through aquaculture wastewater, and inefficient biological uptake by marine organisms. Indeed, nutrient availability in Jeju's coastal waters is strongly related to land-based, anthropogenic activities, such as land-operated fish farms which are present in the vicinity of SH. Wastewater from land-operated fish farms accounts for up to 95% of the seawater ammonium (Kwon et al., 2022), increasing coastal DIN and DIP concentrations (Choi et al., 2021), and generally contributes significantly to the nitrogen budget in the coastal waters of Jeju (Koh et al., 2013; Kim et al., 2022b). Sea water enriched in ammonium is preferred by coralline algae, which dominate SH (Nguyen et al., 2020; Kwon et al., 2022). Moreover, geniculate coralline algae have lower nitrogen amounts in their tissue than brown algae (e.g., *E. cava, U. pinnatifida*), hence incorporating less total nitrogen (Choi et al., 2021). Although, throughout the year, SH showed similar environmental conditions to SS, SH was not dominated by *E. cava*. Canopy-forming algae populations of *U. pinnatifida* and *E. cava* were present at SH but showed much lower coverage percentages than in SS and were only recorded in May. High nutrient concentrations due to sewage effluents can inhibit the germination and photo efficiency of brown algae (Doblin and Clayton, 1995; Scherner et al., 2012), but this substantial difference in benthic composition compared to the abiotic environmental similarity of these sites suggests that other factors may hold a key role in shaping these benthic ecosystems. Overgrazing by sea urchins and other invertebrates is known to cause decrease in kelp forests (Kang, 2010; Bekkby et al., 2015; Ling et al., 2015), and a high abundance of such grazers at SH compared to SS could explain the low coverage of canopy-forming algae despite the apparent favorable environmental conditions. Such information is not reported in Jeju's literature, and personal observations did not attest to high abundance of grazers. Still, additional ecological factors, such as intensity and frequency of extreme weather-related events (Smale and Wernberg, 2013) and biotic interactions (Negri et al., 2001; Tebben et al., 2015), can all hold essential roles in shaping benthic communities, and additional study including these parameters is warranted. Additionally, DO measurements were significantly lowest at SH, especially in August, which may be caused, in parts, by the elevated nutrient levels, as increased nitrogen and phosphorous content lowers the amount of dissolved oxygen in the water (Dodds, 2006). The overall lower water quality at SH mirrored in the high coverage percentages and diversity of Bryozoa, Porifera, and soft corals. Sponges and bryozoans have been found in large species numbers and percentage cover on hard bottoms of highly disturbed environments, and especially bryozoans are reported to thrive in low light conditions, while soft corals can tolerate high eutrophication and sedimentation environments (Corriero et al., 2007; Baum et al., 2016; Evseeva and Dvoretsky, 2023). In contrast to the southern coast, the benthic community composition in the northern coastal waters may be more influenced by topography and additional localized anthropogenic stressors rather than natural abiotic parameters. Similarly, the impact of global warming on the community composition of the northern barren grounds may be comparably low, as CCA communities are less sensitive to rising SST (Krieger et al., 2023).

Third, water depth did not much influence any of the observed community dynamics, although depth is directly correlated with light and nutrient availability and, as such, impacts the vertical zonation of marine benthic species (Kang and Kim, 2012; Muir et al., 2015). Generally, photosynthetic species, such as canopy-forming brown algae and hermatypic scleractinian species, always showed higher coverages at the shallower depth. At BM, the hard corals *M. millepora*, *P. profundacella*, and *P. albopicta*, and geniculate coralline algae were more abundant at 10 m depth. As light is a major limiting factor in high-latitude ecosystems, particularly in winter, hard corals carrying photosynthetic

symbionts living above 30° latitude tend to thrive best in shallow areas that receive more sunlight (Muir et al., 2015). Interestingly, there was no depth-related trend in the coverage of *A. japonica*. This may be because the reported depth range of this species around Jeju Island is much wider than those of *M. millepora* and *P. profundacella* (5–25 m and < 10 m, respectively; Sugihara et al., 2014). Geniculate coralline algae usually dominate at shallower depths (1–10 m depth; Kang et al., 2023) because of their higher tolerance to wave action. Similarly, the photosynthetic brown algae *E. cava* and *Sargassum* spp. showed decreasing coverages with depth at SH and SS. These species exhibited maximum abundances at depths between 6 m and 10 m in Jeju waters, explained by their higher light demand and lower tolerance to strong physical forces (Kang et al., 2023). On the contrary, encrusting red algae (e.g., CCA and *Peyssonnelia* sp.) and *G. angusta* have increasing coverages with depth due to their lower demand for light (Kang et al., 2023). At SH, the soft coral *D. gigantea* was more abundant at 15 m depth (coverage ≈ 4% in May and November), which may be explained by its non-photosynthetic lifestyle, i.e., not requiring sunlight for energy acquisition, and its generally high stress-tolerance to sedimentation, turbidity, and eutrophication (De'ath and Fabricius, 2010; Powell et al., 2014; Baum et al., 2016; Lalas et al., 2023). These traits enable *D. gigantea* to thrive in poorer quality waters while avoiding increased competition at shallower depths. Likewise, the sampling months accounted for a minor part of the variability observed in the benthic community. For instance, the decrease in canopy-forming algae and high-latitude hard corals at SS and BM, respectively, can be attributed mainly to, in the absence of other extreme events, destruction by super typhoon Hinnamnor, which reached Jeju Island in September 2022. Lee K.-T. et al. (2023) reported a 42% loss of *E. cava* at 10 m and 34% at 15 m in September 2022 compared to May 2022 at SS, which is coherent with our results. This decline in canopy density has led to an artificial increase in the percentage cover of underlying species in November, such as rhodophytes *Plocamium* sp. and *G. angusta*. Similarly, the seasonal decline of *A. japonica* at BM by roughly half its coverage from May (61% at 10 m; 71% at 15 m) to November (37% at 10 m; 30% at 15 m) was also likely caused by typhoon Hinnamnor. Numerous dead and bleached *A. japonica* were observed on photo-quadrats in September 2022, right after Hinnamnor had hit. At the same time, the increase at all three sites and two depths of turf-forming algae, substrate, red algae, and coralline algae may have been promoted by space, light, and resources availability, as well as species-specific invasion capacity of a newly disturbed area (Sousa, 1984; Airoldi, 1998; Kim T. et al., 2022). Life history traits can also contribute to this observed monthly divergence (Darling et al., 2012). Whereas the dominant *E. cava* and *A. japonica* have a perennial life cycle and are known to have an overall annual stable coverage (Haroun et al., 1989; Vieira et al., 2016), *U. pinnatifida* is an annual species living as macroscopic, diploid sporophyte from January to July, and the rest of the year, as microscopic, haploid gametophyte (Schiel and Thompson, 2012). In its microscopic stage, its presence cannot be identified by image analysis, which can explain its absence in the November results. This study investigated the current spatial variability in Jeju's benthic communities and local environmental conditions, and seasonal variability of these marginal ecosystems needs further assessment.

5 Conclusion

Marine climatic transition zones are emerging as geographic hot spots of scientific interest in climate warming-related ocean changes. Increasing temperatures threaten the survival of the heat-sensitive temperate species living at the limit of their physiological tolerance while driving the arrival and expansion of species with warmer climate affinities. Therefore, benthic habitats of marine climatic transition areas are subject to extensive faunal turnover, driven by an interplay of extinction, outbreak, and migration events.

This study greatly improved the understanding of Jeju benthic community dynamics on an annual scale and demonstrated the importance of considering environmental parameters in understanding benthic community distribution in climatic transition zones. It clearly suggests that a combination of hydrographic, meteorological, and topographic parameters structures coastal benthic communities in the temperate transition zone of Jeju Island. Statistically, winter water temperature, nutrient concentration, water motion (derived from wind speed and direction), and transparency were the most significant in setting the particular environmental conditions around the island. These local environmental conditions were congruent with the distribution, composition, and coverage of sessile foundation species.

Although the underlying drivers of Jeju benthic communities need to be further investigated, our study suggests that site divergence in winter environmental conditions may play a significant role. Higher spatio-temporal resolution abiotic and biotic data are needed in future studies to improve our understanding of marginal benthic community dynamics. Moreover, experimental research is necessary in the mostly overlooked, temperate transition zone of Jeju to investigate the controlling factors of these marginal communities further. Having such information will help clarify the role of ecological variables in driving biogenic habitat shifts, assessing how each affects sessile communities, including, among others, effects on the physiology of foundation species, antagonistic and synergistic relationships, and food web interactions.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

GP: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. AJ: Conceptualization, Validation, Visualization, Writing – review & editing. K-TL: Data

curation, Investigation, Methodology, Writing – review & editing. LP: Formal analysis, Investigation, Visualization, Writing – review & editing. H-SY: Investigation, Project administration, Writing – review & editing. YS: Investigation, Validation, Writing – review & editing. H-SP: Funding acquisition, Project administration, Resources, Writing – review & editing. D-HK: Funding acquisition, Project administration, Resources, Writing – review & editing. TK: Conceptualization, Data curation, Investigation, Methodology, Supervision, Validation, Visualization, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1345518/full#supplementary-material

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Observing change in pelagic animals as sampling methods shift: the case of Antarctic krill

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Understanding and managing the response of marine ecosystems to human pressures including climate change requires reliable large-scale and multi-decadal information on the state of key populations. These populations include the pelagic animals that support ecosystem services including carbon export and fisheries. The use of research vessels to collect information using scientific nets and acoustics is being replaced with technologies such as autonomous moorings, gliders, and meta-genetics. Paradoxically, these newer methods sample pelagic populations at ever-smaller spatial scales, and ecological change might go undetected in the time needed to build up large-scale, long time series. These global-scale issues are epitomised by Antarctic krill (*Euphausia superba*), which is concentrated in rapidly warming areas, exports substantial quantities of carbon and supports an expanding fishery, but opinion is divided on how resilient their stocks are to climatic change. Based on a workshop of 137 krill experts we identify the challenges of observing climate change impacts with shifting sampling methods and suggest three tractable solutions. These are to: improve overlap and calibration of new with traditional methods; improve communication to harmonise, link and scale up the capacity of new but localised sampling programs; and expand opportunities from other research platforms and data sources, including the fishing industry. Contrasting evidence for both change and stability in krill stocks illustrates how the risks of false negative and false positive diagnoses of change are related to the temporal and spatial scale of sampling. Given the uncertainty about how krill are responding to rapid warming we recommend a shift towards a fishery management approach that prioritises monitoring of stock status and can adapt to variability and change.

KEYWORDS

ecosystem monitoring, population change, Antarctic kill, fishery management, new technologies

1 Introduction

Pelagic animals are key components of marine ecosystems. In this paper we use the term "pelagic animals" to refer to species from zooplankton to small pelagic fish that tend to form dense aggregations and are mainly sampled in the upper few hundred metres of the water column. These animals support biodiversity at higher trophic levels, carbon export and important commercial fisheries, functions that are changing in response to a variety of pressures such as climate change (Siegel and Watkins, 2016; Cavan et al., 2019; Meyer et al., 2020). Understanding of such changes is based on large-scale spatial and temporal observations (Benway et al., 2019) but the approaches, scales and technology used to sample pelagic animals are also changing. It has long been possible to acquire high volumes of data including *in situ* images, multi-frequency acoustics and molecular samples, but only recently have we gained the computer processing power and machine learning capabilities to effectively process the terabytes of data involved. Concurrently it has become increasingly difficult to maintain large-scale and long-term sampling programs using traditional nets and bottles, with humans identifying the individual species including their ontogenetic stages (Benway et al., 2019). A key issue is that research vessels have significant financial and environmental costs (Kintisch, 2013) and lower cost, lower carbon platforms are preferred. Here we use the specific case of Antarctic krill (*Euphausia superba*, hereafter "krill"), which shows signs of long-term change (Atkinson et al., 2022) and is the target of the largest fishery in the Southern Ocean (SO) (Meyer et al., 2020), to assess how evolving sampling technology maps onto the information requirements for understanding and protecting a globally important pelagic species.

Krill has an enormous biomass, perhaps 400 Mt (Siegel and Watkins, 2016), and plays a central role in pelagic foodwebs (Figure 1), as a key prey species for a diverse range of predators including many SO endemics (McCormack et al., 2020; Cavanagh et al., 2021b), and as a major grazer (Yang et al., 2022). The huge faecal production (tens of Mt C yr^{-1}) resulting from this grazing contributes to carbon export to deep water and therefore long-term removal from the atmosphere (Cavan et al., 2019). Krill are also important in the regeneration and translocation of limiting nutrients (Schmidt et al., 2016). Krill fishery catch has tripled since 2000 and now accounts for c. 97% of the SO catch of all species, although it

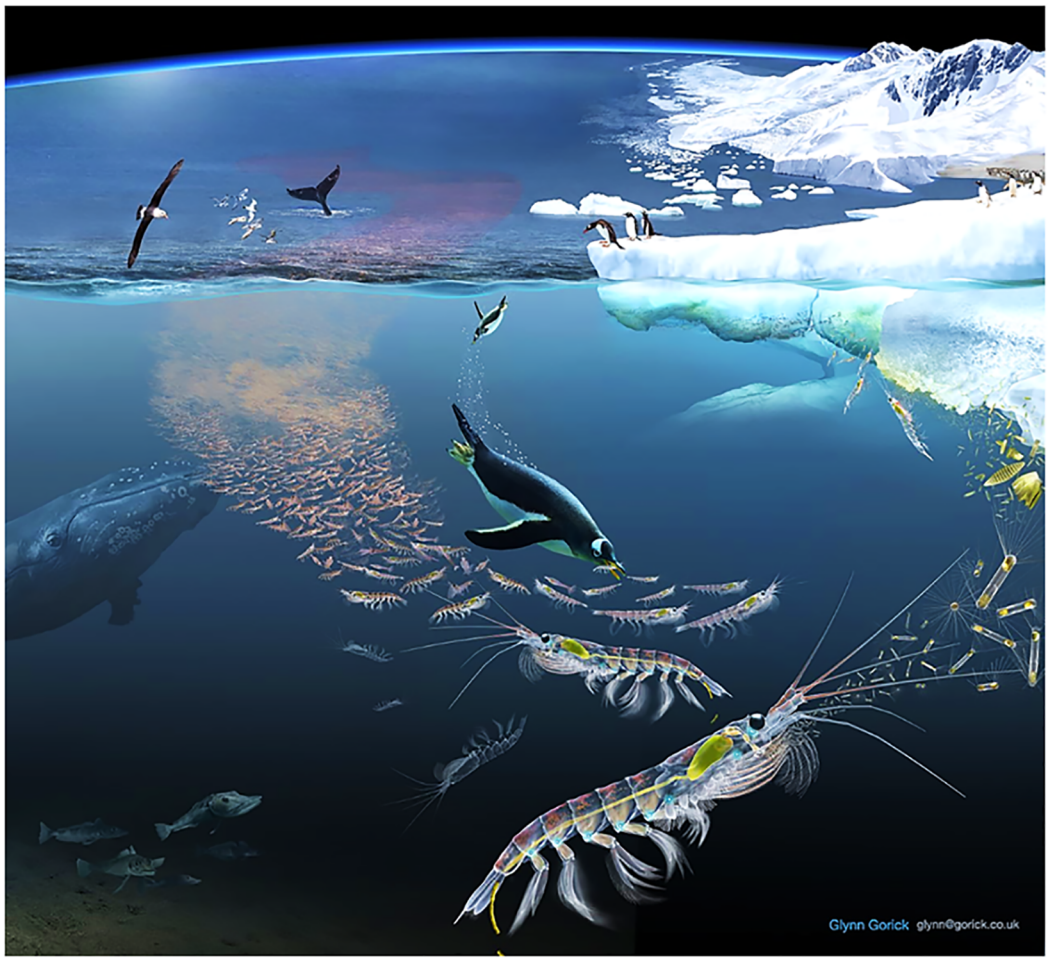

FIGURE 1
Traditional view of the krill-based food web. This schematic highlights an anthropocentric emphasis on organisms that are beautiful (e.g. diatoms, albatrosses), large (e.g. whales), charismatic (e.g. penguins) or land breeding and slightly easier to sample (e.g. seals). By contrast the ectothermic predators, illustrated bottom right by icefish species, are perhaps the major krill consumers in this food web, but the relative contributions of the various groups (icefish, Antarctic cod, myctophids, and squid) is poorly known. Sampling to detect changes within this krill-based food web is therefore challenged by the fact that we have an insufficient overview of the web itself. Previous over-exploitation of a small subset of major krill predators (fur seals, then whales then fish) has added to the effects of climate in perturbing this food web. While it is clear that some of the links in the food web are changing over time, the reasons are not yet always clear.

represents an apparently small (<1%) fraction of krill biomass. The fishery is concentrated in the Southwest Atlantic sector of the SO which is also a major krill population centre and the area where most krill sampling has occurred but has experienced rapid warming and sea ice loss (Meredith et al., 2019) (Figure 2).

While the ecological and economic importance of krill ensure that it is a focus of SO research and monitoring (Siegel and Watkins, 2016), understanding of krill populations, including how their biomass changes between years, remains highly uncertain. Catch limits for the fishery are based on historic catches rather than any estimate of population status (Siegel and Watkins, 2016; Meyer et al., 2020). Meanwhile there is a debate over whether long-term population change has occurred in the Southwest Atlantic (Cox et al., 2018; Atkinson et al., 2019; Cox et al., 2019; Hill et al., 2019; Candy, 2021). Given the central role that krill plays in the SO pelagic ecosystem and the services it provides (Cavanagh et al., 2021a), understanding krill population dynamics is critical to gauge the ecosystem response to climate change. It is also a major information requirement for improved fishery management (Nicol and Foster, 2016).

The Scientific Committee on Antarctic Research Krill Action Group (SKAG), an international community of Antarctic krill scientists, which has now become an Expert Group (SKEG), held an online workshop in April 2021 to evaluate existing and emerging sampling technologies against the information requirements for understanding population change and improving fishery management. The workshop was attended by 137 krill researchers from 19 countries (Atkinson et al., 2021) and its outcomes and recommendations are reported here. The general nexus of SO ecosystems, krill and climate change impacts and projections has been well covered by a suite of reviews over the last decade (Flores et al., 2012; Constable et al., 2014; Siegert et al., 2019;

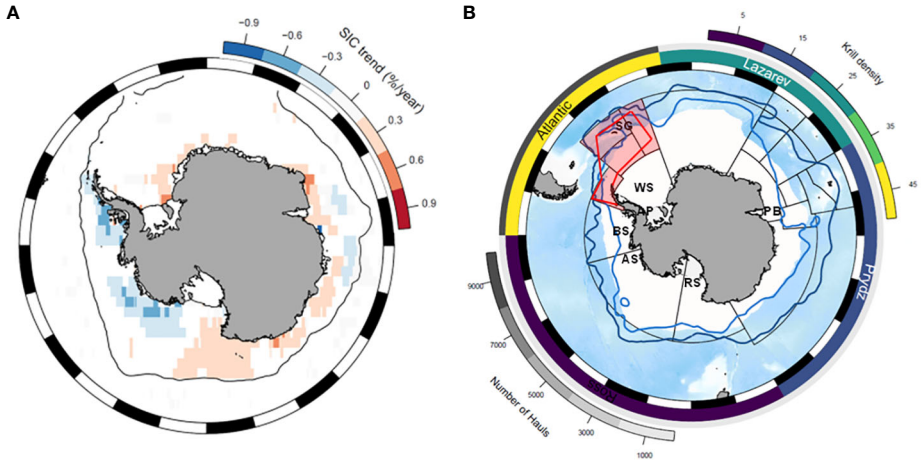

FIGURE 2
(A) Significant (p<0.05) interannual trends in sea-ice concentration (1978-11-01 to 2021-12-01). Calculated from monthly averages of daily gridded sea-ice concentration from NSIDC (https://nsidc.org/data/G02202/versions/3), and binned to a 1x1 degree grid. Trends were calculated for each grid cell by fitting monthly SIC using a GAMM with two terms: (1) a periodic spline in day of the year to capture the seasonal trend; and (2) a fixed linear term for the index in the time series to capture the multi-year trend; and also including an AR1 correlation coefficient for year. If the linear interannual trend was significant, then the slope of the trend (in %/year) is shown in the colour ramp for that grid cell. This figure was produced in the R Statistical Computing Environment (RCoreTeam, 2021) using the SOmap package (Maschette et al., 2019) and the NSIDC sea ice files were accessed using the raadtools package (Sumner, 2018). **(B)** Long-term sampling effort relative to krill numerical density observed in four sectors of the Southern Ocean. The grey scale (outermost) annulus shows the number of net hauls recorded in the KRILLBASE dataset, and the coloured annulus shows the average krill numerical density (number per m^2) indicated by these net hauls. Grey lines are CCAMLR management units. The four subareas in the Southwest Atlantic sector are shaded pink and the approximate outer boundaries of the large scale-acoustic survey conducted in 2000 are shown in red. The dark blue and light blue lines represent the Polar Front and the southern Antarctic Circumpolar Front. SG: South Georgia; WS: Weddell Sea; AP: Antarctic Peninsula; BS: Bellingshausen Sea; AS: Amundsen Sea; RS: Ross Sea; PB: Prydz Bay.

Rogers et al., 2020; Johnston et al., 2022; Kawaguchi et al., 2024), and we do not repeat these here.

We provide context for our overview of sampling methods through a brief recap on the krill fishery and climate change (section 2) and a survey of workshop participant views on priority issues for understanding krill populations (section 3). We then describe the strengths and limitations of each sampling method (sections 4-6). Those methods that have been used to sample krill have been applied over different timescales, in different locations, and often for different purposes. This precludes detailed analysis of their relative performance. However, we were able to compare the methods in two ways. First, we asked workshop participants to score the suitability of each method for addressing key current problems in the understanding of krill populations (section 7). Second, we assessed the characteristics of methods used to infer stability or change in the Southwest Atlantic krill stock to identify the relationship between the conclusion reached and the sampling approach used (section 8). We conclude with a series of tractable recommendations for the SO research community and its funders (section 9).

2 Krill fishing and environmental change

Antarctic krill catches have varied over the past 50 years, peaking at 528,000 t in 1982 before declining to 66,000 t in 1993. Catches have steadily increased over the past decade to reach a three-decade peak of 450,000t in 2020 (the catch was 416,000t in 2022). In the 1980s fishing occurred in the Atlantic, Pacific and Indian Ocean sectors but since the 1990s it has occurred almost exclusively in the Southwest Atlantic sector. The fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) which is also responsible for managing the impact of the fishery on the wider state of the ecosystem (Constable, 2001). To date, this responsibility has largely been focused on the protection of land-based krill predators, especially penguins and fur seals and has resulted in catch limits much lower than those in other fisheries for high-biomass species (Hill et al., 2020). Nonetheless catches in the Southwest Atlantic have never reached the effective catch limit set in 1991, indicating limited demand.

Management of the krill fishery in the Southwest Atlantic sector (Figure 2) includes three incremental levels of precaution. Only one of these, the nominal catch limit (5.6 million t yr^{-1}), is based on sampling of the krill stock, specifically during a single survey in 2000 (Hewitt et al., 2004). The nominal catch limit divides long-term krill production at the large scale (c. 3.5 million km^2) between the fishery, predators and recruitment to the krill stock, but a lower effective catch limit (620,000 t yr^{-1}) applies until a system for managing the risks associated with spatially-concentrated fishing has been agreed. There are also lower catch limits (<279,000 t yr^{-1}) for four subareas (c. 0.5 to 1 million km^2) within the sector, intended as an interim measure to manage these risks (Hill et al., 2016). This measure expired in 2021 but CCAMLR has maintained it on a temporary basis while working on a more robust alternative (SC-CCAMLR, 2023).

CCAMLR recognises that progress is "urgently needed" as current catch limits "are not related to the status of the stock" and it identifies "feedback management" as a mechanism to "improve future management of krill, and the spatial allocation of krill catches" (CCAMLR, 2021). Thus, the intention within CCAMLR is to develop a management approach based on regularly updated information on the status of the krill stock (SC-CCAMLR, 2019).

Changes in the krill fishery have occurred against a backdrop of rapid environmental change within the Southwest Atlantic sector. This has had a notable effect on fishing patterns, with catches at the Antarctic Peninsula becoming increasingly concentrated in the austral winter and to the south of the South Shetland Islands following declines in sea ice extent and duration. Various potential environmental influences on krill populations and distribution have been reported (Meredith et al., 2019; Henley et al., 2020; Morley et al., 2020), including a strong link between the Southern Annular Mode (SAM), the leading mode of Southern Hemisphere atmospheric circulation variability, and krill recruitment (Atkinson et al., 2019). Critically krill is a cold-water species which is sustained by localised high primary production and which has a lifecycle that includes significant associations with sea ice, and apparent dependence on a limited number of spawning sites (Siegel and Watkins, 2016; Meyer et al., 2020; Atkinson et al., 2022). Prognostic studies generally suggest that krill populations and habitat extent are likely to be negatively impacted by future climate change. A series of studies suggest that there have already been climate-related changes to the distribution and, possibly, abundance of the krill population in the Southwest Atlantic. More detail, including on the drivers of change, is available in recent reviews (Meredith et al., 2019; Morley et al., 2020; Cavanagh et al., 2021b; Johnston et al., 2022).

3 Prioritisation of key topics and actions for change

The 137 participants in the 2021 SKAG workshop were mainly active krill researchers, including about one-third early career scientists, with some stakeholders from the krill fishery, management and NGOs (Atkinson et al., 2021). This engagement, enabled by the novel wholly-online format, provided a good sample size to assess expert opinion on scientifically-based management of the krill fishery in a changing climate. We asked participants via online multiple-choice polling, repeated at the start and end of the workshop, to identify priorities to improve krill fishery management (Figure 3). Only 3% of respondents supported "no real need for change" with the majority indicating an appetite for change in how the krill fishery is managed.

In both polls, around 80% of replies supported improved generation of scientific data relevant to management, and on the final day, 66% also supported improved communication between scientists and managers. Support for "improved consensus among the scientific community" fell from 50% to 31%, after the meeting. This followed discussion in which the opinions of some appeared to shift from seeing uncertainty over past krill stock declines as an impediment to management to seeing it as an indicator of the need for precaution.

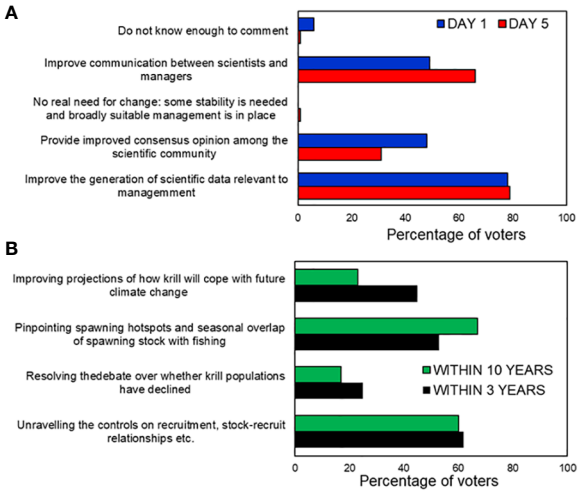

FIGURE 3
Results of online polling among approximately 100 workshop participants with mainly scientific backgrounds. Respondents were asked to vote for up to two responses and the results are expressed as percentages of voters who chose each option, rather than percentage of votes. **(A)** Polling at the start and end of the workshop in response to the question "What do you think are the most attainable ways to improve management of the krill fishery over the next five years?". **(B)** Previous work (text box 2 in Meyer et al., (2020)) has identified four main scientific priorities for helping towards improved management of the krill fishery. The question posed was "which of these are most important to prioritise over a timescale of 3 years and over the next decade?".

Previous work identified four major research foci to help krill fishery management (Meyer et al., 2020) (Improving projections of how krill will cope with climate change; Pinpointing spawning hotspots and seasonal overlap of spawning stock and fishing; Resolving the debate over whether krill populations have declined; and Unravelling the controls on recruitment). We asked participants to identify which of these to prioritise over timescales of 3 and 10 years (Figure 3). Participants strongly support prioritisation of two of the foci (pinpointing spawning hotspots and unravelling the controls on recruitment) on both timescales. Pinpointing spawning was particularly well supported (67%) over the shorter timescale as it represents a potential quick win, whereby spatial protection could be targeted at a vulnerable life-history stage. Understanding recruitment processes was likewise identified as a priority in a workshop a decade ago (Flores et al., 2012).

These research priorities require direct collection of krill from the sea as this is the only approach currently available for determining their life stage. Sampling of krill with nets has greatly declined in recent years. Acoustic surveys have also been impacted and there is an active shift to newer approaches which will take years to develop time series. These alternative methods present additional challenges such as the small spatial scales covered by individual moorings and gliders, or the limited size range sampled by commercial fishing nets. The workshop addressed this issue by evaluating the strengths and weaknesses of traditional and emerging methods (Sections 4 to 6) – and mapping them onto the priority

issues (Section 7). The diversity of krill sampling methods is illustrated schematically in Figure 4 and described below.

4 Insights on change over multiple decades

4.1 Molecular approaches

Molecular genetics is an emerging approach for investigating ecosystems, which is compatible with a wide range of sampling methods. For example, krill DNA can be obtained from scientific or commercial nets, predator diets, archive specimens or the environment. One application relevant to krill population dynamics has been to determine whether there are distinct breeding stocks. While some studies have suggested weak stock structure (Zane et al., 1998; Batta-Lona et al., 2011), there is no conclusive evidence of genetically separate groups at any scale from swarm to circumpolar (Deagle et al., 2015; Jarman and Deagle, 2016; Dong et al., 2019). By contrast, genetic analyses of the bacteria associated with krill exoskeletons have shown geographically distinct assemblages (Clarke et al., 2019). This indicates separation of host populations over a timescale of months and suggests that the method might be useful for investigating separation over longer timescales. DNA sequence data has also been used to infer past population sizes. This suggests that the population generally increased over the last 400,000 years but levelled off or declined in the most recent 20,000 years, although uncertainty is high (Goodall-Copestake et al., 2010; Dong et al., 2019). All of these analyses have been hindered by krill's unusually large and repetitive genome (Jeffery, 2012; Deagle et al., 2015). RNA sequencing of krill has also been applied to investigate responses to the environment, with early results showing effects of CO_2 levels, light, and food availability (Martins et al., 2015; Hunt et al., 2017; Sales et al., 2017).

Improvements in DNA sequencing technology, decreasing cost and increasingly robust bioinformatic tools should give higher resolution to address questions of population size and structure, including identifying any subtler structure only detectable in genomic regions under selection. Use of environmental DNA to measure the presence or abundance of krill in an area through DNA in water samples is potentially a high temporal and spatial resolution technique for monitoring krill populations, and problems of quantification (Yamahara et al., 2019) may be reduced by developing appropriate standards. Likewise,

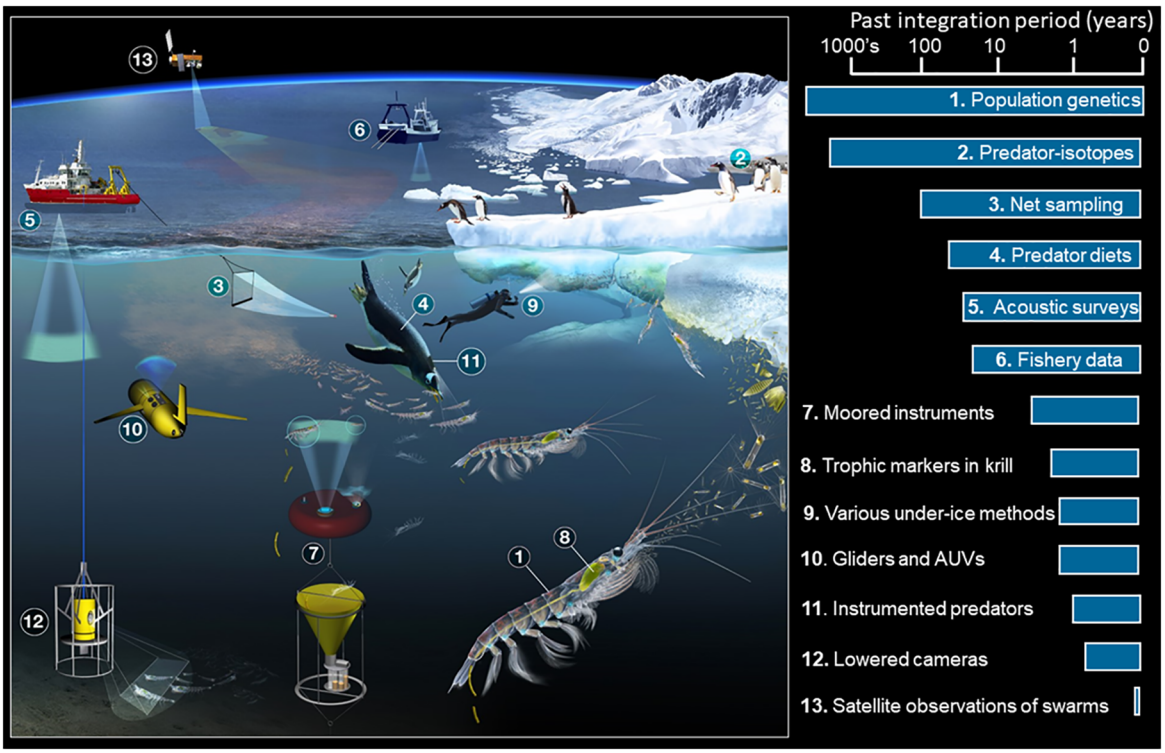

FIGURE 4
Traditional, emerging and future approaches to detect change in the krill-based food web. Illustrated are single-image depictions of groups of approaches; for example, the diver used to depict under-ice observations (No. 9) represents a suite of methods including diver-observation and sampling, a suite of net types and pumps, ROVs and AUVs. Moored instrumentation can also sample under ice and likewise includes various approaches including ADCPs and sediment traps. The fishery includes data from observers and from fishery statistics as well as newly developing opportunities (for example to sample krill in similar ways to research vessels). Imaging systems are also typically deployed from ships and other surface platforms, and can also be mounted on AUVs. For these reasons the right-hand scale can show only an approximate timescale over which these approaches can integrate. Importantly, the newer technology and approaches may be better at providing more direct, high-resolution observation, from ice crevices to abyssal seabeds, but so far the time scales are too short to yield evidence of multi-decadal change. Conversely, longer time series have greater statistical power but can face issues of interpretation of the trends observed.

monitoring of krill transcriptional activity (RNA), feeding, and/or symbionts may develop into a useful rapid indicator of stresses on krill populations, able to detect perturbations before effects are measured at the level of stock sizes.

4.2 Millennial, centennial, and decadal time paleo reconstructions

Paleoenvironmental proxies are commonly used to reconstruct krill-based food web dynamics prior to the era of direct krill sampling. The microscopic, geochemical, isotopic, and molecular analyses of ice cores, marine and limnological sediments, ornithogenic soils, and historic museum collections provide insights on SO climate and food-web dynamics over millennial, centennial, and decadal timescales. Collectively, these provide proxy records of past climate [e.g. isotopic and chemical analysis of ice cores (Mulvaney et al., 2012)], sea ice conditions [e.g. marine diatom sedimentary records (Taylor and Sjunneskog, 2002)], oceanic productivity [e.g. biogenic silica sedimentary records (Johnson et al., 2021)], sea-ice algal productivity [e.g. highly branched isoprenoid sedimentary records (Vorrath et al., 2020)] shifts in krill predator populations [e.g. bio-element, faecal sterol, and radiocarbon analyses of ornithogenic soils (Emslie et al., 2014)], and changes in krill predator diets over time [e.g. bulk tissue and compound-specific stable isotope analyses (McMahon et al., 2019; Kalvakaalva et al., 2020)].

While these paleoenvironmental proxies provide insights into how krill-based food webs have changed, no single proxy directly measures krill abundance over time. They are innately patchy in time and space and their use requires an understanding of the relationships between climate, productivity, krill abundance, and predator population and foraging dynamics. For example, multiple paleoenvironmental proxies in the Ross Sea were used to show that changes in atmospheric circulation and oceanographic conditions between ~1600 and ~1850 AD increased primary productivity, krill and silverfish (*Pleuragramma antarctica*) abundance, providing greater open-water access for krill predators relative to today (Yang et al., 2018). Compound-specific stable isotope analyses provided support for the hypothesis that historic anthropogenic exploitation and recent climate change reduced the availability of krill to their predators in the Antarctic Peninsula over the past century (Johnson et al., 2021).

The development and validation of zooplankton and possibly krill-specific paleoenvironmental biomarkers in sedimentary and ornithogenic archives represent an important future research need (Yang et al., 2021a). This could allow future studies to better relate variation in krill abundance over time with past climate, productivity, and krill-predator dynamics to understand longer-term changes in krill-based food webs.

4.3 Time series from net surveys

Net sampling is the longest-running sampling method for krill, with the earliest available data coming from the *Discovery Investigations* in 1926. These data provide our foundational understanding of krill (Fraser, 1936; Marr, 1962; Mackintosh, 1972, 1973). Net surveys are unique in their ability to provide quantitative data on different krill life stages, length-frequency distributions, and physical samples for laboratory-based research [e.g (Conroy et al., 2020; Steinke et al., 2021)]. However, net sampling comes with disadvantages such as mesh selectivity (Siegel, 1986), net avoidance (Wiebe et al., 2004), escapement, damage and integration (Watkins, 2000), and net feeding (Hirota, 1984). Nearly a century of circumpolar net-catch data are available in the standardised, composite KRILLBASE database (Atkinson et al., 2017), a historical reference to which new data can be added. These data have been used for a variety of purposes, for example to estimate krill biomass and annual production (Atkinson et al., 2009) and to identify habitat partitioning between life stages (Perry et al., 2019).

Analyses of net time series reveal spatial differences in multidecadal krill abundance trends. This topic has raised some controversy and section 8 enlarges upon the issue of detecting time trends in krill populations from a series of sampling methods including nets. Importantly, scientific netting remains the most viable method to capture and quantify the pelagic early larval stages of krill (eggs to furcilia) which indicate spawning, nursery and recruitment areas (Perry et al., 2019; Rombolá et al., 2021; Atkinson et al., 2022). However, the recent decline in net sampling surveys, in part due to competing demands for ship time, is expected to continue and presents a major challenge for detecting long-term change in krill populations.

4.4 Scientific ship-based acoustics

Acoustic instruments, deployed on research or fishing vessels, have been the main tools used by CCAMLR to assess krill density and distribution since they were first used to survey krill biomass in the 1980s (Siegel and Watkins, 2016). Large scale (i.e. ≥0.5 million km^2), often multi-vessel, surveys require significant ship time and as a result happen infrequently (Krafft et al., 2021). Smaller-scale, single-vessel surveys (10^3 - 10^5 km^2) have provided annual assessments of krill biomass in three areas in the SW Atlantic sector. These are the US-AMLR time series, north of the tip of the Antarctic Peninsula [1996 – 2012 (summer), 2014-2016 (winter), with subsequent surveys conducted by a Chinese fishing vessel (2013-present)] (Reiss et al., 2008, 2017) (WG-ASAM, 2019) the Norwegian South Orkney time series (2011 – present) of krill biomass in a krill fishing hotspot (Krafft et al., 2018), and the Western Core Box area north of South Georgia has been sampled by the British Antarctic Survey annually since summer 1997 (Fielding et al., 2014). Each survey provides a snapshot of biomass, but a time series built on such snapshots might be sensitive to phenology, amongst other factors. These time series tend to show high inter-annual variability in krill biomass and no evidence for an overall trend (see section 8).

Annual acoustic surveys provide key datasets contributing to the understanding of inter-annual variability in krill populations. Additional data such as net samples and predator observations are collected at the same time. Historically these surveys have been

undertaken by research vessels but research fleet sizes are declining (Kintisch, 2013). Subsequent sections describe parallel acoustics from commercial fishing vessels, autonomous vehicles and gliders, and the approaches needed to ensure that estimates from different platforms are comparable, and trends can be detected.

4.5 Data from the krill fishery

The krill fishery has reported catches and operational details for nearly five decades. Haul-level data from the fishery can be used as proxies for describing krill horizontal and vertical distribution, and catch per unit of effort (CPUE), calculated at the haul-level and averaged per year over appropriate spatial units provides an indirect indicator of krill stock state (Ribic et al., 2008; Santa Cruz et al., 2022). The capacity to process catches sets an upper limit on CPUEs beyond which they are insensitive to increases in abundance. Conversely, fished species can maintain high densities within aggregations, maintaining high CPUEs even as overall abundance falls. CPUE can also be affected by shifts in location. These issues are compounded by the fact that the krill fishery is experiencing radical shifts in technology and strategy, and becoming increasingly concentrated in areas of reliable catches (Santa Cruz et al., 2018; Krüger, 2019). Nonetheless, there is some correspondence between spatially and temporally averaged CPUE time series and acoustic series for similar locations (Ribic et al., 2008). Decreases in spatially averaged CPUE were observed as the fishery expanded southwards in the Antarctic Peninsula region in the last two decades and fishing operations also shifted temporally to begin later in the summer-autumn season (Santa Cruz et al., 2018; Krüger, 2019; Santa Cruz et al., 2022). These changes also resulted in increased fishing depth (Krüger, 2019). Disentangling the various influences on CPUE data will require comparison with independent estimates of biomass, which could be based on acoustic transects provided by fishing vessels following scientific protocols.

The presence of scientific observers on krill vessels has increased from low levels in the 1990s to the current 100% coverage and this provides a valuable source of information on biological characteristics, especially krill size. Nonetheless, these data must be interpreted cautiously since sampling locations, swarm sizes, depths and biological characteristics such as body condition and feeding status are selected to suit fishery objectives, and commercial nets are too coarse to quantitatively sample smaller (<30mm) individuals.

4.6 Monitoring diet and foraging behaviour of krill predators

Long-term studies on central-place krill predators, including penguins and seals, provide the majority of data to CCAMLR's ecosystem monitoring programme which monitors the life history parameters of these foragers to help detect changes in the abundance of harvested species, especially krill, and determine whether such changes are driven by fishing (Agnew, 1997).

The availability of krill to these predators is a function of krill biomass and its accessibility. Unravelling predator responses to changes in krill availability therefore requires consideration of factors beyond biomass estimates from traditional net or acoustic surveys. For example, accessibility of krill can vary due to diel vertical migration, tides and near-shore currents, prey depletion, annual on-shelf migrations, and episodic krill recruitment events (Wilson et al., 1993; Ribic et al., 2008; Ballance et al., 2009; Lowther et al., 2018; Nardelli et al., 2021). It is increasingly recognized that availability is a multivariate phenomenon and that understanding predator responses to changes in prey availability benefits from integrated sampling approaches (Boyd et al., 2017; Waggitt et al., 2018).

Despite these caveats, studies monitoring predator diets and foraging effort reveal predator sensitivity to changes in krill availability. For example, diet samples from krill predators reveal regional-scale coherence in krill sizes with foraging trip durations that correlate negatively with mean krill sizes (Hinke et al., 2007). Furthermore, years with longer foraging trips exhibit lower offspring production and growth (US AMLR, unpublished data). At Bird Island, South Georgia, where krill abundance is more dependent on advection/migration (Murphy et al., 2004), periodic variability in its availability, in turn correlated with variation in the physical environment, correlates with subsequent fluctuation in vital rates of predators, particularly those that are more dependent on krill (Murphy et al., 2007; Forcada et al., 2008). Together, the weight of evidence helps to link changes in size structure of the krill population with predator foraging behaviour and vital rates and reaffirms the utility of predator monitoring for understanding changes in krill populations.

5 Emerging and novel approaches to observe and monitor krill

5.1 Moored instrument arrays

Mooring arrays offer the potential to deliver temporally extensive (sub-daily and monthly) data on krill and, with concurrent oceanographic data, can help us understand intra- and inter-annual variations in their density, behaviour and population dynamics (Brierley, 2006). For example, moored echosounders and Acoustic Doppler Current Profilers at South Georgia have revealed a seasonal cycle in krill density, with peaks in summer and troughs in winter, which may be associated with seasonality in temperature, swarming behaviour and/or depth distribution (Saunders, 2007; Saunders et al., 2007). However, methodological challenges with this approach include ground-truthing and robust species identification, which may be improved using new multi-frequency echosounders. Innovative methods using moored sediment traps that collect krill moults can also provide alternative approaches to measure krill density, population structure, recruitment and carbon flux (Manno et al., 2020). Elsewhere, acoustic moorings in the Amundsen Sea coastal polynya have revealed seasonal and climate-related trends in zooplankton vertical migration behaviour (La et al., 2015, 2019).

In addition to identifying the scatterers, a major challenge with moorings for monitoring krill is the requirement to set their small-

scale, point observations into a broader spatial context. To address this, integration of mooring-based observations with larger scale observations will be required.

5.2 Gliders and autonomous underwater vehicles

Remotely piloted and self-propelled Autonomous Underwater Vehicles (AUVs) are able to sample marine ecosystems autonomously for long periods of time, even in inaccessible, inhospitable and challenging regions (Testor et al., 2019). The current summary focuses on the buoyancy-driven glider (Webb et al., 2001; Schofield et al., 2007), while the later "under ice" section considers Remote Operating Vehicles (ROVs) dedicated to observing the ice-water interface.

Gliders can sample across a wide range of scales, from micro to macro, in both space and time, but there are limitations to where they can operate, especially in near-shore environments. Multiple gliders can simultaneously sample multiple locations and scales. Gliders outfitted with echosounders can measure krill distribution and biomass in a comparable manner to ship-based acoustic surveys (Reiss et al., 2021) while additional sensors for parameters including temperature, salinity and fluorescence (Testor et al., 2019) help to resolve relationships between krill distribution and the physical environment at scales not achievable from ship-based surveys (Nardelli et al., 2021). These scales range from sub-meso (10s of kilometres and days to weeks) (Cimino et al., 2016; Hann, 2021; Nardelli et al., 2021), to macro (100s of kilometres and months to years) (Reiss et al., 2021) (Guihen et al., 2014). Glider-borne acoustic surveys of Antarctic krill have illuminated predator-prey interactions (Cimino et al., 2016), examined krill diel vertical migration patterns (Nardelli et al., 2021), and assessed krill-salp distribution overlap (Hann, 2021). Acoustic data obtained from glider-borne echosounders are often less noisy than data collected from vessels (Hann, 2021) and, because they traverse the water column, clear acoustic signals can be detected at great depths, which are limited to lower frequency echosounders in ship-based surveys.

Target validation and length frequency determination from net tows pose a challenge for gliders. However, new techniques are being developed to overcome this, including the use of imaging (Ohman et al., 2019). Acquiring and maintaining a glider fleet is costly and logistically challenging and might limit the scales of the questions that can be addressed by any single research group. However, by pooling resources to develop programs that coordinate AUV fleets, a research community can begin to conduct truly transformative science (Testor et al., 2019).

5.3 Instrumented air-breathing predators

Instrumented predators can provide valuable insight into the distribution, availability, and density of krill. Predators such as penguins and seals consume large amounts of krill, concentrating their foraging efforts in the areas and depths where krill occur in high densities. Recent developments in biologging (the study of marine life via animal-borne instruments) have allowed us to monitor the movements, diving behaviour, feeding rates, and prey field of these predators at multiple spatial (<1 – 100s km) and temporal (minutes to decades) scales (Hindell et al., 2020).

Recent successful uses of biologgers include a study of crabeater seals, a highly-specialized krill predator, showing how their foraging effort related to sea ice, water temperature, and bathymetry across the western Antarctic Peninsula (WAP) (Hückstädt et al., 2020). Forward projection of seal habitat use indicated that krill distribution will expand offshore and towards southern sectors of the WAP in response to future environmental conditions. A study on Adelie penguins in East Antarctica found that their feeding rates while diving for krill (a putative indicator of krill density) were higher in a year of less extensive fast-ice than in extensive fast-ice years (Watanabe et al., 2020).

These studies suggest that changes in krill distribution, density and availability, and their links to environmental fluctuations, can be inferred from instrumented predators, although this approach is biased towards areas where these predators aggregate (e.g., breeding colonies). While long time series of predator behaviour data from biologgers are not yet available, simultaneous monitoring of feeding behaviour and *in-situ* environmental characteristics will expand our ability to understand fine-scale links between the environment, krill, and their predators (Keates et al., 2020; Kokubun et al., 2021).

5.4 Developments in under ice krill sampling

Sea ice is an important habitat for early life stages of krill, and its study provides insight into their life cycle, recruitment and population dynamics. A variety of methods have been used to sample at different spatial and temporal scales.

SCUBA divers (O'Brien, 1987; Meyer et al., 2009, 2017) and ROVs help us understand how krill use sea ice on a scale of meters (Marschall, 1988; Nordhausen, 1994). Divers can also provide data on stage structure and condition, and are unique in their ability to collect pristine live krill (Meyer et al., 2009). Specialized nets for sampling under ice, such as the Surface and Under-ice Trawl (SUIT), can survey across the water/ice interface on the kilometre scale while providing samples for assessing stage and condition (van Franeker et al., 2009). Traditional oblique Rectangular Midwater Trawl (RMT) and vertical nets (Bongo) deployed from a ship in ice provide similar information but vertically integrate the water column (Nordhausen, 1994; Schaafsma et al., 2016; Reiss et al., 2020). Acoustic methods can integrate biomass over many km^2 but are limited in their ability to assess the water/ice interface (Brierley et al., 2002; Reiss et al., 2020). In a recent study synthesizing different methods, abundance estimates were 2-3 orders of magnitude higher in the same location using acoustic and diver methods than SUIT and vertical net methods and one-order of magnitude higher than RMT or ROV methods (Meyer et al., 2017). The methods used reflect the research questions and available time. While nets can be deployed relatively quickly from research vessels, divers and ROVs require great logistical efforts, for instance over

weeks from winter ice camps on stable ice floes (Meiners et al., 2017; Meyer et al., 2017).

5.5 Direct visual observations of krill

Direct observations of krill behaviour in the water column, particularly through the use of divers and various camera systems, have provided much information about how individual krill behave (Hamner and Hamner, 2000; Nicol and Brierley, 2010; Atkinson et al., 2012; Tarling and Fielding, 2016). While krill behaviour within surface swarms was described from the *Discovery Investigations* (Marr, 1962), divers provided some of the first observations of krill behaviours in the water column and continue to be valuable under sea ice (Kils, 1981; Hamner et al., 1983; O'Brien, 1987; Stretch et al., 1988; Meyer et al., 2017). Acoustic systems are ideal for observing collective krill behaviour over larger spatial scales (De Robertis et al., 2003; Klevjer and Kaartvedt, 2003; 2006; 2011; Lawson et al., 2008; Klevjer and Kaartvedt, 2011), but cannot currently resolve the finer-scale behaviours of individual krill (Kils, 1981; Kawaguchi et al., 2011). Camera systems, deployed either on static rigs, ROVs, AUVs, ships, or even krill predators (Kawaguchi et al., 1986; Jaffe et al., 1998; Kokubun et al., 2013; Letessier et al., 2013; Watanabe and Takahashi, 2013; Kubilius et al., 2015; Schmid et al., 2016; Handley et al., 2018; Kane et al., 2018) provide these finer-scale observations, and can be adapted to determine the abundance of zooplankton and possibly other pelagic organisms (Jaffe et al., 1998; Letessier et al., 2013; Kubilius et al., 2015; Schmid et al., 2016; Kane et al., 2018, 2021). They can be used at deeper depths than scuba divers or acoustics can operate (Kawaguchi et al., 1986; Gutt and Siegel, 1994; Letessier et al., 2013; Kubilius et al., 2015; Kane et al., 2018; Zabroda et al., 2020; Kane et al., 2021), but importantly, can also be used to ground-truth acoustics data.

Direct observations of individual krill from divers and camera systems, as well as indirect observations from acoustics, have enabled us to document krill anti-predatory behaviours (O'Brien, 1987), seasonal changes in movement (Kane et al., 2018, 2021), interactions between individual krill (Hamner and Hamner, 2000; Kawaguchi et al., 2011), and with their environment. Camera observations of their behaviour at the seabed have brought about a paradigm shift in our understanding of krill-seabed interactions, showing that krill regularly interact with the seabed, in contrast to the earlier assumption that such interactions were rare (Gutt and Siegel, 1994; Clarke and Tyler, 2008; Kawaguchi et al., 2011; Schmidt et al., 2011; Zabroda et al., 2020; Kane et al., 2021).

Despite these advantages, direct, *in situ* observations of individual krill remain scarce, which hampers our ability to generalise their individual behaviours, including swimming, feeding, and mating. Nevertheless, improvements in image capture and processing technologies will enable us to better observe krill interactions with each other and their environment at small scales. These observations will allow laboratory results to be placed into better context, and help to elucidate the relationship between individuals and population dynamics.

5.6 Remote detection of krill swarms

The biomass and distribution of near-surface swarms of krill are poorly quantified by conventional sampling, and remote detection by satellites or aerial vehicles offers one potential solution. Historical records indicate that large surface swarms can change the water colour, so ocean colour satellites, which measure the surface ocean synoptically, should theoretically allow measurement of near-surface krill swarms at high spatial and temporal resolution. Such data have already been used to detect aggregations of the pelagic copepod *Calanus finmarchicus* and global patterns of diurnal vertical migration (Basedow et al., 2019; Behrenfeld et al., 2019). A pilot study (Belcher et al., 2021) has shown that water containing krill indeed has a different reflectance spectrum, thus providing proof of concept for remote detection of surface swarms.

To develop earth observation methods for krill swarms, more ground-truthing is needed. This requires the use of unmanned aerial vehicles mounted with spectroradiometers and/or cameras, in concert with surface net tows from a ship under cloud-free conditions. Cloud cover presents a challenge for ocean colour satellite measurements, thus the use of LIDAR from autonomous aerial vehicles must also be considered. Nevertheless, remote detection has the potential to provide unparalleled resolution of near-surface krill swarm distribution, which could facilitate a step-change in our ability to map and monitor this species over large areas of the SO.

6 Detecting change in the krill-based food web

The methods described in previous sections provide indices of numerical or biomass density or availability to predators over various time and space scales. This section describes other complementary indices of change in the krill-based food web, namely in recruitment, population structure and krill trophic position.

6.1 Changes in krill recruitment and population structure

Indices of krill recruitment, the replenishment of the adult population by approximately one-year old animals, are generally based on length-frequency distributions from multi-decadal series of length measurements based on net tows (Atkinson et al., 2019) and predator diet data (Saba et al., 2014). Such data are mainly available for the Atlantic sector, with some coverage in other areas such as the Indian sector (Nicol et al., 2000; Kawaguchi et al., 2010). Recruitment indices provide critical information on krill population dynamics, including on possible causes of large interannual variations in stock size. Nonetheless, there are potential biases in such data due to potential size-selectivity of sampling and uneven distribution of recruits (Ducklow et al., 2007).

Analyses of trends in recruitment are sensitive to scale and location. At sector-wide scales, strong declines in recruit density, related to summer, autumn and winter SAM anomalies emerge (Atkinson et al., 2019), but as the spatial scales of study decline, recruitment time series become increasingly fragmented (Ducklow et al., 2007; Veytia et al., 2021), and conclusions are often dependent on the region and time-period of study. For example, in the early 21st century, relationships between localised recruitment indices and sea ice extent or duration (Quetin and Ross, 2001; Wiedenmann et al., 2009), supported findings of southward shifts in recruitment with declining sea ice (Ross et al., 2014). However more recent observations suggest that the processes underpinning recruitment are regionally variable (Jia et al., 2016; Meyer et al., 2017; Walsh et al., 2020), or changing to become less reliant on sea ice habitats (Walsh et al., 2020).

Understanding of krill recruitment requires progress in data analysis, including integrated modelling (Kinzey et al., 2018) to handle the statistical challenges of comparing proportional and absolute recruitment data. It also requires an improved sampling strategy to coordinate across science programmes and target the spatiotemporal scales at which krill recruitment plays out. This implies a role for modelling to optimize sampling design (Peel et al., 2013). Because measuring recruitment requires direct sampling and identification of small (~20 mm) krill, which are the same size as the adults of other euphausiid species, there is a continuing need for traditional net sampling and identification skills until reliable alternative methods are available.

6.2 Tracing krill diet and resource allocation

Analyses of krill diet and body condition provide insights into the processes affecting population change. A suite of methods have shown that krill exploit a broad range of food items from phytoplankton blooms and sea ice algae, micro- and mesozooplankton, to seabed detritus (Hopkins et al., 1993a, Hopkins et al., 1993b; Martin et al., 2006; Passmore et al., 2006; Schmidt et al., 2011; Cleary et al., 2018; Schmidt et al., 2018; Pauli et al., 2021). Krill also accumulate substantial lipid reserves for overwintering (Hagen et al., 2001), but importantly for understanding recruitment, overwintering strategies vary between sectors and latitudes (Schmidt et al., 2014). At an interannual scale, differences in sea ice dynamics and phytoplankton abundance are reflected in krill diet, body conditions and fecundity (Quetin and Ross, 2001; Jia et al., 2016; Ericson et al., 2018; Bernard et al., 2019; Walsh et al., 2020). However, we are not aware of any long time series of krill diet/body condition that accompanies those of recruitment or density.

As krill sampling methods evolve in future, two types of approach may prove promising. First, creating biomarker time series on frozen or formalin-preserved krill to understand temporal-spatial changes in the krill food web. Studies elsewhere have shown that biomarkers such as bulk stable isotopes ($\delta^{15}N$, $\delta^{13}C$), amino acid $\delta^{15}N$, highly branched isoprenoids and even DNA of preserved tissue can provide robust data that reflect changes in trophic level or diet in relation to climatic events (Rau et al., 2003). As scientific sampling with nets diminishes, the krill fishery can provide a valuable source of material; for example, frozen winter-caught specimens have been used for lipid content and various diet and condition indices (Schmidt et al., 2014). Secondly, a wider perspective on how krill-based food webs are faring under climate change can also be obtained by sampling other plankton alongside krill to understand changing body composition of "winners" and "losers" under varying climatic conditions.

7 Mismatch between key research areas for krill and emerging sampling methods

Thirty-three of the workshop participants, spanning discipline areas, career stage and experience, contributed to Table 1 which maps methods of sampling and analysing krill onto key areas in current research. Table 1 identifies a mismatch between priority issues identified for improving management (e.g. larger scale and longer term population trends, sampling of larval or newly-recruited krill) and the emerging methods that in many cases are partially replacing traditional ship-based scientific surveys. Paradoxically, the new methods allow us to sample krill on ever smaller scales of space and time, while the pressing issues of climate change and habitat occupancy concern much larger scales. All of the new methods received lower support than ship-based methods for their ability to assess long-term population trends, and only gliders/AUVs received a similar level of support to ship-based methods for their ability to assess large-scale distribution.

8 The influence of sampling approach on perceptions of change

A debate about whether krill have declined in the last 50 years within the SW Atlantic sector (Cox et al., 2018; Atkinson et al., 2019; Cox et al., 2019; Hill et al., 2019; Candy, 2021) provides an opportunity to examine the influence of sampling scale and location and time series length on perceptions of change in a pelagic population. Resolving this debate has previously been identified as a key step towards better understanding of future change in krill populations (Meyer et al., 2020). This controversy results, in part, from a lack of large-scale monitoring during the 1980s, the main period of the reported decline. Just one large-scale survey (0.5 million km^2) was conducted during this period (Siegel and Watkins, 2016) and two further surveys (2 million km^2) were conducted, in 2000 and 2019 (Krafft et al., 2021). This lack of large-scale monitoring has led to attempts to fill the information gaps, including the CCAMLR Ecosystem Monitoring Programme (Agnew, 1997) and the compilation of KRILLBASE data (Atkinson et al., 2017).

We compiled and compared analyses reporting changes or stability in the krill population over multiple years (Figure 5 and Supplementary Table 1). This shows that many of the apparently

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TABLE 1 Mapping established and developing krill sampling methods onto some of the key current research areas.

Measurement	Long-term, large scale..		Inference it provides on krill..				Small scale
	Long-term stock trajectory	Large-scale Distribution (meso, basin, circumpolar scale)	Recruitment long-term (multi-decadal) trends	Changing availability to Predators	Inference on how the krill-based food web operates	Behaviour, Swarming, seasonal-to decadal and verti-cal distribution	Growth reproduction, energy budget, Biogeochemical role.
Population genetics	20	18	12	11	17	4	13
Paleo- isotopes and other proxies	28	14	7	31	37	1	15
Net-sampling	45	59	62	40	40	47	52
Ship-borne acoustics	50	65	22	53	29	61	14
Predator diets & foraging indices	26	32	42	55	53	24	21
Fisheries data: catch/effort/position	28	37	18	24	11	21	5
Fisheries data: observer pop structure	24	18	48	23	18	16	36
Fisheries data: acoustic info	31	39	16	24	16	44	2
Moorings, *in situ* instrumentation	24	19	22	30	27	47	20
Instrumented predators	7	34	15	59	46	47	9
Under ice sampling/ observation	7	16	27	31	46	58	43
Gliders, AUVs	20	54	13	38	26	56	7
Lowered cameras	0	4	9	21	27	59	14
Earth observation	12	33	7	16	5	17	2
Trophic markers	4	6	9	34	55	1212	56

Each participant scored each combination of measurement and inference as 2 (Useable), 1 (Useable)? or 0 (not relevant) and the scores were summed per cell. The colour coded results table shows the total scores for each cell. Cell score totals ranged from 0 to 65 of a total of 66, and cells are colour-coded as below:

< 20	20-29	30-39	40-49	50-59	60-66

conflicting interpretations can be explained by sampling differences. Suggestions of a decline are based on data series that have one or more of the following features: a) net or predator-based data; b) a start date before the late 1980s; c) more than 20 years of observations; d) spatial coverage that includes the northern (warmer) part of the range of krill, particularly north of 60°S. Conversely, most studies which report an absence of directional trends are based on combinations of a) acoustic or fisheries methods; b) data series starting in the 1990s or later; c) fewer than 20 years of data; d) sampling only south of 60°S.

Beyond these factors, repeated analyses of the net-based data in KRILLBASE have either supported (Atkinson et al., 2004, 2019; 2022; Candy, 2021; Yang et al., 2021b) or not supported (Cox et al., 2018; Candy, 2021) a decline in the late twentieth century. This partly reflects differences in the selection of data for inclusion in the analysis, the covariates included, and the statistical method used. A recent analysis (Candy, 2021) presents a series of models in which the significance of a decline reported north of 60°S[9] varies from highly significant (P<0.001) to non-significant (P>0.05) depending on the formulation of the model. Likewise, the statistical significance of the decline depends on whether larval or post-larval data are used and whether they are aggregated by year or multi-year period, and presented as mean densities or swarm frequency (Atkinson et al., 2022). The finding that declining

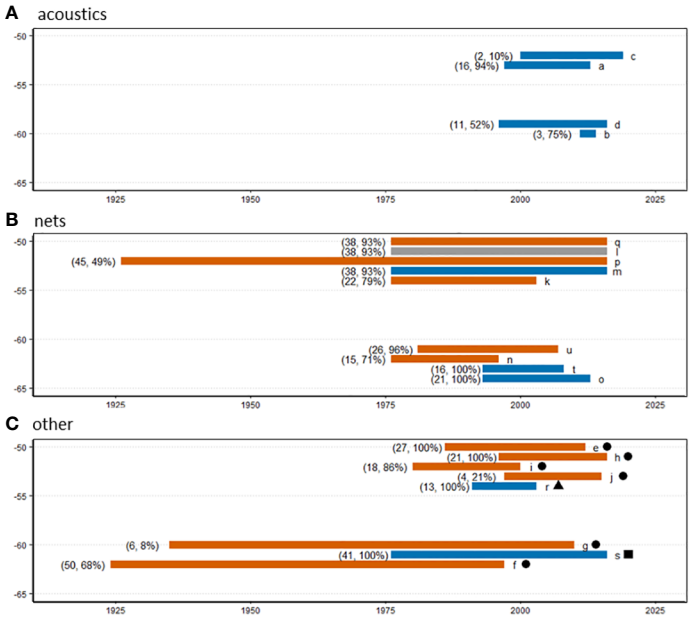

FIGURE 5
Summary of studies reporting on krill trends within the SW Atlantic sector, showing the time span, northern latitude (vertical axis: 5° bins) and findings of the study (orange = a negative trend, blue = no trend, grey = ambiguous). Panels group studies by data source: **(A)**=acoustics, **(B)**=nets, **(C)**=other methods indicated by the symbol: solid circle = availability to predators, solid triangle = fishery CPUE, and solid square = integrated assessment of multiple data sources. Additional values in parentheses are the number of years of data and the percentage of years sampled in the time span of the study. The study reference (Supplementary Table 1) is indicated by a letter on the right of each bar. In our synthesis of evidence, we have included only studies which report previously unreported data or present analyses that provide direct information about changes in indices of krill population size (including population density, biomass and recruitment strength). We have not included reviews, opinions expressed in papers without supporting data and papers only reporting trends in indirect indicators such as predator population parameters.

mean densities of krill were reflected in declining frequencies of high (swarm) densities (Atkinson et al., 2022) requires further study, because it supports earlier suggestions (Brierley and Cox, 2015) that changes in density of aggregating species like krill are associated with changes in swarm frequency rather than swarm size.

Importantly, none of the various sampling methods provides a direct estimate of the biomass or abundance of the whole population. Predator and fishery-based indices are likely to be highly non-linear indicators, as explained in section 4. Acoustic and net surveys often miss krill dispersed in mid-water layers and at the seabed (Kane et al., 2021). Nor is there a simple relationship between numerical density (from nets) and biomass density (from acoustics). Net sampling suggests that a dramatic decline in small (~20 mm) krill over 20 years resulted in a 40% increase in mean mass of individuals, due to a significant increase in mean krill length (Atkinson et al., 2019). Thus, declines in abundance could occur with little or no parallel change in biomass. In addition, acoustic methods [typically using transducers with frequencies in the range 38-120 kHz (Krafft et al., 2021)] and net sampling have different selectivities for krill in the affected size range. Each of these factors might contribute to discrepancies between krill trends observed with acoustics and nets (Figure 5).

When trends have been reported they explain only a fraction of the observed variance (e.g. 8% (Atkinson et al., 2019)). Great inter-annual variability in recruitment translates into significant, possibly cyclic, interannual fluctuations in post-larval density. Periods of rapid change punctuated by periods of relative stability are also possible. This high variation makes secular trends difficult to evaluate statistically without long data series. The spatial scale of sampling is also important because changes in krill distribution, from inshore-offshore migration (Cleary et al., 2018) to longer-term range shifts (Atkinson et al., 2022) could mask or exaggerate changes in population size.

While we did not seek consensus on the interpretation of these data, the prevailing view of workshop participants was that uncertainty over krill trends strengthens the case for management based on repeated sampling of the krill stock. Importantly, short data series tend to have a higher risk of type II error (falsely assuming that lack of statistical support for a trend means stability). Sampling at scales much smaller than the population carries risks of both type I (falsely identifying a trend, or falsely assuming that a trend applies to the whole population) and type II error. Conversely the debate over krill trends indicates a concern that analyses of large-scale krill population trends carry a high risk of type I error. These risks are important and need to be communicated to fisheries managers. An abrupt shift to new methods could mean starting afresh with very short data series and exacerbating the type II risk.

9 Future outlook and recommendations

Workshop participants supported change in how the krill fishery is managed, with the majority identifying improved

communication and the provision of data as tractable steps towards more scientifically-based management. A key priority is improving understanding of the combined impacts of climate change and fishing on krill. Other priorities, including better understanding of recruitment, spawning areas and time trends were articulated a decade ago (Flores et al., 2012) but remain largely unresolved. Consensus on time trends seems unlikely but better quantification and explanation of uncertainty in reports of both time trends and stability is required. The scale of this uncertainty is a strong argument for management that is able to adapt to change and a key requirement for such management is regularly updated information on the state of the krill stock.

There are clear benefits in new sampling methods, which can be applied to krill and other pelagic animals. These methods diversify the types of data obtained, require fewer personnel, and often have lower costs and carbon footprints than research vessel surveys. However, newer sampling methods generally focus on finer scales of space and time while tracking change, for management or ecosystem monitoring, requires larger-scale and longer-term data. Many methods could potentially be scaled up to provide such coverage, for example by developing coordinated fleets of gliders. There is a clear need to plan the transition to new methods to minimise the risk of a loss of coverage. A key risk is a lack of comparability between old and new data to the extent that it becomes impossible to disentangle ecological change from methodological change.

Coupled to these issues is the changing skill set among the scientific community. Only 65% of established researchers had handled live krill. The percentage was lower (58%) amongst early career researchers and the ability to identify pre-adult life stages was lower still (13%). Multiple complementary approaches are useful for studying a behaviourally flexible species and it is important to retain fundamental field biology skills even as science becomes more reliant on new technology. We have shown here that diversification of approaches has the added benefit of providing complementary (and sometimes alternative) insights into long-term change in the krill-based food web.

To meet these challenges, Box 1 provides a series of key solutions arising from our workshop. Continued ship-based monitoring, which includes net-sampling of live animals, is necessary to minimize the risks associated with a transition to new methods, improve understanding of demographics and physiology, and ensure that researchers are able to learn and practice handling and identification skills. This requires ship-time and experimental facilities, the cost of which has led to some key monitoring programmes (e.g. the summer AMLR surveys) being discontinued. Several acoustics-based monitoring programmes using moorings and AUVs have started in the last decade, but these use very different techniques to ship-based surveys, so lengthy intercalibration periods are necessary to allow continuity and comparability between old and new methods.

An ongoing issue, exacerbated by the smaller scales of newer methods, is that fieldwork focusses on localised areas, while the vast majority of the pelagic habitat is poorly sampled. To help rectify this, workshop participants strongly supported developing strategies to network individual observations and allow for easier

BOX 1

Potential solutions to mismatches between the information requirements for managing the krill fishery and the capabilities of new sampling methods

Improve overlap and intercalibration of new and existing methods: Despite challenges of expense and availability of research vessels, it is imperative that traditional capture of krill with nets is maintained, alongside scientific acoustic survey techniques. With acoustic krill monitoring, for example from gliders and moorings, we need to verify acoustic target identification and provide intercalibration time series. Given the importance of understanding recruitment and spawning hotspots it is vital to sample with sufficiently fine mesh nets to capture larval and juvenile krill, and that experience is retained in the community to handle live krill and to identify these stages.

Harmonise, network and upscale the capacity of national sampling programmes: Despite challenges of administrative load, national preferences and history of sampling approaches, we urgently need to scale up localised data collection efforts (for example glider tracks or survey grids, fixed moorings) to the ocean basin scales occupied by krill stocks. Multiple programmes are much easier to compare if sampling methods are similar, and looking forward, key targets for harmonising to provide better comparability of study are: mesh size and type of nets; acoustic frequencies; sampling depths of nets and moorings. Some of these best practice procedures are already in place for zooplankton (Harris et al., 2000) or exist within the Ocean Best Practices System (OBPS); these can be adapted for krill by using existing networks such as ICED or SKEG. Likewise, efforts to combine and network data (for example CCAMLR observer programme, and BIOMASS, COPEPOD and KRILLBASE databases) should be supported and funded, with open provision and FAIR (https://www.go-fair.org/fair-principles/) access to data being the default.

Make greater use of the fishing industry, as a provider of data and as a research platform: Fishing vessels are not optimised for science, have competing commercial interests and use nets too coarse for catching juvenile krill. Their great advantages, however, are in the fact that they are a cheaper method of collecting large amounts of krill year-round, year after year and the data provided by the fishery have a wide variety of uses. Currently, through the Science-Industry Forum (SIF), there are also opportunities to use fishing vessels in a more scientific capacity, for example to repeat scientific acoustic survey transects year after year (Krafft et al., 2021) and to collect krill with finer mesh nets alongside environmental data.

Cross-cutting recommendations to achieve these solutions:

Coordination: Multiple institutes and nations have Antarctic interest, typically with each country working in "their" sector. Given the circumpolar and multinational issues around krill all three of our proposed solutions require multinational organisations, including SKEG, to take the lead in coordinating research to advertise ship opportunities, promote inter-lab visits, training, harmonisation of efforts and networking of data coverage.

Calibration: many of the debates about krill highlighted in this synthesis arise from use of different methods and approaches and for all three of our proposed solutions it is imperative that the multiple methods are used alongside each other for substantial periods of time, or at the very least that objective approaches are used to compare and to intercalibrate them to better understand their strengths and weaknesses.

Training: with a shift in approaches to sample krill we need to retain traditional skills, for example in identification and ability to handle live krill for experiments. Likewise, skills in handling the large volumes of new data may need to embrace rapidly developing fields: for example, machine learning. For all these skills the training of early career researchers is paramount.

Alignment of funding: the funding routes for national research programmes around krill are diverse, varied and often short-term. Achievement of the research to enable CCAMLR to manage the fishery safely requires a much more joined-up and longer-term approach.

and effective international collaboration and sharing of resources. A newly created Science-Industry Forum (SIF) aims to coordinate the use of fishing vessels as science platforms, improving access to an underused resource. Nonetheless the capabilities of fishing vessels are currently limited by the available gear and facilities and the operational priorities of the industry. Consequently, there remains a need for the science community to better coordinate its own resources. An internationally coordinated approach to addressing the major gaps in our knowledge on key pelagic species could include developing standardised methods approved through the Global Ocean Observing System (GOOS) Ocean Best Practices System (OBPS) and specialised training of ECRs. Antarctic krill research is generally funded by national governments, so there is also a need for higher-level intergovernmental agreements that support collaborative research and sharing of polar facilities. Similar agreements will be needed for other pelagic species whose distributions typically extend across political borders and into areas beyond national jurisdiction.

Author contributions

SLH: Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Visualization, Writing – original draft, Writing – review and editing. AA: Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Visualization, Writing – original draft, Writing – review and editing. JA: Writing – original draft, Writing – review and editing. AB: Writing – original draft, Writing – review and editing. SB: Writing – review and editing. KB: Writing – original draft, Writing – review and editing. AC: Writing – original draft, Writing – review and editing. JC: Writing – original draft, Writing – review and editing. RD: Writing – original draft, Writing – review and editing. SF: Writing – original draft, Writing – review and editing. HF: Writing – review and editing. JF: Writing – original draft, Writing – review and editing. SH: Writing – review and editing. JH: Writing – original draft, Writing – review and editing. LH: Writing – original draft, Writing – review and editing. NJ: Writing – review and editing. MK: Writing – original draft, Writing – review and editing. SK: Writing – original draft, Writing – review and editing. BK: Writing – original draft, Writing – review and editing. LK: Writing – original draft, Writing – review and editing. HL: Writing – original draft, Writing – review and editing. CL: Visualization, Writing – original draft. BM: Writing – original draft, Writing – review and editing. EM: Writing – original draft, Writing – review and editing. EP: Writing – review and editing. FP: Writing – original draft, Writing – review and editing. AP: Writing – original draft, Writing – review and editing. MP: Writing – original draft, Writing – review and editing. KR: Writing – original draft, Writing – review and editing. CR: Writing – original draft, Writing – review and editing. ER: Writing – review and editing. RS: Writing – original draft, Writing – review and editing. KS: Writing – original draft, Writing – review and editing. ZS: Writing – review and editing. AT: Writing – original draft, Writing – review and editing. GT: Writing – original draft, Writing – review and editing. PT: Writing – review and editing. DV: Visualization, Writing – original draft, Writing – review and editing. GW: Writing – original draft, Writing – review and editing. JX: Writing – review and editing. GY: Writing – original draft, Writing – review and editing.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1307402/full#supplementary-material

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Defining operational objectives for nature-inclusive marine infrastructure to achieve system-scale impact

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The marine environment faces continuous anthropogenic pressures, including infrastructural developments at a global scale. Integration of nature-inclusive measures in the design of infrastructural development is increasingly encouraged, but a lack of coordination results in fragmentation of project-based measures, failing to meet the desired overall effects. To realize impact at system-scale, i.e. the seascape dimension required to achieve the set objective for a selected ecosystem component, overarching policies with shared targets towards effective nature-inclusive marine infrastructure are needed. We present a stepwise approach to work towards operational objectives for promoting selected ecosystem components that can be species, habitats or ecosystem processes, in which ruling policies, environmental conditions and the use of infrastructural development are aligned, and agreement on achievable ambitions is reached. Having clear targets will provide guidance to project developers in designing the infrastructure nature-inclusive, and in setting up relevant monitoring programs to evaluate the measures taken. We demonstrate how this stepwise approach could be applied to derive operational objectives for the design of nature-inclusive marine infrastructure in the context of offshore windfarm development in the North Sea, currently one of the most prominent infrastructure developments that changes the marine environment drastically. The European flat oyster *Ostrea edulis* has been selected as target species in the case study, as its once abundant population is now nearly extinct from the North Sea due to human disturbances, and there's growing interest to restore its reefs. The application of the stepwise approach indicates the potential for oyster reef restoration in the area, based upon a clear match between ruling policy, environmental conditions, and habitat suitability within offshore wind farms. An agreement between the main stakeholders on achievable ambitions can likely be established and would translate into the operational objective to actively introduce oysters to reach an initial critical mass and optimize settlement habitat in all future offshore wind farms in an area with suitable habitat

characteristics. Such an agreement on overarching objectives is crucial to align separate initiatives to promote targeted ecosystem components and to jointly become most effective, which is ultimately in the best interest of the larger community using the system.

KEYWORDS

offshore wind, policy, restoration, nature-inclusive, infrastructure, oyster

1 Introduction

Rapid changes in the marine environment are taking place, driven by human usages and climate change (Halpern et al., 2019; Smale et al., 2019). One of the most extreme human modifications to global seascapes is the extent of marine construction (Bugnot et al., 2020). Marine infrastructure comes in many forms and covers functionalities for multiple usages, including recreation, residency, fisheries, coastal defense, and offshore energy installations (Dafforn et al., 2015b). It is primarily designed to meet engineering and financial criteria, without considering its value as habitat (Browne and Chapman, 2011; Laboyrie et al., 2018). Marine infrastructure modifies seascapes by replacing natural habitats and changing environmental conditions critical to habitat persistence (Bishop et al., 2017; Bugnot et al., 2020). While these effects are primarily viewed as negative, marine infrastructure can also be designed to incorporate ecological principles that benefit marine life (Dafforn et al., 2015b; Laboyrie et al., 2018). This so-called 'nature enhancement' and derivatives thereof are prone to broad interpretation. To avoid ambiguity, we refer primarily to 'nature-inclusive marine infrastructure', which we define as marine infrastructure designed to improve the condition of targeted components of the ecosystem during its operational lifetime. These components would be selected species, habitats or ecosystem processes, and improvement refers to comparison with their condition prior to the infrastructural development. In recent years, a wide variety of nature-inclusive designs were applied to real projects (e.g. O'Shaughnessy et al., 2020 for review). However, the fragmented character of individual measures has so far not led to significant impact at system-scale (Abelson et al., 2020; Duarte et al., 2020), by which we refer to a seascape of the dimension required to achieve a set objective for the targeted ecosystem component. The variety in measures applied in individual projects could partly be due to underlying competitive differences between the developers. Without shared objectives, parallel efforts to include nature-inclusive elements in the design of marine infrastructure might not lead to a desired overall effect, and could even interfere with each other. To achieve a significant system-scale effect, individual initiatives to promote selected ecosystem components should be defragmented into a coordinated system-wide approach, following shared objectives. The process of setting those objectives for different systems involving different usages, would benefit from a generic stepwise approach to do so.

When defining objectives for ecological values as part of infrastructural development in the marine environment, one should aim to limit the negative environmental impact, and try to stimulate positive impact with the usage function. Such potential impact on the environment of marine infrastructural development is generally evaluated through an Environmental Impact Assessment (EIA) (e.g. Carroll et al., 2020). In practice, as most infrastructural designs are optimized for their economic and technical objectives, the EIA process subsequently applies mitigation measures to reduce any significant negative effects identified. But a recent development is that an EIA also addresses the potential of a project to have beneficial effects to the environment, both natural and socio-economic (Laboyrie et al., 2018). Furthermore, priority should be given to the implementation of monitoring programs, in order to be able to assess the long-term effects of newly build infrastructure (Dafforn et al., 2015b). In the end, it is up to authorities in close cooperation with the scientific community and other stakeholders, to determine an approach for implementing the environmental goals and policy objectives for the infrastructural development within the system.

A well-established tool to structurally align policy objectives with technical solutions to meet these objectives is the 'Frame of Reference' approach (Van Koningsveld, 2003). It cyclically defines both a strategic and an operational objective and operationalizes these objectives in a 4-step decision recipe determining (i) a quantitative state concept, (ii) a bench marking procedure, (iii) an intervention procedure and (iv) an evaluation procedure (see Figure 1). Originally derived to evaluate and re-define a sustainable coastal policy for the Netherlands (van Koningsveld and Mulder, 2004), the 'Frame of Reference' approach has since then been applied successfully for a range of civil engineering disciplines. For example, it was used to define coastal management policies for beach areas (Jiménez et al., 2007; Gault et al., 2011; Sutherland and Thomas, 2011), to develop environmental monitoring schemes for offshore renewable energy projects (Garel et al., 2014), and proposed as a tool to assess the sustainability of for example dredging (Laboyrie et al., 2018) and port and waterway projects (Van Koningsveld et al., 2023).

A key element of establishing a coordinated, system-wide approach for implementing nature-inclusive elements within infrastructural development, is to define the strategic and

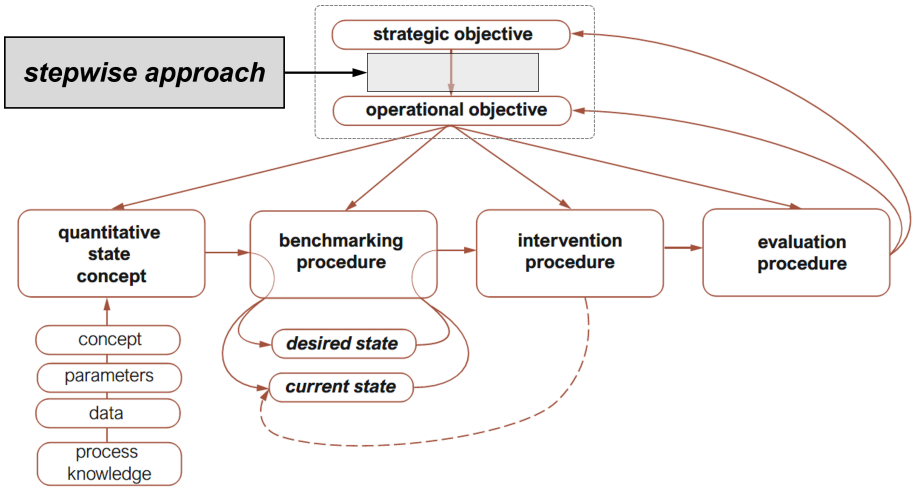

FIGURE 1
The basic Frame of Reference for policy development by Van Koningsveld (2003). The grey rectangle indicates the fit of the stepwise approach for alignment towards operational objectives. (Figure after Van Koningsveld et al., 2023).

operational objectives and to break these down into a number of logical elements (De Vries et al., 2020b). Strategic objectives provide the long-term context for a policy, express the vision for a system and its usage, and tend to change slowly (Van Koningsveld et al., 2005). Operational objectives are the concrete implementation of strategic objectives, by expressing how to handle the system and its usage, and include and explicit indication of the spatial and temporal scales involved (Van Koningsveld et al., 2005). Turning strategic objectives into operational ones, as also shown in the 'Frame of Reference' methodology, is a crucial though complicated process. It would benefit from a generic approach that is applicable for different systems involving different usages. Such an approach should include standards for defining the objectives as well as for implementing targets to achieve them, both temporarily and spatially. Although the need to specify clear operational objectives in coastal and marine management is generally recognized (e.g. Van Koningsveld, 2003; Cormier et al., 2017; De Vries et al., 2020a), a methodology for facilitating the process of turning strategic objectives into operational ones has not yet been described. This paper is the first in its kind to address an approach to set effective operational objectives for promoting targeted components of the subtidal ecosystem, i.e. the environment below the surface of the sea, in areas designated for infrastructural development. It entails a structured methodology, that aligns the ruling socio-economical and environmental conditions of the system with the potential offered by nature-inclusive marine infrastructure to achieve long-term benefits for selected ecosystem components. This stepwise approach is demonstrated by setting operational objectives for the nature-inclusive design of offshore windfarms the Dutch part of the North Sea. We selected offshore wind farms as it is currently one of the most prominent infrastructure developments that severely changes the marine environment (Ter Hofstede et al., 2023a). This rapid development in renewable energy production has been attributed to the goals set in the Paris Agreement (UNFCCC, 2018), aiming at the reduction of CO_2 emissions, and by several of the Sustainable Development Goals of the "2030 UN Agenda for Sustainable Development" (UN, 2015) (Danovaro et al., 2024). We selected the Dutch part of the North Sea as incorporation of nature-inclusive measures in offshore wind farms is highly encouraged by the Dutch government (Ministry of Economic Affairs, 2018). A key driver behind this encouragement is commitment to European policies such as the Green Deal, stating that the development of economic activities should "Do No Significant Harm" to the EU environmental objectives (European Commission, 2019), and the Marine Strategy Framework Directive (MSFD) targeting Good Environmental Status (GES) of the EU marine ecosystems (European Commission, 2008). However, current initiatives for implementation of nature-inclusive design measures in offshore wind farms in the Dutch part of the North Sea are yet uncoordinated and likely not meeting their full potential. Therefore, clear objectives are needed to ensure that the condition of targeted ecosystem components is at least maintained to meet the existing policies, or can even be improved effectively through interventions taken along with the development of offshore wind farms.

2 Approach for alignment towards operational objectives

When considering the design of nature-inclusive marine infrastructure, one should first identify the strategic objectives for the ecosystem in which the development is planned, and then define operational objectives to achieve desired environmental targets. Although the inherent dynamic variability of ecosystems makes it difficult to design marine infrastructure such that it contributes to an improved condition of certain targeted components, setting operational objectives is fundamental to enable the

implementation of nature-inclusive design measures (De Vries et al., 2020a). This applies for individual infrastructure projects, but even more so for the combined effect of multiple interventions on a system-scale. Addressing large-scale issues will reveal the true impact of measures and support their well-considered selection and implementation to enable their full potential (De Vries et al., 2020b). However, current practices focus too little on their collective impact to reach system-scale effects. On the contrary, current designs of nature-inclusive marine infrastructure still result in an uncoordinated sprawl of individual measures that each may be effective to achieve their individual project objectives, but collectively don't contribute to the system-scale objective to achieve the desired impact for the targeted ecosystem component (De Vries et al., 2020b). To mitigate this shortfall, we present a stepwise approach for alignment of the nature-inclusive designs of marine infrastructure that is to be developed in a system, to support setting operational objectives for making an impact at system-scale (see Figure 2). The approach starts with assessing three fundamental elements of the system that are to be aligned: Policy assessment (I), identifying and prioritizing the objectives of existing and future policies and legislation towards nature; Environmental assessment (II), identifying and prioritizing the potential of the environmental conditions for improving ecosystem components; and Infrastructural assessment (III), identifying and prioritizing the potential of nature-inclusive marine infrastructure, including defining design modifications. Next, matchmaking (IV) has to be done between ruling policy, environmental conditions, and infrastructural potential, to determine whether the identified measures don't conflict with each other, preferably even have mutual positive effects, and to achieve a set objective for the targeted ecosystem component, which we defined as system-scale impact. Finally, an achievable agreed ambition (V) between the relevant stakeholders for implementation of potential measures is needed, for which operational objectives can be defined.

2.1 Step I - policy assessment

Policies adhere to (inter)national laws, regulations and treaties, and implementing nature-inclusive elements in infrastructural designs is subject to legislative frameworks and associated permitting processes. Sometimes these processes are complex and uncoordinated, thereby impeding the implementation of nature-inclusive design measures in infrastructural development projects (Shumway et al., 2021). For instance, legislation may require specific requirements of constructions being built using certain materials, inhibiting the use of nature-inclusive elements (Dhakal and Chevalier, 2017). Another example is the observation that local legislation in the Netherlands does not allow sand borrow pits to exceed 2 m in depth, though it has been observed that creating a seabed with deep pits of 20 m during sand extraction would increase benthic biodiversity (De Jong et al., 2015). On the contrary, policy and legislation can also enable incentives for the implementation of nature-inclusive infrastructural development, when policy makers adhere to these, such as the United Nations Decade of Ocean Science for Sustainable Development (2021–2030), the United Nations Decade of Ecosystem Restoration (2021–2030), and the European Green Deal (Abelson et al., 2020). The EU Floods Directive, for example, has inspired at least 26 EU member states to include nature-based solutions in their water retention plans (Gerritsen et al., 2021). Another example, but at a local level, exists in Maryland (USA) where living shorelines are promoted by the Living Shoreline Protection act from 2008, stating that by default natural and nature-based infrastructure should be used for shoreline protection, unless a property owner can demonstrate the need to put in a built feature (Sutton-Grier et al., 2018). Depending on the ruling authority, policies vary in extent from local to international seascapes, which should be recognized when defining feasible objectives for nature-inclusive marine infrastructure.

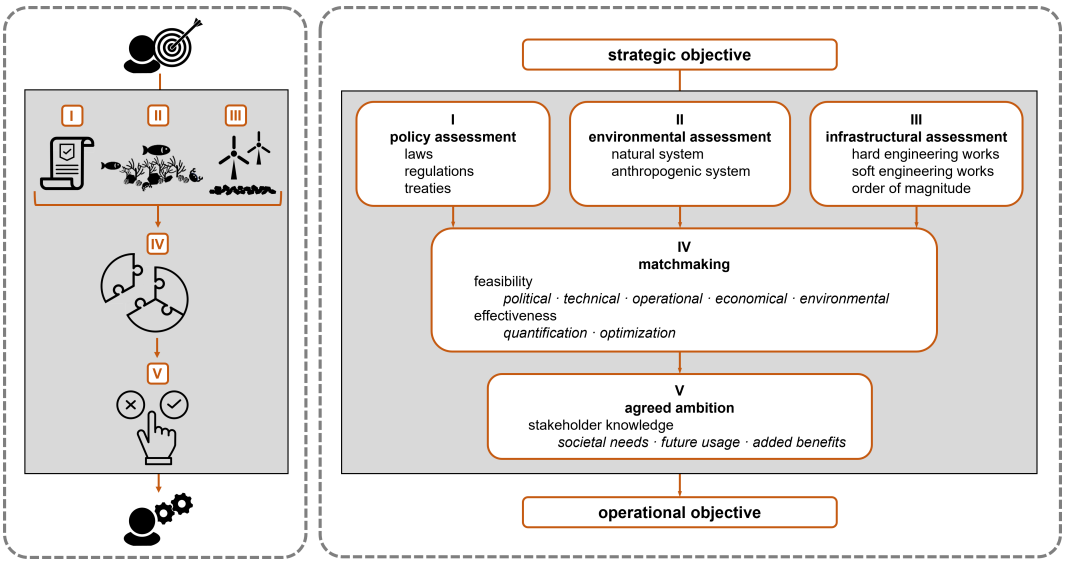

FIGURE 2
Stepwise approach for alignment towards operational objectives for designing nature-inclusive marine infrastructure.

2.2 Step II - environmental assessment

For nature-inclusive marine infrastructure to achieve its full potential at the system-scale, a thorough understanding of the functioning of that system is required. It is important to consider both the historic and present situation (Ter Hofstede et al., 2023a), but also future site conditions given current projections of global climate change and changes in ecosystem services (Suding, 2011; Howie and Bishop, 2021). The local environment contains both the natural system, which includes abiotic as well as biotic components, and the anthropogenic system. For the description of the conditions of a system is it advisable to adhere to those provided in a standard procedure as commonly used for an Environmental and Social Impact Assessment (Laboyrie et al., 2018), such as to the one mandatory in the European Union, the EU's Environmental Impact Assessment Directive (European Commission, 2014), or to principles practiced more globally and provided by the International Association for Impact Assessment (www.iaia.org/best-practice.php). An impact assessment generally covers basic variables of the physical environment (e.g. geology, meteorology, hydrology, water and air quality, etc.), biological environment (e.g. fish and benthic communities, marine megafauna, birds, etc.), the anthropogenic environment (e.g. fisheries and aquaculture, socio-economic profile, traffic and navigation, cultural and archeological heritage, etc.) (Laboyrie et al., 2018).

Essential for nature-inclusive design of marine infrastructure is to clearly define which components of the ecosystem are to be targeted. One could for example strive for establishing more biodiversity, or for promoting threatened species or habitats. Consensus on the nature-inclusivity target allows for the selection of measures to be incorporated in the design of the foreseen marine infrastructure, and the determination of the system-scale required to achieve the target. Sometimes a specific species is considered to represent a range of co-occurring species, which are assumed to co-develop similarly as that species (Fleishman et al., 2000; Lengkeek et al., 2017). Selecting such a so-called umbrella species as target for nature-inclusive design can be favored, as focusing on one species eases the design process of measures, while the effect of the measures is assumed to benefit a range of species. Also, when monitoring the effect of the measures, it is often more cost-effective to only sample one species than an entire assembly (Fleishman et al., 2000). However, it is always preferred to monitor the impact of a rigorous intervention such as the construction of marine infrastructure on all abiotic and biotic components of the system, in order to determine whether the desired effect has been achieved and side-effects have occurred.

2.3 Step III - infrastructural assessment

Man-made marine infrastructure such as dredged channels, breakwaters, sea-walls and scour protection can provide important habitat for marine organisms to spawn, to nurse, to forage, or to find shelter (Dafforn et al., 2015b; Ter Hofstede et al, 2023b). There is a vast potential to include elements that can benefit selected ecosystem components in the design of the infrastructure. The generally long-term lifetime of marine infrastructure allows the associated marine life at and around it to develop, and designs can be optimized to target desired species, habitats or processes (Ter Hofstede et al., 2023b). Marine infrastructure can be categorized under hard engineering works and soft engineering works. Hard engineering comprises marine infrastructural development using hard structures, including rubble mound structures (e.g. breakwaters), gravity-based structures (e.g. seawalls), pile foundations (e.g. offshore platforms) and floating structures (e.g. offshore wind turbines). Soft engineering involves human control on natural processes primarily through dredging works, including for example beach nourishment, salt marsh creation and capital dredging of channels. Within both categories, conventional engineering solutions can already benefit marine ecosystem components, and optimizations in the design can further increase these benefits.

In order to the determine the potential of using infrastructure development for promoting ecosystem components, one should first identify which design options are available and could function in the system. Second, one should consider design optimizations (Ter Hofstede et al., 2023b). It is recognized that marine construction works first serve human needs, not nature goals, but optimizing the infrastructure does provide an opportunity to benefit ecological values at system-scale. This should never be used as excuse to ignore or down-play the negative impact that infrastructural developments may have on a marine system (Firth et al., 2020). However, marine construction works can be synergized with the functioning of the ecosystem in which they are build much better than is currently practiced, and one should always strive for nature-inclusive features in their designs (Pioch et al., 2018; Ter Hofstede et al., 2023b).

2.3.1 Hard engineering works

The hard substrate used in marine infrastructure is known to act as artificial reef substrate (e.g. Bishop et al., 2017; Coolen et al., 2020; Degraer et al., 2020), though the associated communities are often observed to be less diverse and abundant than natural assemblages and nonindigenous species due to their low surface complexity and non-natural materials (Glasby et al., 2007; Gittman et al., 2016). Hard engineering works can be adjusted to increase the habitat complexity by bringing in more variety in use of materials and their texture, shape and dimensions, which is expected to result in a higher biodiversity (e.g. Dafforn et al., 2015a; Pioch et al., 2018; Strain et al., 2018). For example, the use of calcareous rock such as limestone or marble will trigger increased settlement by shellfish (Hidu et al., 1975; Soniat et al., 1991). If concrete is used as a construction material, it can be enriched with calcium carbonate, making it potentially a more preferable settlement substrate for shellfish larvae (Cuadrado-Rica et al., 2016; Potet et al.). The texture of concrete can also be roughened to mimic natural rock to promote the colonization by pioneering species (Moschella et al., 2005; Potet et al., 2021). The downside of using concrete is its toxicity as the cement mortars often leach trace metals over time (Hillier et al., 1999; Wilding and Sayer, 2002), which can be reduced by using

nature-friendly adhesives in the mortar (Perkol-Finkel and Sella, 2014). Irregular extensions of infrastructure in both vertically and horizontally directions will increase surface area and provide leesides for marine organisms to shelter (Firth et al., 2014; Consoli et al., 2018; Ter Hofstede et al., 2023a). Narrowing down the rock grading in rubble mound structures will results in more crevices, and variation in rock size at different locations will increase habitat diversity, serving a wide range of rock-dwelling species (Ter Hofstede et al., 2022). All such measures can be incorporated into the design of nature-inclusive marine infrastructure.

2.3.2 Soft engineering works

Soft engineering works may also positively affect marine species (e.g. Todd et al., 2014). For instance, dredged channels were observed to be favored over other habitat types by dolphins as the structural features aid to trap prey (Allen et al., 2001), and beach nourishments can be used to restore or create nesting habitats for shorebirds and turtles (Jones & Mangun, 2001). The potential optimization of soft engineering works to achieve benefits for the ecosystem lies particularly in the contours created in the seabed. Leaving borrow areas with steep sand ridges and deep pits after sand extraction, leads to a decrease in bed shear stress and settlement of fine sediment and organic matter. This diversity in bedform can result in a 10- to 20-fold higher biomass of benthic and demersal organisms than would be the case with a plane seabed (De Jong et al., 2014; 2015). Applying a mega-nourishment for coastal protection instead of regular nourishment strategies would increase beach volume and the opportunity to vary habitat relief, leading to distinct communities and higher species richness of coastal fauna (Van Egmond et al., 2018).

2.3.3 Order of magnitude

Actions to promote targeted components of an ecosystem should be executed at a scale large enough to be functionally successful and cost effective (Abelson et al., 2020). Making use of infrastructural development can support this by offering technological advances to reach both efficiency of scale (Abelson et al., 2020) and economy of scale (Price and Toonen, 2017). To estimate the potential effect on ecosystem components, and to determine the required scale of interventions to be taken to become significantly effective, one should quantify the potential effects of the measures prior to their implementation (Ter Hofstede et al, 2023a). The outcomes may support decision-making when designing nature-inclusive marine infrastructure to contribute to the desired system-scale impact. Predicting the effects of such measures will provide insight into the magnitude of effort required to reach the desired impact (Ter Hofstede et al., 2023a).

2.4 Step IV - matchmaking

Matchmaking is the process of evaluating the system against its ruling policy (I), its environmental conditions (II), and its foreseen infrastructural development (III), to determine its potential for benefitting selected ecosystem components. These three elements should match in a manner that their combination reveals opportunities for nature-inclusive design at the required system-scale, promoting effectively a targeted component of the ecosystem within the area. An example of a good match, though not at system-scale, is the development of the Sand Motor in front of the Dutch coastline, a large foreshore nourishment of 128 hectares to contribute to long-term coastal protection. The design of the Sand Motor included a lagoon area with the target to become an appealing feeding and resting place for birds, and indeed was observed to have a positive effect on some species of waders, seagulls and cormorants (Huisman et al., 2021). In the case of the Sand Motor, local policy (I) states to protect all wild bird species and to protect and restore their habitats (e.g. European Commission, 2009). Furthermore, the area lies within the distribution range of many of these birds and offering a suitable environment (II) to host them, and the infrastructural design (III) was optimized with the lagoon area to provide optimal feeding and resting grounds. A similar match would not apply in the area if the infrastructural element would be for example a wind farm, which is recognized for causing negative impact on bird populations (e.g. Furness et al., 2013; Garthe et al., 2023). Although this nature-based foreshore nourishment solution is likely able to create an impact at system-scale if also implemented at other locations along the Dutch coastline, the potential effect of multiple applications has yet not been assessed (De Vries et al., 2020b).

Part of matchmaking is checking the feasibility and effectiveness of potential nature-inclusive measures to meet the prospective. A feasibility check comprises for example assessing the political, technical, operational, economical, and environmental elements. The feasibility assessment includes political, technical, operational, economical and environmental aspects. Political feasibility relates to the societal readiness for the implementation of measures, whether these are possible within the local regulations and socially acceptable. Technical feasibility concerns assessing whether the implementation of a foreseen measure is technically possible, for which the Technology Readiness Level (TRL) is a good parameter. The more mature a technology is, the more likely it can be implemented. The operational feasibility includes organizational issues, operability, accessibility of a location, required effort and limitations due to legal aspects. Economical feasibility relates to the costs of a measure to be successful, strongly determined by being active or passive, the latter generally being less expensive, as this requires less labor, technologies and personnel, e.g. the limitation of fishing activities (Fox et al., 2019). Environmental feasibility concerns whether any proposed intervention with the intention to promote selected ecosystem components would fit within the ecological boundaries of the system.

Assessing the effectiveness of measures involves quantifying their potential effect, determining the required scale for implementation, and optimizing designs to achieve the highest results. A quantitative assessment of each intervention would be based upon existing knowledge and should take into account the prevailing conditions in the designated area (Ter Hofstede et al., 2023a). Knowing the potential effect will allow to make informed decisions on the selection of measures for implementation.

2.5 Step V - agreed ambition

Once the potential has been identified for designing nature-inclusive marine infrastructure to benefit targeted ecosystem components, it is required to reach agreement on achievable ambitions for the system in which actions are foreseen. For this step, knowledge of the system is key, as weighing and ranking ambitions depends on multiple aspects such as, societal demands for the system, whether the identified required scale of a measure fits the system, knowing the future usage of the area, and any additional side-benefits from a measure. During this process of marine spatial planning, the spatial and temporal distribution of human activities in marine areas are analyzed and allocated, with the aim to achieve ecological, economic, and social objectives (Ehler and Douvere, 2009). It has been accepted as a practical tool to sustainably manage the marine environment through a participatory approach around the globe, though it is recognized that the process of stakeholder engagement still faces some challenges (e.g. Ehler, 2021; Santos et al., 2021). Profound stakeholder engagement will ensure that all knowledge from different user groups is incorporated when defining interventions that can promote selected ecosystem components. The combination of engineering, ecological and governance perspectives can yield new opportunities to improve the feasibility of nature-inclusive infrastructural development projects in sensitive environments while meeting societal demands and legislative constraints (Laboyrie et al., 2018). To achieve success after implementation, all relevant users of the system should commit to jointly set objectives, long-term as well as financially (Saunders et al., 2020). Tools for stakeholder involvement are available to ensure that their ideas, interests, and concerns are consistently addressed, and include for example open collaboration in policy modelling through building ICT-based scenario's (Wimmer et al., 2012), engaging panels of experts through surveys such as the Delphi method (Linstone and Turoff, 1975), or group model building that includes simulating policy choices through role playing (Vennix et al., 1996).

During the process of agreeing upon an achievable ambition, the potential impact of measures on the original environment should carefully considered. For example the addition of hard structures in a sandy environment will change the available habitats, affecting the diversity and function of the system (Davis et al., 1982; Martin et al., 2005; Bulleri and Chapman, 2010). The losses of the original habitat need be assessed and in general be minimized if possible (Dafforn et al., 2015b). In situations where hard structures cannot be avoided, or are even desired, there is the potential for eco-engineering to mitigate the impacts of these structures and to maximize potential ecological outcomes (e.g. Chapman and Blockley, 2009).

Once an agreed ambition has been reached, the operational objectives can be defined to achieve the desired ecological impact. These objectives are fundamental for making the design of a nature-inclusive infrastructural development. The 'Frame of Reference' approach can be used to transfer the operational objectives into functional engineering designs, and to assess their performance once applied in practice (Van Koningsveld, 2003; De Vries et al., 2020a; Figure 1).

3 Application of the approach

To be able to exploit the full potential of infrastructural development to strengthen the ecological values of a system, it is key to set clear operational objectives. Our stepwise approach to determine such operational objectives for a system involves the assessment of the ruling policies in an area, the local natural and anthropogenic system, and the benefits of potential infrastructural developments. Next, an inventory of potential design measures for nature-inclusive marine infrastructure is made and assessed for their feasibility and effectiveness. Finally, an agreed ambition on measures to be taken should be reached between relevant stakeholders, for which then operational objectives can be defined. The functionality of this stepwise approach will be demonstrated in a fictive case for setting operational objectives to promote components of the subtidal ecosystem in the Dutch North Sea, aligned with offshore windfarm development.

3.1 Case description

3.1.1 Offshore windfarm development in the Dutch North Sea

The offshore wind energy industry is rapidly growing in the North Sea. In the southern North Sea alone, 62 windfarms with total surface of 3,388 km^2 and capacity of 20,6 GW have been installed during the first two decades of this millennium, and the tenfold in surface area is designated to develop offshore wind energy production (Ter Hofstede et al., 2023a). These areas are generally closed for bottom-disturbing activities such as bottom-dwelling fisheries or sand extraction during the lifetime of the wind farms. They also offer hard substrate by means of the wind turbine foundations and rock material placed at the base of the turbine foundations and on top of cable crossings to prevent scouring of the seabed (Ter Hofstede et al., 2023a). For these reasons, offshore wind farms provide an environment ideal for the development of the epibenthic ecosystem, offering opportunities for biogenic reefs to develop and other organisms to forage and find shelter from human disturbances (Petersen and Malm, 2006; Coolen et al., 2020; Degraer et al., 2020).

The Dutch government has the strategic objective to rehabilitate the North Sea ecosystem, and to make offshore wind farms (see Figure 2) contribute to it through implementing nature-inclusive design measures (e.g. Ministry of Economic Affairs, 2018). However, in order to reach strategic objectives, one requires a coherent overarching realization scheme for such measures (De Vries et al., 2020b). Enabling large scale ecosystem restoration and/or ecological development in offshore wind farms requires setting up an overarching coordinated framework that sets clear targets. Otherwise, well-meant initiatives are bound to range widely in technical solutions per wind farm, being suboptimal or even ineffective at the larger scale (De Vries

et al., 2020b). The systematic approach that we present supports in this process to identify and align applicable policies, the ruling environmental conditions, and the potential of the infrastructure, and determine measures that could promote targeted components of the subtidal ecosystem at offshore wind farms in the Dutch part of the North Sea (see Figure 3).

3.1.2 Evolving ecological requirements for offshore wind farms

Efforts to protect and improve ecosystem components in the Dutch part of the North Sea using offshore wind farms are evolving. The first Offshore Wind farm Egmond aan Zee is in use since 2007 and its development did not include any nature-inclusive measures, though its impact on the environment was concisely monitored (Lindeboom et al., 2011). The installation of following wind farms Princess Amalia (2008), Luchterduinen (2015) and Gemini (2017) focused mainly on the protection of marine organisms such as mammals and fish from impulsive underwater sound caused by piling of the turbine foundations. A decade after the construction of the first offshore wind farm, their development required an 'obligation to undertake demonstrable efforts' to contribute to the strengthening of a healthy sea and to the preservation and sustainable use of endemic species and habitats in the Netherlands. This commitment was firstly formally included in the site decision of Borssele OWF lots I in 2016 (Staatscourant, 2016), and is considered an effort to utilize the momentum of the large-scale development of offshore wind farms for ecological benefits. Also the extension of the Borssele windfarms (2020) and Hollandse Kust Zuid (2021) and -Noord (2022) required to adhere to this commitment. Currently, preserving and improving the ecology of the North Sea has even become a strong requisite in the design, construction and operation of offshore wind farms, being a determinative component in the most economically advantageous tender (MEAT) criteria for offshore wind farms Hollandse Kust West Lot IV (Staatscourant, 2022) and IJmuiden Ver Lot Alpha (Staatscourant, 2023). Processes like these lead to the commercial incentivization of ecosystem restoration and creation in offshore wind farms (Stechele et al., 2023a).

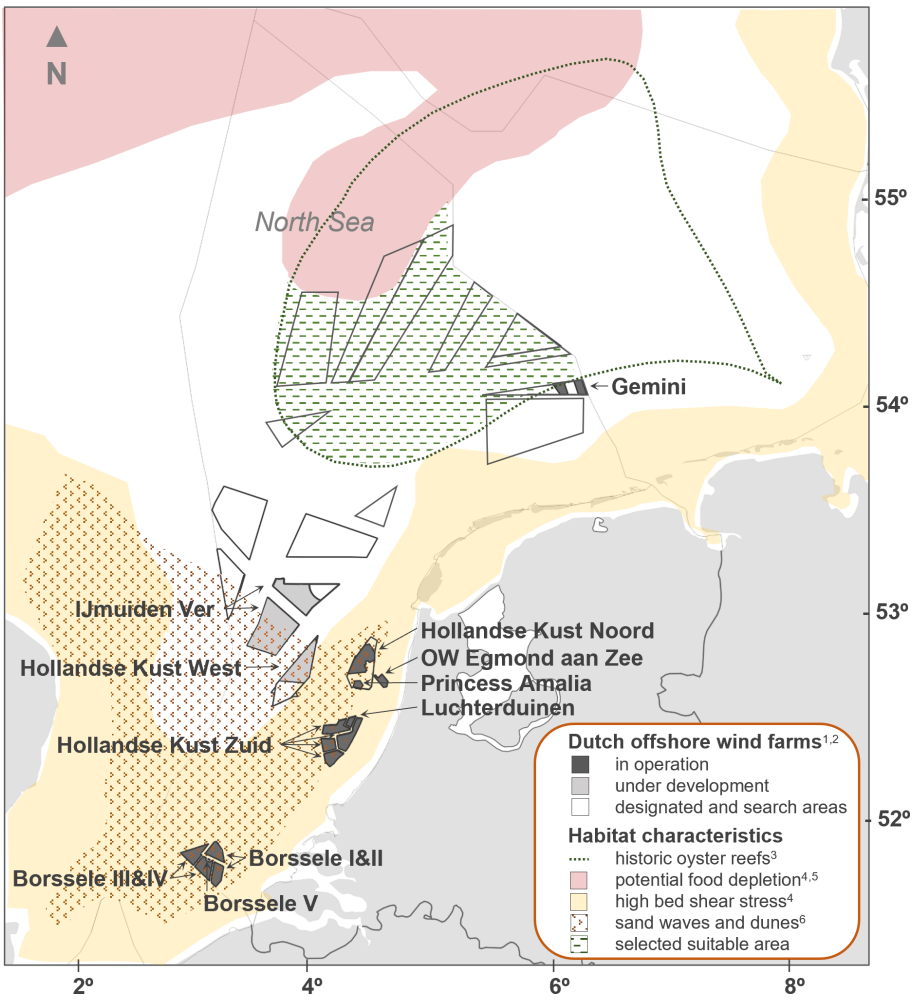

FIGURE 3
Offshore wind farms in the Dutch part of the North Sea. Compiled with QGIS 3.22; data sourced from [1]emodnet.ec.europa.eu; [2]Ministry of Infrastructure and Water Management, 2022, [3]Bennema et al., 2020; [4]Kamermans et al., 2018a; [5]Van Leeuwen et al., 2015; [6]Van der Veen et al., 2006.

A way of integrating nature-inclusive designs in offshore wind farms is to promote target species, e.g. being either umbrella species covering 'overall native biodiversity' or policy relevant species (Lengkeek et al., 2017). The umbrella species Atlantic cod *(Gadus morhua)* and policy relevant species European flat oyster *(Ostrea edulis)* were explicitly addressed in the Site Decisions for the recent Dutch wind farms Hollandse Kust Noord (Staatscourant, 2019) and Hollandse Kust West (Staatscourant, 2022). In the Site Decision for the latest offshore wind farm development project IJmuiden Ver, a new policy-relevant species was introduced, namely the biogenic reef building species Ross worm *(Sabellaria spinulosa)* (Staatscourant, 2023). To illustrate the process of the stepwise approach for setting operational objectives for nature-inclusive design of offshore wind farms in the Dutch part of the North Sea, we've selected the *European flat oyster as target species* (see Table 1).

TABLE 1 Overview of the main outcomes when applying the stepwise approach on the case study to derive operational objectives for oyster reef development in offshore wind farms in the Dutch part of the North Sea.

Step	Result	Source
Strategic objective:	**Development of flat oyster reefs in Dutch offshore wind farms**	
I policy assessment	MSFD target D6T5 'return and recovery of biogenic reef structures including flat oyster beds'	Ministry of Infrastructure and Water Management et al., 2018; Ministry of Infrastructure and Water Management, 2022.
II environmental assessment	Area suitability primarily based upon seabed stability (low bed shear stress, no sand waves), food availability (low seasonal stratification), historical presence.	Kamermans et al., 2018a, b; Herman and Van Rees, 2022; Van Duren et al., 2022; Stechele et al., 2023b, 2023.
III infrastructural assessment	Offshore wind farm areas offer suitable habitat by means of undisturbed seabed and hard substrate infrastructure. Optimization potential primarily in scour protection adaptations.	Kamermans et al., 2018b; Degraer et al., 2020; Ter Hofstede et al., 2022, 2023a.
IV matchmaking	Government set requirements in site decisions. Developers and scientific community showed potential through pilot studies. Cost-effective through incorporation in project design. Suitable environmental conditions present around 54° latitude. Human interventions needed to initiate self-sustaining reefs.	Staatscourant, 2019, 2022; Didderen et al., 2019; Ter Hofstede et al., 2022, 2023a; Kamermans et al., 2018a, b, 2020; Van Duren et al., 2023.
V agreed ambition	Commitment to required joint effort in focal area to create a self-sustaining oyster population with the potential to develop into a magnitude as historically present.	Probable outcome of stakeholder engagement (this paper).
Operational objective:	**Actively introduce oysters to reach an initial critical mass of 100,000 individuals and optimize settlement habitat in all future offshore wind farms in the area with suitable habitat characteristics.**	

3.2 Step I - policy assessment

The nature policy for the Dutch part of the North Sea is driven by the strategic objective "to restore and conserve the integrity of the ecosystem and sustainably use the ecosystem services and products" (Ministry of Infrastructure and Water Management, 2022). The objective is practiced through commitment to European treaties, primarily by the Marine Strategy Framework Directive providing 11 Descriptors for Good Environmental Status (2008/56/EC; European Commission, 2008), which have the characteristics of operational objectives, and complemented by the Birds- and Habitat Directives (2009/147/EC; European Commission, 2009) (Mulder, 2022). With respect to the development of offshore wind energy, the Dutch nature policy focuses on the nature-inclusive design, installation and operation new wind farms. This approach offers opportunities for strengthening species populations and habitats that occur naturally in the North Sea and for carrying out nature restoration projects within wind farms (Mulder, 2022).

A Dutch policy relevant for the development of the European flat oysters comes from commitment to the European Marine Strategy Framework Directive. Dutch government has set the environmental target (D6T5) for the 'return and recovery of biogenic reef structures including flat oyster beds' in part 1 of the Dutch Strategy for the period 2018–2024 (Ministry of Infrastructure and Water Management et al., 2018), and incorporated it as well in the Dutch North Sea Program 2022–2027 (Ministry of Infrastructure and Water Management, 2022).

3.3 Step II - environmental assessment

Wind farm locations relatively suitable for oyster reef development have been appointed based upon habitat suitability, larval retention, food availability, and historical presence (Smaal et al., 2017; Kamermans et al., 2018a, b; Herman and Van Rees, 2022; Van Duren et al., 2022; Stechele et al., 2023b, 2023). The most important characteristics of habitat suitability relate to the presence of a stable seabed, meaning little seabed mobility (sand waves), low bed shear stress, and a composition that provides a consolidated foundation, such as stable sands, stiff muds, shells or rock (Héral and Deslous-Paoli, 1991; Houziaux et al., 2008; Smaal et al., 2017; Hughes et al., 2023). Larval retention is assumed to be highest in areas at or near their production, and therefore its assessment accounted for the source locations and dispersal rates (Herman and Van Rees, 2022). Food availability is related to the stratification of the North Sea during the summer season, reducing the transport of the main food source phytoplankton to the seabed. Areas with high seasonal stratification are therefore assumed less suitable for oyster reef development, opposed to areas that are nearly fully mixed (Van Leeuwen et al., 2015; Kamermans et al., 2018a; Stechele et al., 2023b). For estimating the historical presence of oyster reefs, data was used from Olsen (1883), Houziaux et al. (2008), and Bennema et al. (2020). Note that the potential for oyster reef development offered by the infrastructure in offshore windfarms (Ter Hofstede et al., 2023a), in particular in terms of hard substrate offered by the

rock material used as scour protection, was not taken into account in these studies. Other main factors of importance for the survival of flat oysters are oxygen content in the water and food availability by means of phytoplankton, but these are not limiting in the Dutch part of the North Sea (Van Leeuwen et al., 2015; Van Duren et al., 2022). The potential suitable area for oyster reef development in the Dutch part of the North Sea is visualized in Figure 3, drafted from their historic distribution (Bennema et al., 2020) and the prime environmental factors that hamper their development, i.e. bed shear stress (Kamermans et al., 2018a), sand waves (Van der Veen et al., 2006), and potential food depletion based upon stratification (Van Leeuwen et al., 2015).

3.4 Step III - infrastructural assessment

Once in operation, offshore wind farms provide an undisturbed seabed and hard substrate infrastructure which both make them suitable for oyster reef development (Kamermans et al, 2018b; Degraer et al., 2020; Ter Hofstede et al., 2022, 2023a). For safety reasons, the wind farm developers have successfully excluded bottom disturbing activities such as bottom-trawl fisheries from the concession zones around their underwater infrastructure such as turbine foundations and cable routes. The exclusion of disturbing activities from these concession zones has resulted in quasi-marine protected areas providing refuge for benthic habitats and species such as oysters (Hammar et al., 2016). The infrastructure of offshore wind farms inherently provides artificial habitat, allowing long-term development of targeted ecosystem components, and its design can even be optimized to target desired species (Ter Hofstede et al., 2023b). The type of infrastructure used for offshore wind farms is dependent upon the system in which it is build. In particular the support structures for the wind turbines will vary, either fixed-support or floating. The fixed-support types are gravity-based and the turbines are placed on for example monopile foundations or jackets. Their primary constraint is the limited depth in which they can be build, as in waters of over 60 m depth, they become commercially inviable due to a considerable increase in costs (The Carbon Trust, 2015). Floating wind turbines are held in place through mooring cables connected to the seabed. Their costs are generally higher than gravity-based turbines, and also significantly increase with water depth (Kausche et al., 2018). Gravity-based designs of wind turbines can likely include the highest benefits for increasing epibenthic biodiversity, in particularly when placed on sandy substrate. Here they require a scour protection, generally by means of rocky substrate, which forms a suitable habitat for the development of marine flora and fauna (Petersen & Malm, 2006; Degraer et al., 2020; Glarou et al., 2020). Such benefits for epibenthic biodiversity should be taken into account when selection the type of windfarm in the design process. To increase biodiversity or the presence of targeted rock-dwelling species using scour protection, small adaptations in material use, texture, and shape can improve the conditions for settlement, growth and use by a variety of marine organisms even more, while keeping the function of the scour protection intact (Ter Hofstede et al., 2023a). In case of oyster reef development, the main adaptations in the scour protection design for would include the use of calciferous rock material such as limestone or marble, containing a high amount of calcium which is beneficial to shellfish species (Hidu et al., 1975; Soniat et al., 1991). Furthermore, the scour protection should be designed with rock material of a grading size large enough to provide stable substrate (Van Velzen et al., 2014), as moving rocks cause physical damage or even mortality to the oysters. Also, extending the dimensions of the scour protection would increase the area of hard substrate for settlement by oyster larvae, and variation in shape could create areas with reduced flow velocity to improve the opportunities for settlement (Korringa, 1940; Smaal et al., 2017). Over time, the oyster reef development is even expected to contribute to the stabilization of the scour protection by effectively binding the rocks, in particular those of a smaller grading size (Domisse, 2020).

3.5 Step IV - matchmaking

The combination of the ruling policy, environmental conditions, and presence of offshore wind farms in the Dutch part of the North Sea offers great potential for oyster reef development. This match is based upon an assessment of both the feasibility and effectiveness of the potential measures that can be taken to establish oyster reefs using the infrastructure in offshore wind farms.

3.5.1 Feasibility

The feasibility assessment includes political, technical, operational, economical and environmental aspects.

From a political perspective, it is highly feasible to develop oyster reefs in Dutch offshore wind farms, as there's general support from government, developers, scientists, and the public society. The government has been setting requirements for oyster reef development in the site decisions for new wind farms, e.g. in windfarms Hollandse Kust Noord and -West (Staatscourant, 2019; 2022). Wind farm operators have shown their willingness by taking measures to initiate reef development in wind farms Gemini, Borssele 3&4, Borssele V, and Luchterduinen (e.g. Didderen et al., 2019). The scientific community has stressed the potential to use wind farms for oyster reef restoration practices (e.g. Lengkeek et al., 2017; Kamermans et al., 2018b). From public society, no opposition has been reported, and oyster reef development is generally advocated by non-governmental organizations (e.g. Sas et al., 2019; Vrooman et al., 2019).

From a technical perspective, Dutch offshore wind farms offer great potential for oyster reef development. The seabed in the area refrains from disturbance as no bottom disturbing activities are allowed during the operational lifetime of the wind farms. The infrastructure of the windfarms by means of the scour protection at the base of the turbine foundations and at the cable crossings, offers excellent substrate for settlement of larvae. The infrastructure could

even be further optimized by making small adaptations in material use, texture, and shape to further improve settlement conditions (Ter Hofstede et al., 2023a).

From an operational perspective, multiple pilot studies have shown that interventions can be taken in offshore wind farms to trigger oyster reef development. For example, adjustments to the scour protection were made to facilitate oyster larvae settlement in several Dutch offshore wind farms: In Borssele 3&4, 20 m^3 of clean shell material was placed in the scour protection at the base of 8 wind turbines foundations; in Hollandse Kust Zuid, a sprinkler layer of marble rock was placed at 4 cable crossings; and in Hollandse Kust Noord, berms of marble rock were placed at the scour protection of 42 wind turbines. In addition, to initiate larvae production and kickstart reef development, oyster broodstock was installed in wind farms Borssele 3&4, Borssele V, Luchterduinen, and Gemini (Didderen et al., 2019), and at all locations the broodstock was shown to survive, grow and reproduce after installation.

From an economical perspective, feasibility relates to the costs of a measure to be successful. All activities in the offshore environment are generally considered to be costly due to the required vessel time. However, the fact that many activities have already taken place to develop oyster reefs in offshore wind farms, demonstrates their feasibility, independent of the costs. Cost reductions can be achieved by wisely selecting and implementing interventions. For example on a small scale, the deployment of oyster broodstock fixed on stable structures will provide a dense and lasting source of adult oysters to ensure local larvae production, while deployment via loose distribution would require a far greater amount of oysters to ensure the same sized broodstock over time, due the high risk of losses caused by severe hydrodynamic conditions. On a larger scale, costs of vessel time include the expensive mobilization and demobilization of a vessel for a specific purpose. The longer a vessel can be at sea, the daily costs of the activity becomes relatively lower. Therefore, it is recommended to combine as much as feasible the various activities that are aimed at promoting targeted ecosystem components, or even align them fully with the standard wind farm installation and operation activities. For example, the deployment of calciferous rock aimed at increasing oyster larvae settlement rates should be executed in line with the installation of the functional scour protection, and preferably even be fully integrated in its basic design; post-construction deployment as an add-on should be avoided at all times to save on costs.

From an environmental perspective, offshore wind farms in the Dutch part of the North Sea are generally considered suitable for oyster reef development. The environmental conditions however vary throughout the region, leading to different levels of suitability. Although all current and likely future Dutch offshore wind farms offer substrate for oyster reef development by means of their scour protection at the base of the turbine foundations, the vast seabed area in between the turbines does not. Oysters require a stable seabed with low hydrodynamic forces such as bed shear stress. These conditions are not present in the southern part of the Dutch EEZ (Kamermans et al., 2018b; Van Duren et al., 2023; see Figure 3). In order to utilize wind farm areas for oyster reef development to its full potential, meaning not only at the scour protections, but also at the seabed in between, it is therefore recommended to focus efforts to establish oyster reefs in the current and future wind farms in the northern part of the Dutch EEZ (Van Duren et al., 2023). However, the tip of the Dutch EEZ around 55° latitude is considered unsuitable due to poor food availability in the summer season as a consequence of stratification (Kamermans et al., 2018a; see Figure 3). These considerations would leave an area assumed most suitable for oyster reef development around the 54° latitude (see Figure 3).

3.5.2 Effectiveness

In order to select measures to establish oyster reefs in offshore wind farms, their potential effect needs to be quantified first. Knowing the impact of the presence of the wind farm itself, and of the additional interventions to increase it, allows to make informed decisions in setting the operational objectives for oyster reef development in an area. The quantification provides insight in the required order of magnitude of the potential effects, needed to determine the type and scale for selecting measures to achieve a desired result. A stepwise procedure designed in particular to guide the selection of appropriate interventions and their required scale for pro-actively facilitating flat oyster reef development in offshore wind farms, was presented by Ter Hofstede et al. (2023a). The procedure makes use of available knowledge, allowing inclusion of most recent insights. An assessment of the wider Southern North Sea bordered by England (UK) on the west, and Belgium, The Netherlands, Germany and Denmark on the east, learned that oyster reef development in offshore wind farms at least requires a human-induced accumulation of broodstock in the wind farms due to the lack of connectivity with the scarce natural reefs (Ter Hofstede et al., 2023a). Succeeding development of oyster reefs within a wind farm area is suggested to be facilitated by providing suitable substrate for larvae settlement. Provision of clean shell material would be the most beneficial, in potential offering oyster densities 150 times higher than on rock material and 8000 times higher than on a soft seabed. However, the supply of shell material is not unlimited, and also not without impact on the existing environment when being collected. Therefore, a focus on providing suitable settlement substrate using rock material, such as already applied in the scour protections in wind farms, would be a good alternative. Optimization of these scour protections for oyster reef development can be achieved by using most suitable rock material, and adjustment of the conventional shape. Calciferous rock material such as marble could in increase settlement rates by factor 1.33 (Tonk et al., 2020), and simply extending the scour protection horizontally would increase settlement opportunities linearly, particularly if done for the armour layer which won't disappear on a layer of sand as is the case for the filter layer (Ter Hofstede et al., 2022).

3.6 Step V - agreed ambition

Now that the potential for oyster reef development in the Dutch part of the North Sea has been identified, it is needed to reach agreement on achievable ambitions to do so, for which operational objectives can be defined next. The ambition should be agreed upon

by relevant stakeholders, of whom their knowledge of the political and environmental system and of the potential for implementation of interventions are key to ensure that the ambition will be achievable. The main four stakeholder groups for this case study would at least include i) relevant Dutch Ministries having legislative authority of the area, ii) research institutes with knowledge about the environmental conditions, iii) marine contractors providing engineering solutions, and iv) wind energy developers being the owners of the offshore wind farms.

The demonstration of the functionality of our stepwise approach is merely applied for a fictive case. Therefore an actual stakeholder involvement process was not performed, but we confined ourselves to assuming a probable perspective for each of the four stakeholders towards oyster reef development in Dutch offshore windfarm: Governmental authorities (i) would be supportive, following their incentive to "return and recover biogenic reef structures including flat oyster beds", and have the powerful tool of setting requirements to enforce oyster reef development in site decisions for new offshore wind farms. The scientific community (ii) would stress the need for windfarms to have suitable environmental conditions, and a connected, preferably continuous, areal large enough to host a self-sustainable population. The wind farm developers (iii) would be willing to invest in taking nature-inclusive measures to meet contractual obligations and to strengthen their corporate image, though a predictable income from energy production should be guaranteed. Marine contractors (iv) would offer the capability to design and implement engineering solutions to support oyster reef development, but require guidance on the required type and extent of interventions.

Considering the stakeholder perspectives, it can be concluded that habitat suitability would be the main driver for agreeing upon development of oyster reefs in specific offshore wind farms, as it is the only aspect that varies across the Dutch part of the North Sea (see Figure 3). On the contrary, the Dutch policy (to recover flat oyster beds) and the type of existing and future wind farm infrastructure (a monopile foundation with rocky scour protection at its base), are generally more uniformly distributed.

An area suitable for oyster reef development that offers a stable seabed and year-round food availability, is present in the Dutch part of the North Sea broadly around the 54° latitude (Kamermans et al., 2018b; Van Duren et al., 2023; see Figure 3). The area is partly overlapping with the historic presence of oyster beds (Olsen, 1883; Houziaux et al., 2008; Bennema et al., 2020). The highest potential to establish oyster reefs successfully is generally thought to be in an area with both suitable environmental conditions and historic presence of oyster reefs (Kamermans et al., 2018a, b; Stechele et al., 2023b). Therefore, the area around 54° latitude and between 4° and 6° longitude could be appointed to initiate oyster reef development in the Dutch part of the North Sea (see Figure 3). This area also includes search areas for future offshore wind farms (see Figure 3), eventually offering the valuable infrastructure for hosting oyster reefs, which could be optimized even further to provide the most suitable conditions.

Currently, observations of flat oyster reefs presence have not been reported for the area, nor is connectivity with existing reefs to be expected (Ter Hofstede et al., 2023a). Therefore, active introduction of oysters for local larvae production to initiate reef development would be required. A preferred starting population would be one that can become self-sustaining over time. An amount of 20,000 oysters was suggested as the minimum starting population size to exceed a limited critical mass of 100,000 oysters (at high densities of 82 m^{-2}) within 3 years (Smyth et al., 2016; Kamermans et al., 2020). For such a population to be able to develop into a size as used to be present in the late 19th century, a large area, exceeding individual wind farms, is needed (Ter Hofstede et al., 2023a). This means that all future offshore wind farms in the area should embrace the ambition to host oyster reefs. Further increase of the oyster population can be achieved by optimizing the wind farm areas to provide suitable hard substrate habitat. Optimizations could include increasing the habitat complexity of conventional scour protection by bringing in more variety in use of materials, shapes and dimensions (Ter Hofstede et al., 2023a), and the installation of longlines hosting vertical mussel reefs that provide a continuous supply of shell material and will thereby provide most suitable settlement substrate for oyster larvae (Ter Hofstede et al., 2023a, b).

The agreed ambition between the prime stakeholders to restore oyster reefs in the Dutch part of the North Sea could be threefold, i.e. 1) to concentrate efforts in the future offshore wind farms located in the area that is considered most suitable for oyster reefs, i.e. around 54° latitude and between 4° and 6° longitude (see Figure 3); 2) to initiate oyster reef development by deploying sufficient broodstock for the population to become self-sustainable; and 3) to provide settlement substrate as part of the wind farm infrastructure for the oyster reefs to thrive upon in higher densities than at the existing seabed. The operational objective would accordingly become: Actively introduce oysters to reach an initial critical mass of 100,000 individuals and optimize settlement habitat at all future offshore wind farms in the area with suitable habitat characteristics. This operational objective would provide the starting point for the next step, i.e. defining and actually implementing quantified technical solutions needed to reach the objective, using a tool like the 'Frame of Reference' approach (see Figure 1). The application of this approach was demonstrated to further stimulate the integration and cooperation of science, policy and management during the process of defining functional engineering designs and assessing their performance (Van Koningsveld, 2003).

4 Discussion

Marine infrastructure offers huge potential to improve the ecological functioning of the system in which it is build (Dafforn et al., 2015b; Laboyrie et al., 2018), and it is becoming more and more common to include nature-inclusive elements in marine construction projects (e.g. Borsje et al., 2011; Firth et al., 2014; Ter Hofstede et al., 2023a). In most cases, these nature-inclusive measures are designed to meet individual project requirements, fragmented, and insufficiently taking into account the opportunity to make a system-scale impact. To do so, a coherent overarching

realization scheme of design measures for nature-inclusive marine infrastructure is required, with clear objectives to make the efforts effective at a larger scale beyond individual projects (De Vries et al., 2020b). Strategic objectives are required to address the desired future condition of a system, defining a long-term plan with clear priorities, along with a means to monitor and assess progress (Tunnicliffe et al., 2020). Operational objectives are needed to provide tangible direction to implement strategic objectives, with a clear indication of the spatial and temporal scales involved (Van Koningsveld et al., 2005).

Our paper presents a stepwise approach for defining clear operational objectives for nature-inclusive marine infrastructure to achieve impact at system-scale, in which ruling polices, environmental conditions and the potential use of marine infrastructure are aligned. It includes careful consideration of the full potential nature-inclusive infrastructure can offer, based upon an assessment of the feasibility of measures and their estimated effects. Our approach can support policy makers in achieving their environmental targets, while at the same time meeting societal demands for infrastructural development. For example member states of the European Union have set policy targets to achieve a Good Environmental Status of their marine ecosystems, being implemented by the Marine Strategy Framework Directive (European Commission, 2008), while at the same time their marine environment is increasingly used for wind energy production in order to meet renewable energy goals (European Commission, 2023). Using our approach could facilitate EU member states in the planning process of their marine waters, by identifying measures that can be implemented in the future marine infrastructure to optimize the potential benefits for ecosystem components targeted by the MSFD. Herewith policy makers might overcome the struggles they face during the marine spatial planning process, e.g. in establishing a shared transboundary vision and in aligning the different interests of stakeholders (e.g. Fraschetti et al., 2018; Santos et al., 2021). The final selection of operational objectives for a system is still to be made through strong involvement of these stakeholders. This is to ensure that all required knowledge and expertise from various disciplines are covered, and to achieve commitment to the jointly established objectives. For example, inclusion of the scientific community, allows for the assessment of the objectives to determine their ecological feasibility and their consequences, which is often too little understood by decision makers and developers only (Lackey, 2003). Scientists provide advice on the ecological, social and economic repercussions of the objectives, and can determine courses of actions to be taken (Cormier et al., 2017). However, scientists might also display implicit preferences and advocate a certain ecological state for a system, which should be avoided when providing advice for setting objectives (Lackey, 2003). This illustrates the importance of a balanced stakeholder engagement process, in which the various relevant disciplines are evenly represented.

Reaching agreement upon achievable ambitions between different stakeholder disciplines can be a difficult process. For example, going from overarching strategic objectives towards clear operational objectives was observed to lead to confusion about terminology, baseline and reference states, and defining them quantitatively (Leadley et al., 2022). The process of setting operational objectives for including nature-inclusive elements in the design of marine infrastructure requires strong leadership and political will. A lack of motivation to improve legislation, vested interest in conventional infrastructural development, and insufficient funds and resources will hamper the development and implementation of measures that could benefit marine life (Dhakal and Chevalier, 2017; Johns, 2019). Stakeholder engagement during the stepwise approach to reach operational objectives for nature-inclusive marine infrastructure allows all relevant users of the system to express their interests, essential to reach long-term commitment to the set objectives.

Our stepwise approach to define operational objectives to embed nature-inclusive measures into marine infrastructure has been demonstrated for use to promote oyster reef development in offshore wind farms in the Dutch part of the North Sea. To establish oyster reef restoration in the North Sea, it is recommended to follow a coordinated basin-wide approach to reach connectivity between natural oyster beds, restoration sites, offshore infrastructure, and aquaculture sites (Stechele et al., 2023a). Such can only be achieved if an overarching vision is developed for an area, including the setting of clear operational objectives for implementing measures wisely. Assessing the three major elements within the Dutch North Sea system, i.e. policy, environment and infrastructure, it is concluded that these elements match when striving for oyster reef development in offshore wind farms. The European flat oyster has been characterized as a 'policy relevant species' (Lengkeek et al., 2017) and is already explicitly addressed as a target species in Site Decisions for new offshore wind farms (Staatscourant, 2019; 2022). The environmental conditions are considered most suitable for oyster reefs around the 54° latitude and between 4° and 6° longitude (see Figure 3), which is primarily influenced by food availability, the presence of a stable seabed with low hydrodynamic forces, and their historic presence (Kamermans et al., 2018a; b; Bennema et al., 2020; Van Duren et al., 2023). The area is furthermore prone to offshore wind farm development in the near future (Ministry of Infrastructure and Water Management, 2022), providing infrastructure that offers suitable substrate for oyster reef development. Considering the interests of the main stakeholders, it is highly likely that an agreement on achievable ambitions can be established, which would result in the operational objective to actively introduce oysters to reach an initial critical mass and optimize settlement habitat in all future offshore wind farms in the area.

Offshore wind farms outside of the identified area with the most suitable habitat characteristics should not be completely discarded from consideration to support oyster reef restoration. In general, at the base of each wind turbine foundation and on top of cable crossings, rock material is placed to prevent scouring of the seabed, providing good conditions for oyster reef formation (Ter Hofstede et al., 2023a). Although the majority of the seabed within a wind farm in the southern part of the Dutch Nort Sea might not be stable enough for oyster reef development, their scour protections do

provide suitable substrate, and could function as steppingstones for the spread of oyster larvae (Adams et al., 2014), thereby contributing to oyster reef restoration throughout the North Sea. The suitability of scour protections within these offshore wind farms can also be further optimized for hosting oyster reefs by the design of their shape and dimension and by the type of rock material used (Ter Hofstede et al., 2023a). Whichever design optimizations in a scour protection are feasible while still preserving its primary function to prevent seabed erosion, is location-specific and depends on the willingness of the developer to invest, if a cost-increase is applicable.

The final selection of which and where to implement design measures for nature-inclusive marine infrastructure is always to be made through careful consideration of the different interests of relevant stakeholders. If only individual interests are pursued, there's a risk of an uncoordinated fragmentation of well-intended though ineffective measures to promote ecosystem components, which fail the need to strengthen one another, or even may be counteracting. In order for interventions to be truly benefitting marine life, it is required to implement measures at a predetermined scale, large enough to be create impact within the larger system (Abelson et al., 2020; Ter Hofstede et al., 2023b). When feasible, one should even consider targeting cross-habitat effects, by facilitating positive interactions that occur when processes generated in one habitat benefits other (Vozzo et al., 2023). For effective improvement of targeted components of the ecosystem, an interdisciplinary approach with the involvement of different stakeholders is needed, covering all required aspects with regards to knowledge, expertise, finance, and legislation (Gann et al., 2019; Saunders et al., 2020). Finding mutual ground and reaching agreement on achievable ambitions between all relevant parties is key for setting operational objectives to take measures for nature-inclusive design with and within marine infrastructure at a system-wide scale. This can be achieved through following our stepwise approach in which the potential for nature-inclusive marine infrastructure is determined by matching the ruling policy, its environmental conditions, and its foreseen infrastructural development, followed by jointly determining the most effective operational 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 author/s.

Author contributions

RH: Conceptualization, Data curation, Investigation, Methodology, Project administration, Software, Visualization, Writing – original draft, Writing – review & editing. Mv: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare 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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Towards environmental sustainability: further evidences from decarbonization projects in Kenya's Blue Economy

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Kenya is committed to the global efforts on climate change mitigation and adaptation as seen through investments in various sustainable green and blue economy projects. In this review paper, we present the current status of what has been done, particularly on the blue carbon offset initiatives undertaken in the mangrove and seaweed ecosystems as well as the decarbonization activities at the port of Mombasa and which should form reference information for local, regional, bilateral/multilateral partners, scientists and other climate change stakeholders. The blue carbon offset projects involve mangrove conservation, reforestation and carbon credit sale as well as seaweed farming. The initiatives have several unique features amongst which are the community-led income generation systems that simultaneously act as an inducement for ecosystem preservation, co-management and benefits sharing which are recipes for economic, socio-cultural, and environmental sustainability. A notable project impact is the conferment of economic power to the locals, particularly the women and the youth The model used embraces a collaborative approach involving multisectoral engagements of both the government, multilateral organizations, NGOs, and local communities. This integrated top-down (government) and bottom-up (local community) method deliberately targets the strengthening of economic development while ensuring sustainability.

KEYWORDS

sustainability, mangroves, seaweeds, decarbonization, carbon credit

1 Introduction

Global warming and the attendant climate change are worldwide challenges that are mainly driven by emission of greenhouse gases (GHG) particularly the carbon dioxide (CO2) (IPCC, 2022). GHG emissions keep on increasing due to unsustainable use of resources particularly energy, land use and land-use changes (IPCC, 2022). Other causes include lifestyles, consumption patterns, and methods of production within regions,

countries and amongst individuals (IPCC, 2022). The incessant increase in CO2 emissions is a major threat to a sustainable environment as it is raising the temperatures and increasing weather anomalies in every region across the globe with heatwaves, floods, droughts and tropical cyclones a common occurrence (Clarke et al., 2022). Since the environment is a finite resource central to the survival of our planet and humanity, achieving environmental sustainability has become another international challenge in addition to climate change and its effects. As has been observed that carbon dioxide emissions are produced chiefly by the burning of fossil fuels, energy consumption is therefore considered a principal driver of climate change (Xue et al., 2021). Consequently, environmental sustainability therefore requires making a gradual transition from use of non-renewable energy sources (in the form of fossil fuel) to sustainable and low-carbon energy sources such as wind, geothermal, solar, and hydro energy (IRENA, 2020).

Although Africa is one of the lowest contributors (less than 10 percent) to global GHG emissions, its limited adaptation ability renders it one of the most susceptible continents to the effects of climate change (Wang and Dong, 2019; Bouchene et al., 2021; Trisos et al., 2022; Yang et al., 2022). It is worth mentioning that climate change and associated threats have a massive impact on the continent largely due to environmental and public health related challenges such as poverty, poor planning, disease burdens, illiteracy and corruption. Both Yameogo et al. (2021) and Aleman et al. (2017) further suggest that the weak policy environment around sustainable use of resources in the continent is another contributor to the continual increase in global warming and climate change. Indeed, global warming and the changing climate is already severely affecting key development sectors and infrastructure and impacting the social fabrics and livelihoods of millions of African families (Adekunle, 2021).

As is the case in most African countries, Kenya's economy relies heavily on natural resource-related sectors which are extremely susceptible to climate change and variability (Government of Kenya (GoK), 2016). To address these vulnerabilities, the government, through various mitigation, adaptation, and resilience-building measures is promoting investment in sustainable resource efficient green development initiatives that use renewable energy while reducing GHG emissions (Government of Kenya (GoK), 2016). One such project is the Lake Turkana Wind Power Project, a wind farm which generates 310 MW of clean energy. Another project is the Olkaria Geothermal Development Company project generating over 500MW of clean energy from geothermal sources and which makes Kenya a pioneer in geothermal energy exploitation. As a consequence, in terms of climate change mitigation, up to 90% of Kenya's energy generation is now from renewable sources (40% geothermal, 35% hydro-generated, 13% wind power and 2% solar). Furthermore, the country has embraced the M-Kopa Solar project which is providing affordable solar power to households all over Kenya thus helping reduce reliance on use of kerosene.

Like most countries participating in the REDD+ program, Kenya has developed a National REDD+ Strategy as required by the Cancun Agreement to UNFCCC (Government of Kenya (GoK), 2021; UN-REDD+, 2018) and implemented the "Greening Kenya Initiative" geared towards expanding the country's forest cover to total 10% of its land areas. This project has seen the planting of millions of trees, which help to mitigate the effect of climate change by absorbing atmospheric carbon dioxide as well as promoting biodiversity. More recently, the country commenced the Kenya Climate-Smart Agriculture program which promotes sustainable farming practices that increase productivity, ensures food security and sustainable livelihoods while reducing GHG emissions and building resilience to climate change risks.

Kenya's commitment to the pursuit of sustainable natural resource exploitation is further evidenced by signing and ratifying key multilateral environmental conventions, treaties, and agreements including United Nations Framework Convention on Climate Change (UNFCCC), the Kyoto Protocol, and Paris Agreement. Furthermore, to demonstrate leadership in climate action, the country has enacted several climate-specific policies including; National Climate Change Strategy (2010), Climate Change Act (2016), Climate Finance Policy (2018), National Climate Change Action Plan 2018-2022 (which is a 5-year rolling plan), and National Adaptation Plan (2015-2030) which guides the climate actions of the National and County governments and other stakeholders. Others include; Energy Act 2012, Environmental Management and Coordination (Amendment) Act 2015, Green Economy Strategy Implementation Plan (GESIP) (2016-2030), and Vision 2030.

Kenya firmly believes that Blue Economy (BE) is an integration of green growth and sustainable development and essentially to promote social,economic, and community development (Government of Kenya (GoK), 2023) Taking cognizance of the BE potential for employment creation, alleviation of poverty, nutrition and food security, and its role as an economic driver (OECD, 2016; World Bank and United Nations, 2017; UN Habitat, 2018; United Nations Development Program (UNDP), 2018; Taillardat et al., 2018; AU-IBAR, 2019; Childs and Hicks, 2019; Intergovernmental Authority on Development (IGAD), 2020), the Government of Kenya (GoK) has made BE one of the key sectors to be prioritized in order to achieve the country's long-term development blue print; the Kenya Vision 2030 (AU-IBAR, 2019; Rasowo et al., 2020). Recognizing the multiple ecosystem services provided by mangroves and associated blue carbon ecosystems, Kenya included blue economy (BE) climate commitments to the earlier land-focused (green economy) interventions in her updated Nationally Determined Contributions (NDCs) and subsequently increased the target of abating its carbon emissions from 30 percent to 32 percent by 2030 (Government of Kenya (GoK), 2017a; GoK, 2020). In 2023, the country's National Blue Economy Strategy 2023-2027 was formulated and aligned to the BE Strategies of the African Union (AU) and Intergovernmental Authority on Development (IGAD), (AU-IBAR, 2019; Government of Kenya (GoK), 2023).

In the past five years, Kenya has taken a global leadership role by spearheading various high-profile BE engagements. The country, in 2018, co-hosted with Canada and Japan, the first "Sustainable Blue Economy Conference". Again, in collaboration with Portugal, Kenya co-hosted the 2022 UN Ocean Conference (UNOC) in Lisbon, Portugal. UNOC came up with the "Lisbon Declaration" which reaffirmed the support to the achievement of Sustainable

Development Goal 14 (referred to as Life below water), the Paris Agreement, and the implementation of UN Decade for Ocean Science (2020-2030). Furthermore, Kenya is currently the champion for the sustainable blue economy sector in the Commonwealth Blue Charter (Commonwealth Blue Charter, 2021). Meanwhile, Kenya is a key partner in the 14-member states of the High-Level Panel for a Sustainable Ocean Economy (referred to as The Ocean Panel), a panel which functions as a global pillar for sustainable BE undertakings. In December 2020, Kenya together with other members of the High-Level Panel, pledged to sustainably control 100% of the ocean area under their national jurisdiction by 2025. Furthermore, the GoK has pledged to create a network of Marine Protected Areas (MPAs) encompassing 30% of its Exclusive Economic Zone by 2030.

In this review, we discuss the blue carbon projects being undertaken in the mangrove and seaweed ecosystems and the decarbonization initiatives at the port of Mombasa. We report on carbon offset projects that are integrating mangrove conservation and reforestation while incorporating the sale of carbon credit in the form of payment for ecosystem services. Notably, the seaweed farming is mainly for production of seaweed for food and for sale as a source of income. These two nature-based initiatives balance community livelihood improvement with conservation and are proof that environmental conservation and economic development can be achieved concurrently if well planned.

2 Carbon offset projects in the mangrove ecosystem

2.1 Overview of mangrove functions and uses

Mangroves are amongst the utmost productive ecosystems on planet earth and provide a myriad of valuable goods and ecosystem services to humanity and nature. These include; regulating (e.g. controlling floods, storms and erosion; stopping intrusion of salt water); habitat (e.g. habitat for spawning, breeding and nursery for various marine organisms, refuge for mammals, birds); provisioning (e.g. fruits, charcoal, timber, and fish); cultural services (e.g. sport, aesthetic), and global climate regulation through sequestering carbon dioxide (Lee et al., 2014; Alongi, 2020; Das, 2020; Menéndez et al., 2020; zu Ermgassen et al., 2020; Adame et al., 2021; Afonso et al., 2021; Macreadie et al., 2021; Quirost et al., 2021).

Together with saltmarsh, coral reefs, seaweed, and seagrass ecosystems, mangrove forests have been termed "blue carbon" ecosystems since they can store organic carbon (C) for a long period making them major contributors to marine C burial (Nellemann et al., 2009; Mcleod et al., 2011; Duarte et al., 2013; Macreadie et al., 2019; Jennerjah, 2020; Wang et al., 2020). Mangroves are of special interest since they amass and sequester relatively higher quantities of C than the other ecosystem types (Ezcurra et al., 2016; Atwood et al., 2017; Kauffman and Bhomia, 2017; Adame et al., 2018; Zeng et al., 2021; Chatting et al., 2022). According to evidences adduced from several studies, the high productivity combined with slow rates of decomposition in the soil significantly improves mangroves' capacity to capture and eventually store organic carbon, especially in the soils (Bouillon et al., 2008; Alongi, 2012; Suello et al., 2022). Estimates by Atwood et al. (2017) indicate that organic carbon stowed in mangrove sediments up to a depth of 1 m, globally equates to 2.6 billion Mg of C. Furthermore, above-ground net primary productivity reported for mangroves (8.1 t DW ha−1 yr−1) match the records from highly productive tropical forests on land (11.1 t DW ha−1 yr−1) (Alongi, 2012; Cooray et al., 2021). Research on carbon stocks in the Kenya mangroves report an estimated range of 500-1000 t C ha-1 which is ten times higher than the average carbon content of terrestrial forests in the country (Huxham et al., 2015). Indeed, it is noteworthy that whilst covering only ca. 2 per cent of the world ocean, mangroves effectively account for over 10 per cent of the global carbon sequestration by the world's oceans (Alongi, 2014).

World-wide, mangroves are faced with a myriad of threats particularly from organic and inorganic pollution, wanton deforestation, and sea-level rise with the leading drivers causing these threats being the rapid population growth, climate change, and infrastructural developments in coastal areas (Barbier et al., 2011; Giri et al., 2011). Mangrove conservation and restoration efforts including innovating financing instruments should be speeded up to save these natural blue carbon ecosystems and to ensure that the critical function of provision of goods and services are not destroyed (Laffoley and Grimsditch, 2009; UN Environment (UNEP), 2018).

2.2 Projects in the Kenya mangrove ecosystem

Mangroves occur throughout the coastal Kenya region starting from the north in Kiunga in the Kenya-Somalia border and up to Vanga at the Kenya-Tanzania boundary to the south (Figure 1). The forest inventory show that the mangrove forest area cover about 61,271 ha, 62% of which is found in Lamu County (Figure 2) (GoK, 2017b), and that all the nine species of mangrove recorded to occur in the region of the Western Indian Ocean are also found in Kenya namely: grey mangrove (*Avicennia marina*), oriental mangrove (*Bruguiera gymnorhiza*), tagal mangrove (*Ceriops tagal*), black mangrove (*Lumnitzera racemosa*), red mangrove (*Rhizophora mucronata*), apple mangrove (*Sonneratia alba*), cannonball mangrove (*Xylocarpus granatum* and *Xylocarpus molucensus*) and *Heritiera littoralis*. Unfortunately, the mangroves have experienced loss and degradation with the National Mangrove Ecosystem Management Plan estimating a loss of 40% of the mangroves occurring between 1990 and 2010 (FAO, 2016; GoK, 2017b; Kairo et al., 2021). However, Kirui et al. (2013) reported an annual net mangrove cover loss of 0.7% between 1985 and 2000 with the loss rate dropping to 0.28% between 2000 and 2010. Hamza et al. (2022) estimated a mangrove cover loss of 0.15% per year between 2010 and 2016 indicating a trend of gradual reduction in loss of forest cover (Gitau et al., 2023).

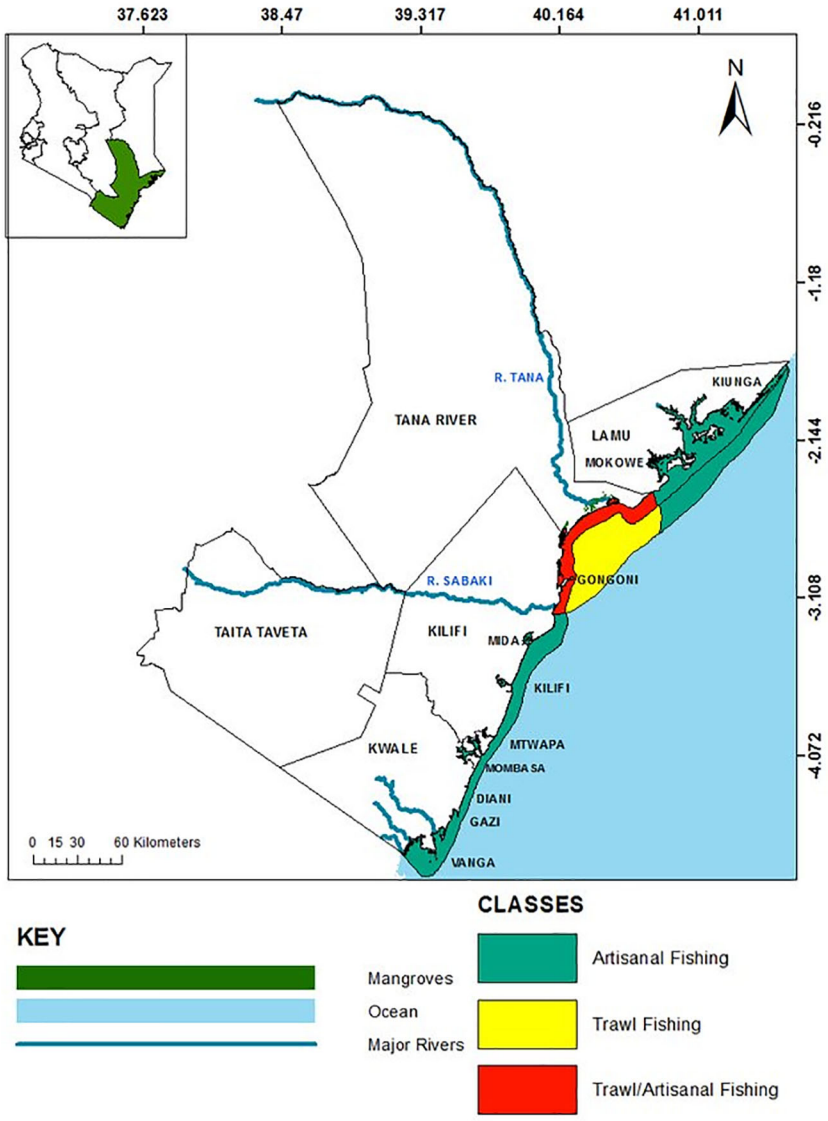

FIGURE 1
Mangrove restoration and conservation and Seaweed farming project sites in Gazi, Vanga, and Lamu (Adapted from Morara et al., 2015).

To further counter the mangrove forest loss and degradation, Kenya has launched several projects in the mangroves aimed at protecting and restoring mangrove forests through avoided deforestation and establishment of new mangrove plantations. Some of the projects have added the aspect of payment for ecosystem services (PES) aimed at providing long-term incentives for restoration and protection of the mangroves through selling blue carbon credits (Locatelli et al., 2014; Huxham et al., 2015). Additionally, the projects encompass establishing community-managed conservation zones and promoting alternative livelihoods such as ecotourism and crab farming. Appreciating the high demand for poles for building and fuelwood and in order to mitigate carbon leakage, the projects support the planting of fast-growing trees, mainly Casuarina spp (*Casuarina equisetifolia)*, to create a maintainable supply of timber for construction, wood for fuel and income from their sale; thus, removing pressure from the mangroves. Here we report on three of such initiatives namely; the Mikoko Pamoja Project, the Vanga Blue Forest Project, and the Lamu Marine Conservation Trust Mangrove Project.

Mikoko Pamoja Project (MKP) is a community-based initiative located in Gazi Bay (Figure 1), some 50 km south of Mombasa in Kwale County. Gazi Bay has a total cover of 615 ha of natural mangrove forest. The forest has suffered major degradation in most areas while in some places total destruction has been recorded due primarily to its proximity to Mombasa city, which offers a quick market to sell mangrove timber (Dahdouh-Guebas et al., 2004; Kirui et al., 2013; Rideout et al., 2013; Musyoka, 2015; GoK, 2017a, b; Omondi, 2017; Plan Vivo Project Design Document (PDD), 2020). The project aims to reduce GHG emissions through protecting and restoring the mangrove forests in the Gazi Bay area. Since its inception in 2012, the project has conserved as well as

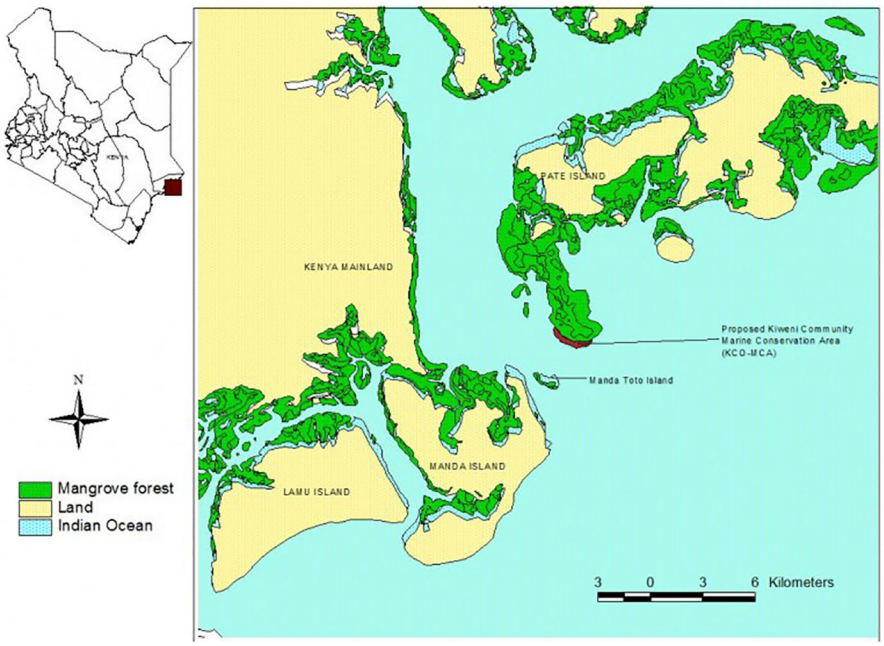

FIGURE 2
Lamu County is home to nearly 62% of Kenya's mangrove forests (SOURCE: Lamu Marine Conservancy).

planted over 117 hectares of mangroves with about 10 hectares out of the 117 ha being newly planted mangrove trees. The MKP is accredited, as per regulatory requirements, by the Plan Vivo System and Standard to trade up to 3000t CO2 for an initial 20-year period. The carbon credits generated by MKP are marketed and sold on the international voluntary carbon market through the Association for Coastal Ecosystem Services (ACES), a charity registered in Scotland (https://aces-org.co.uk/our-projects/). Benefits from the sale are ploughed back into the community to support various community projects including various small and medium enterprise that meet the needs of the Gazi community (Huff and Tonui, 2017; Murungi, 2017; Kairo et al., 2019; Vanga Blue Forest Project Design Document (PDD), 2019).

The Vanga Blue Project (VBF) launched in 2019 as a result of the huge success of MKP, is also located in the south coast of Kenya (Figure 1), approximately 110 km from Mombasa city. The project coverage encompasses the mangroves of Vanga, Jimbo, Kiwegu and Majoreni totaling about 4,428 ha (https://aces-org.co.uk/our-projects/). According to Omondi (2017), a major decline in forest cover in this locality occurred between 1991and 2016, changing the forest cover from 3685 ha to 3234 ha with the drivers of losses and degradation identified as population pressure, poverty and inequality, and poor governance. The VBF project has planted more than 1,000 native mangrove trees since its inception, with future plans to work with neighboring communities in Tanzania to restore mangrove forests along 140 kilometers of the East African coastline. VBF targets avoided emissions of over 100,379 t CO2-eq over the 20 years' crediting period, which approximates to 5,019 t CO2 yr-1 from both the soil carbon and above and below-ground biomass carbon pools (Kairo et al., 2009; Cohen et al., 2013; Huxham et al., 2015; Gress et al., 2017; Vanga Blue Forest Project Design Document (PDD), 2019; Aigrette et al., 2021). Money produced from trading carbon credits is utilized in supporting community-initiated development projects in the area (Kairo et al., 2019).

In Lamu County, the Lamu Marine Conservation Trust (LaMCoT) and The Nature Conservancy, two non-profit organizations work to encourage sustainable and efficient management of marine and coastal resources in the county. The organization has implemented several projects aimed at conserving and restoring mangrove forests in Lamu County, including the establishment of community-based management systems and the promotion of alternative livelihoods such as eco-tourism and sustainable fishing.

3 Carbon offset projects in seaweed ecosystem

3.1 Overview of seaweed functions and uses

Seaweeds, also known as macroalgae, provide diverse ecosystem services such as; supporting (biogeochemical cycles, primary producer, biodiversity conservation, habitat for various organisms), provisioning (source of food, source of energy), cultural (recreation, aesthetics, heritage) and regulating (climate, eutrophication, biological) (He et al., 2008; Chung et al., 2011; Chung et al., 2013; Kraemer et al., 2014; Ferreira et al., 2021; Yong et al., 2022).

Previous exhaustive studies have shown that seaweeds provide bioremediation services as the dissolved nutrients such as nitrogen,

phosphorus and carbon are abstracted by seaweed during growth then removed when the seaweed is harvested (Kim et al., 2017; Wu et al., 2017; Hasselstrom et al., 2018). Further studies have reported that seaweed reduces the hydrodynamic wave energy thus abating erosion of coastal areas from wave forces in addition to protecting tidal zones from erosion (Christianen et al., 2013). Furthermore, growing seaweed, directly on the seafloor in shallow areas or on ropes suspended off the bottom normally in deep areas, adds complexity to growth environment, normally creating a three-dimensional habitat which offers refuge plus more surface for settlement for other organisms as well as more feeding and more nursery areas for a greater diversity of associated marine and terrestrial organisms (Smale et al., 2013).

Seaweed can be used as direct food for human consumption or can be processed into other food additives, animal feeds, medicines, pharmaceuticals, fertilizers and cosmetics among other products (McHugh, 2003; Bixler and Porse, 2011; Wells et al., 2016; Anis et al., 2017). Related research has reported that seaweed species are rich in bio compounds majorly proteins, dietary fibers, proteins, and lipids and contain bioactive elements with a broad range of applications (Fleurence, 2004; Sánchez-MaChado et al., 2004; Macartain et al., 2007; Mišurcová et al., 2011; Pereira et al., 2011). Furthermore, they contain vitamins A (beta carotene), K, B12, and C in addition to being rich in potassium, iron, calcium, iodine and magnesium. From a practical perspective, the very high iodine content of the macroalga makes them ideal for tackling malnutrition in children and pregnant women. Meanwhile, according to the research conducted by Demarco et al. (2022) and Barbier et al. (2019), seaweed contains polyphenols and essential fatty acids since the principal components of their cell membranes are polyunsaturated fatty acids, principally omega 3 (ω-3) and omega (ω-6) although their bioavailability is not clear and is still an area of research. In addition, many studies have enumerated several other properties of seaweed to include anti-cancer, anti-fungal, anti-viral, antidiabetic, antihypertensive, immune-modulatory, anticoagulant, anti-inflammatory, anti-parasitic, and antioxidant among others (Smit, 2004; Mayer et al., 2013; Barbosa et al., 2014; Besednova et al., 2015; Ruan, 2018) consequently making seaweeds beneficial to human health. Seaweeds are routinely used by the cosmetic industry as coloring agents, stabilizers, emulsifiers and are also a source of different compounds used in the skincare sector (Yuan and Athukorala, 2011; Pimentel et al., 2017). Recently, Guillerme et al. (2017) reported that seaweed produce compounds that absorb UV rays, such as mycosporin-like amino acids, phenolics, carotenoids and terpenes, that are normally useful photo-protective elements for the formulation of sunscreen products.

Seaweeds are able to sequester atmospheric CO2 and the surrounding seawater through the process of photosynthesis (Krause-Jensen and Duarte, 2016). During photosynthesis, they absorb CO2 and convert it into organic matter and in the process release oxygen into the surrounding environment. The organic matter produced by the seaweed is used for growth, or can be buried in the sediment at the bottom of the ocean, effectively removing atmospheric carbon and storing it for a long-time duration. In addition to sequestering carbon, seaweed farming has many other environmental benefits, including improving water quality, providing habitat for marine life, and reducing the impact of ocean acidification (Krause-Jensen et al., 2015; Mongin et al., 2016). Ocean acidification is an increasing threat to all the marine ecosystems as decreasing pH levels interferes with the life processes of most marine species.

3.2 Seaweed farming projects in Kenya

After an extensive study of the seaweed resources of Kenya, over 380 species have been documented (Moorjani, 1977; Yarish and Wamukoya, 1990; Oyieke, 1998; Coppejans et al., 2000) with several of the species found to be potential candidates for farming namely: the carrageenophytes *Eucheuma* spp., *Kappaphycus* spp. and *Hypnea* spp.; the agarophytes, *Gracilaria* spp. and *Gelidium* spp.; and the alginophytes *Sargassum* sp *Turbinaria* spp. and *Cystoseira* spp. (Wakibia et al., 2006; Wakibia et al., 2011; Nyundo, 2017; Ollando et al., 2019). The first seaweed farms of *Eucheuma denticulatum* and *Kappaphycus alvarezii* were started in 2010.

Currently, seaweed farming is established in Kwale County with farms concentrated in 10 villages situated in Gazi, Nyumba Sita, Tumbe, Funzi Island, Mwambao, Mkwiro, Jimbo, and Kibuyuni. (Figure 1) The most common technique of seaweed cultivation is the peg and line (off-bottom) monoline method, which involves tying seaweed seedlings to monofilament polypropylene ropes (lines) with the main lines tightly stretched amid two wooden pegs (stakes) drilled securely to the seafloor. Other farming practices including the raft, the net, broadcasting, and floating long-line methods are still being piloted (Kimathi et al., 2018; Nyamora et al., 2018; Brugere et al., 2020; Garcia-Poza et al., 2020; Msuya et al., 2022).

Farming cycles are aligned to the tidal cycles with the farmers working in the farms during the low tides. Low tides occur fortnightly each month and each low tide takes seven days; hence farmers work on their farms for about 10-14 days each month. The planted crop is harvested after 6 weeks of growth (Overbeeke et al., 2020; Msuya et al., 2022). This relatively short cycle of production lasting 6 weeks allows for a fairly quick return on investment and subsequently in a regular income to the farmers. Farming is carried out year-round although the yields are highest when conditions are good during the inter-monsoon season from March through to early May and are low from June to mid-August, during the South-East Monsoon when conditions are not so favorable due to extreme wind and rough sea conditions. Normally, the water temperatures are relatively high from December to February, so farmers halt production until the rainy season (Msuya and Porter, 2014; Largo et al., 2020; Overbeeke et al., 2020). On average, farmers produce 300 - 500kg per each production cycle and are paid between US$ 0.2 and US$ 0.25/kg for dry seaweed product, yielding on average total revenues ranging between US$ 70 – 115 every six weeks during production seasons (Odhiambo et al., 2020; Msuya et al., 2022). This price is averagely high for the farmers considering the opportunity costs and the fact that the farming is not a full-time engagement.

4 Decarbonization through greening Kenya's ports

Maritime transport is the lifeblood of the global trade and the manufacturing supply chain , carrying over 90% of global commercial goods (World Bank, 2023). Shipping is particularly important for Kenya with the ports of Mombasa and Lamu playing a strategic role in the national and international trade as well as serving an extensive hinterland comprising Democratic Republic of Congo, Rwanda, Burundi, Uganda, Southern Sudan and southern Ethiopia. The ports lie in a very busy shipping route with a majority of international ships spending time in Kenyan waters or docked at the ports. However, maritime transport is highly polluting as ships use carbon heavy fuels to power their engines (International Maritime Organization (IMO), 2018).

Kenya has shown its commitment as a member of International Maritime Organization (IMO) by signing the International Maritime Organizations Initial Strategy on Reduction of GHG Emissions from Ships. This strategy targets to reduce GHG emitted from the shipping sector by 50% by 2050 as compared to the levels of 2008 and also includes the goal of reducing carbon intensity in ships by 40% by 2030 (International Maritime Organization (IMO), 2018). Furthermore, after acknowledging that the port of Mombasa (Figure 1) produces high concentration of GHG emissions from ships that are docked at the port as well as from trucks and vehicles hauling cargo, Kenya has taken steps to green the port by undertaking several decarbonization projects. In 2020, the GoK launched the "Greening of Ports" project in Mombasa aimed at reducing GHG emissions related to its port's operations. Kenya Ports Authority (KPA), the government parastatal charged with managing the ports, has developed and is implementing an elaborate Green Port Policy (GPP) aimed at transforming the Kenyan ports into ports of clean fuels and which purposes to allow only new technologies and equipment that use clean fuel to operate at the port. Consequently, KPA is implementing cold ironing at the port after installing a 10MW solar photo-voltaic plant for the generation of renewable energy shore power to provide electrical power at the berths for ships calling at the harbor. As per the GPP, all ships calling at the port of Mombasa are to be compelled to switch off their auxiliary diesel engines and power their vessels using shore electric power while docked. Normally, ships emit enormous amounts of carbon dioxide from their diesel engines while discharging cargo and the switching to shore solar electricity- power to supply clean energy is recommended as best practice for green ports. By embracing green technology particularly the switch to electric cranes, and by aggressively investing in equipment modernization and upgrade, efficiency at the port of Mombasa has greatly improved with the turn-around time for ships calling at the port of Mombasa currently standing at an impressive 2 days only (World Bank, 2023; Kenya Ports Authority Magazine (KPA), 2023).

The shipbuilding sector holds great promise as a future growth area for Kenya's economy. To cater for the increasing demand of shipbuilding and repair services within the country and the region, while helping decarbonise this industry, the government, through public and private partnerships (e.g., Kenya Shipyards Limited), is supporting initiatives that embrace green shipping technology in its production. One example is the use of wind-assisted propulsion technologies (European Maritime Safety Agency (EMSA), 2023) inspired in the ancient technology of wind sails.

5 Discussion and conclusion

As part of the strategies aimed at limiting the rising global temperatures and the reduction of man-induced CO2 emissions, most countries have committed to the aspirations of the Paris Climate Agreement which provides for a climate neutral world by 2050 (IPCC, 2022). Achieving climate neutrality entails reducing GHG emissions as much as possible and then offsetting any residual emissions by investing in projects that actively remove atmospheric carbon dioxide including afforestation, reforestation, and carbon capture and storage technologies until net-zero point is reached.

Through its mangrove conservation and restoration and PES projects, Kenya has been able to trade the carbon in the international market as certified carbon credits. Indeed, with over ten carbon credit projects in the country, most of which involve forest cover restoration or protection, Kenya has been hailed as a continent leader in carbon credit markets (Rasowo et al., 2020). However of late, using carbon credit markets to finance adaptation and mitigation activities is facing criticism on a global scale and their future as a sustainable source of climate finance particularly for Africa and other developing countries is not bright. Arguably, carbon markets appear to legitimize the pollution by the big polluters while seemingly appeasing the low-polluting and unindustrialized nations. It is also debatable whether the revenues that the carbon credit markets earn the developing nations are enough to compensate for the losses and damage caused by climate change which they have contributed least to.

Kenya is in an ecological deficit thus the mangrove conservation and restoration mitigates by reducing Kenya's production footprints while increasing its biocapacity (Marti and Puertas, 2020). Additionally, non-deforestation and forest conservation provides a range of benefits to an ecological deficit country like Kenya by protecting biodiversity, mitigating climate change, regulating water cycles, conserving soil resources, and providing social and economic benefits.

The incomes realized from sale of carbon credit and the sale of seaweed has resulted in financial resilience in the local coastal community, increased the community's capacity towards climate adaptation, and decreased their dependence on the limited local resources. Indeed, research by Rimmer et al. (2021) show that financial betterments precipitate wider economic benefits which eventually build the community's capacity to adapt to climate change. In general, the projects have diversified livelihood opportunities for the communities whose main source of income,

primarily, was fishing. Furthermore, diversification has been shown to be a critical factor for building household economic resilience (Rimmer et al., 2021). In addition to climate mitigation and adaptation, the above projects generate multiple benefits to the community including supporting education services, improving sanitation, provision of clean water, shoreline protection, and various mangrove-based livelihood enterprises (e.g. in bee-keeping, crab farming, small-scale farming, mangrove ecotourism, agroforestry).

Seaweed farming, in particular, has proven attractive to the rural coastal communities due to the low barriers to farmer entry, relatively low cost of input, short cycles of production thus providing regular income, low-technology, and relatively easy to master best farming practices. Since seaweed is produced throughout the year and does not need full-time care (relatively low labor requirement), the farming not only ensures constant cash flow, but also creates supplemental rather than replacement income, hence an appropriate alternative livelihood option to the coastal households (Msuya, 2013; Hurtado and Msuya, 2017). Because of the unique characteristics enumerated above, seaweed farming is a more female-oriented activity with over 90% of the current farmers being women (ODINAFRICA, 2020; Msuya et al., 2022).

In order to expand production space and volumes, the government is mapping the whole Kenya coastline to identify more zones that are ideal for seaweed farming with the aim of expanding production space and volumes produced. In addition, the government is funding infrastructural development in the form of good road networks, electricity, water, education, housing, healthcare facilities (Mirera et al., 2020) and training the farmers on entrepreneurial skills including making business plans, market intelligence as well as on value addition processes and technologies as a strategy to enhance economic returns and sustainability. Further government support is through development of coherent policies on conservation, and setting up frameworks and programs that strengthen governance while promoting equality and inclusion.

These Blue Economy projects are unique in that they have embraced a collaborative approach involving a multisectoral engagement of both the GoK, NGOs, international and the local communities. The integrated top-down (GoK) and bottom-up (local community) management model adopted has deliberately targeted the strengthening of economic development while taking cognizance of sustainability (Baker and Mehmood, 2013; Okafor-Yarwood et al., 2020). Studies have documented that a collaborative approach that emancipates the locals by ensuring their involvement in the processes of decision making and management, results in social equity, better economic outcomes, and ecological sustainability (Simane and Zaitchik, 2014; Butler et al., 2015; Mackenzie et al., 2019; Chen et al., 2020). In a related study, El Asmar et al. (2012) further show that when stakeholders are all involved equally in the project's implementation, it makes them take ownership of the project message eventually ensuring sustainability. Furthermore, the component of education and capacity building particularly of the local partners in a project ensures that the community gain adequate skills to run the project on their own at the end of the project contract period. Government engagements at county, national and international levels jointly with the civil society and private sector can play a critical role in aiding and accelerating development pathways geared towards climate resilience and sustainable development in local communities. This is even more effective when activities, financing, and decision-making processes are integrated across all the various governance levels, the sectors, and the timeframes (IPCC, 2022).

From the experiences gained from the activities undertaken at the port of Mombasa, greening a port requires not only investment in modern equipment that does not consume fossil fuel but also the dedicated participation of all value-chain actors including the government, port managers, terminal operators, ship owners and operators, cargo owners, logistics companies, and the communities around the port. In addition, it requires increased efficiency in the form of short turn-around time for ships in the docks since the longer the ships spend floating in the docks, the more GHC gases they emit in the surrounding environment. In general, decarbonizing the shipping sector needs a combination of technological, regulatory and economic approaches including: utilizing renewable energy sources to generate electricity for on board systems, shifting from fossil fuels to low-carbon green fuels, improving the energy efficiency of vessels, and using more efficient propulsion systems to reduce fuel consumption (International Maritime Organization (IMO), 2018). IMO has already established global targets to reduce emissions from the shipping sector but the individual governments do have the leeway to adopt stricter regulations for ships operating in their waters (International Maritime Organization (IMO), 2018).

In conclusion, the observed outcomes of the projects reveal that they are significantly impactful while contributing to the improvement of the livelihoods of the local communities and in particular, conferring economic empowerment to the women whose livelihoods would otherwise depend solely on their husbands. BE needs compliance with the United Nations Sustainable Development Goal (SDG) 14 (Life below water). It is noteworthy that both the mangrove conservation and seaweed farming ventures address problems associated with the realization of several of the UN SDGs in addition to SDG 14 namely; SDG 1(No poverty), SDG 2 (End hunger), SDG 4(Quality education), SDG 5 (Gender equality), SDG 6(Clean water and sanitation), SDG 8 (Sustainable economic growth), SDG 13 (Action to combat climate change), and SDG 15 (Life on land). Kenya's "Green Growth Economy Strategy" and the "Blue Economy Strategy" policy documents are part of the country's effort to realize the bigger circular economy principle which is part of the SDG 12 (Sustainable consumption and production).

Author contributions

Conceptualization, writing plus editing of this manuscript was undertaken by all the five authors: JR, BN, RO, PO and SO. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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

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Mangrove community-based management in Eastern Africa: experiences from rural Mozambique

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Introduction: This study investigated a community-based management model in a mangrove-dependent community in central Mozambique and its adequacy as a management tool for conservation.

Methods: Satellite images were used to map changes in mangrove cover between 1996 and 2017. Individual interviews and Focus Group Discussions were conducted with community members to understand the mangrove restoration processes and management models.

Results and discussion: After unsustainable exploitation that led to mangrove deforestation, the local community engaged in a restoration and management program that started in the late 1990s. Local norms were delineated by the Natural Resources Management Committee (NRMC) aiming at (1) reducing extractive uses by introducing alternative income generating activities; (2) awareness and mangrove planting and (3) law enforcement. Ten hectares of forest were rehabilitated. However, the management system fails to exclude illegal cutters and to enforce regulatory and sanctioning mechanisms, due to resource limitations. More involvement from government authorities and other stakeholders is needed to enhance law enforcement and explore opportunities for carbon trading, tourism and payment for ecosystem services. Additional recommendations are to develop a community management plan and create alternatives to mangrove products and income. Mangrove community-based management is increasingly advocated in many developing countries to promote sustainable utilization of resources and conservation. Understanding the reasons behind the limited success and lessons learnt at this site will guide similar programs elsewhere in Mozambique and other parts of the globe.

KEYWORDS

mangrove restoration, law enforcement, management of commons, natural resources sustainable management, community engagement

1 Introduction

Despite its high ecological and social-economic importance (Kovacs et al., 2008; De Souza et al., 2017; Mozumder et al., 2018; Machava-Antonio et al., 2020) mangroves are globally threatened by several factors, such as overexploitation, urban development, pollution, aquaculture and climate change (Nfotabong-atheull et al., 2011; Banerjee et al., 2016; Li et al., 2016; Phong et al., 2017). In most developing countries, overexploitation of resources is the greatest threat, along with conversion to agricultural uses, coastal development, and natural extreme events such as floods and droughts as documented at the Volta Estuary (Ghana), Senegal, Mombassa (Kenya) and Mozambique (Rubin et al., 1999; Sakho et al., 2011; Bosire et al., 2014; Macamo et al., 2016; Feka and Ajonina, 2017).

Several global and local initiatives are being adopted to counteract these trends, among them protection of mangroves in different types of conservation areas and the restoration of degraded areas (Esteban, 2008; de Almeida et al., 2016). These measures however may not be effective in the long term if the primary causes of degradation are not tackled, thus new management approaches need to be adopted in the protected or restored areas (de Almeida et al., 2016). Community involvement in natural resources management is increasingly advocated giving its socio-economic and ecological outcomes (Leach et al., 1999; Abou-zeid et al., 2007). There are several examples across the globe of community based management, with varying levels of community involvement in the decision making process, law enforcement and community autonomy (Leach et al., 1999; Lynam et al., 2007; Datta et al., 2012; Bown et al., 2013). However, the outcomes of most of these initiatives were below expectations (Datta et al., 2012) because the collective management of resources is a very complex process, where success or failure depends on a great multiplicity of factors, many of which are totally specific to each site (Leach et al., 1999; Datta et al., 2012).

According to (Agrawal, 2003) the critical conditions for sustainable management of common resources include the characteristics of such resources, the characteristics of the community, the institutional arrangements and the external environment (Figure 1). Mangrove forests match all five resource characteristics that are critical for successful community-based management, but the risk of failure lies on the characteristics of the community, institutional framework and external environment (Ostrom, 1999). argues that having a larger numbers of participants in the management of common resources (particularly if with different cultural backgrounds and interests) may hamper the process of community organization and decision making, because the more diverse a group, the more difficult it is to find common interests and agreements. For instance, a community in a municipal village in the Honduras earned its livelihood from the exploitation of forest resources, with at least eight distinct groups of stakeholders with different interests and perceptions of resource uses – loggers, farmers, resin tapers, handicraft women, municipality, firewood and charcoal producers, a municipal corporation for forest development and a community forest association (Nygren, 2005). The conflicts arose at almost all levels, and the same group of stakeholders could be in conflict with more than one other group. This illustrates how important it is to understand the social and political processes through which the multiple actors interrelate and to promote community participation for effective management of the resources (Nath et al., 2017).

Many community-based models also fail because the relationship between costs and benefits does not encourage the participation of some groups, as seen in Tanzania, were poor groups had a much lower net benefit when compared to middle and rich classes (Meshack et al., 2006). The costs may include time and effort to participate in activities and attend community meetings, while benefits are usually ecosystem goods and services.

Community-based management of common goods also requires the existence of legal institutions that can intervene in favor of the community by controlling external factors that are beyond the jurisdiction of the community, as well as providing additional support for law enforcement and sanctioning (Agrawal, 2003; Berkes, 2006). For example, in the mangrove dependent

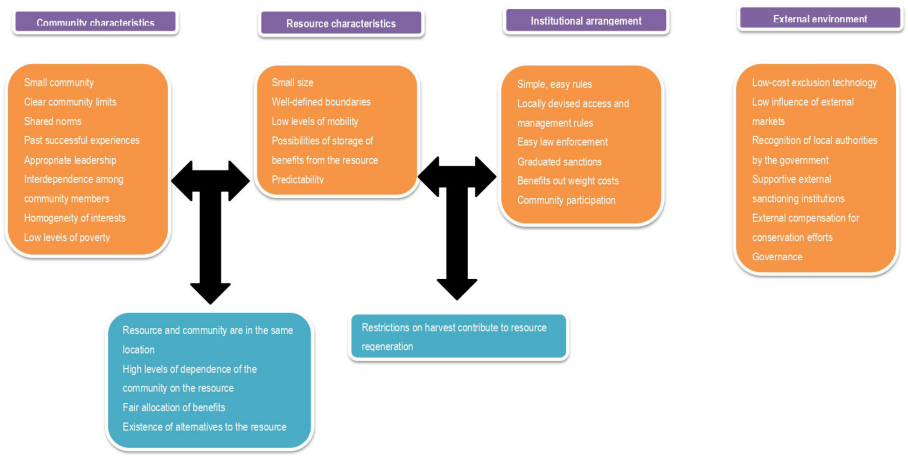

FIGURE 1
Critical conditions for successful; community-based management of common resoiurces. Modified from Agrawal 2003.

community of Koh Sralao (Cambodia), the community managed to organize themselves in a natural resources management committee, creating locally designed rules to protect the forests against illegal harvest of resources, destructive fishing gear and promoting environmental education and mangrove planting. The community also created a reserve area and imposed limits of the mesh size in swimming crab fishing to allow crabs to grow (Berkes, 2006). However, the community did not have appropriate mechanisms to enforce the local regulations to people from other nearby locations, or to exclude incompliant groups of users, even though they had the support from local NGOs and their institutions were recognized by the local authorities. This resulted in the collapse of a community-based management model that had significant outcomes.

Many studies on community-based management models focus on the assessment of only a few of the critical conditions for the success of the model, instead of using more holistic approaches that also try to understand the interrelations between such factors and the implications of the parts on the overall context (Leach et al., 1999; Meshack et al., 2006; Stone et al., 2008). Assessments also rarely detail the community's experience and perception of the outcomes of the management programs (Nguyen et al., 2016).

The aim of this study was to describe the community experience and critically analyze a mangrove community-based management model being implemented in a rural community in central Mozambique. By looking at its failures and success also in terms of the point of view of the community and program managers, the study identifies successful strategies and interventions for improvement that can be replicated elsewhere. The peculiar characteristics of the site include it being one of the few successful mangrove restoration programs in the country (Bandeira and Balidy, 2016), the community experienced traumatic impacts of mangrove degradation and engaged in a mangrove rehabilitation program (by their own initiative) in an area that is vulnerable to wood demands from a nearby town. The study also combines remote sensing techniques to assess the ecological outcomes of the management actions. Understanding the factors behind success and failure of mangrove rehabilitation programs is important in the regional and global context as mangrove rehabilitation and community based management is increasingly used as mangrove conservation and management tools, but few examples of success are known globally (Romañach et al., 2018).

2 Materials and methods

2.1 Description of the study area

This study was conducted at the Nhangau Administrative post, located in central Mozambique, some 30 km away from the second largest town of the country (Beira). Nhangau, with an estimated population of 3 000 inhabitants, features several rural characteristics despite administratively being part of Beira municipality. Agriculture, fishing and small-scale trade are the main economic activities. Nhangau is also a major provider of fishing products to Beira city. The restoration was conducted in Njalane (including Txondja neighbourhood), which is part of Nhangau administrative Post (Figure 2).

The area is part of the Mozambique Channel EBSA (Ecologically or Biologically Significant Marine Area), given its high productivity and species diversity which includes threatened and endangered species (https://www.cbd.int/ebsa/). The climate is tropical, with a rainy season from November to March and a dry

FIGURE 2
Location of the study area, showing Njalane.

season in the rest of the year. The average monthly precipitation is 121.9 mm, and mean temperature 25°C (Estatistica. Estatisticas do Distrito da Beira 2018 -2022. (2023)). Eight mangrove species occur in the area: *Avicennia marina* (Forssk.) Vierh., *Bruguiera gymnorhiza* (L.) Savigny, *Ceriops tagal (Pers.) C.B.Rob.*, *Heritiera littoralis* Aiton, *Lumnitzera racemosa* Willd.(1803), *Rhizophora mucronata* Lam., *Sonneratia alba* Sm., and *Xylocarpus granatum* K.D.Koenig. Marine species in the area include panaeid shrimp *Fenneropenaeus indicus* (H. Milne-Edwards, 1837) and *Metapenaeus monoceros* (Fabricius, 1798) (Gammelsröd, 1992; de Sousa et al., 2006); and sea turtles *Dermochelys coriacea* (Vandelli, 1761) and *Caretta caretta* (Linnaeus, 1758) (Robinson et al., 2016).

2.2 Mapping

High resolution images from the satellite Digital Globe repository on Google Earth were used in its digital format to identify and delineate natural and planted mangrove stands using a participatory approach with community members, members of the local Natural Resources Management Committee and government officials in a meeting (Aheto et al., 2016). The image covered the area between Ladrão and Mutamba Rivers. The participants identified the planted areas and respective year of planting, and all data were recorded. Mangrove planted areas are easy to identify due to the characteristic square-like shape. The geographical coordinates of the limits of each planting block were collected, as well as 50 randomly selected validation points in planted and natural areas. A field visit to all mangrove planted stands and natural areas was conducted afterwards with the same group of people for data validation. Most planted sites had indicative plates with information on the year of plantation, which helped with data validation.

Image processing and supervised classification followed by visual interpretation was carried out using ArcGIS 10.2 and ENVI 5.1. Data validation was done through field work based on the classes produced in the supervised classification. This allowed the correction of misclassifications generated by the supervised classification algorithm. The procedures for accuracy assessment were applied through random validation points from field sampling using a confusion matrix, which shows the proportion of misclassified and well classified pixels in a matrix. Based on this, the calculated overall accuracy and k coefficient were 72.97 and 0.45 respectively. The natural area was mapped as dense and sparse mangrove area and planted mangrove stands that were identified for different years since 1996.

2.3 Mangrove uses, restoration and forest management

Participatory rural appraisal methods were used to collect historical information on causes of mangrove degradation, current and historical uses of mangroves, the restoration process, and details on the management actions for mangrove sustainable use. The data collected were also used to identify the strengths and weaknesses of the Nhangau mangrove replantation and management program. The study incorporated a mixed approach, combining semi-structured questionnaires used to guide open interviews with key informant and focus group discussions (FGDs), and reports available at government institutions.

Focus group discussions were conducted with several members of the community separated by age, gender and main occupation. Some members of the community were interviewed individually when it was not possible for them to attend the formal group discussions (such as mangrove charcoal producers who were unwilling to participate in these discussions). Questions asked were about people's perception of change in mangrove condition, levels of exploitation, provision of goods and services, engagement in management and replantation activities, functioning of the natural resources management committee, assessment of the community management systems, strengths and challenges, among others. Semi-structured interviews were also conducted with key informants on similar subjects (local leaders, managers, NGOs).

The FGD and individual interviews aimed at four main target groups: members of the local Natural Resources Management Committee (NRMC); Managers and key informants (influential people from the community; government, NGO representatives and local authorities); local community (common mangrove users), and community rangers. Within the community, the main user groups were identified with the help of the NRMC. These were fisherman, fish traders, women (fuel wood and invertebrate collectors), mangrove pole cutters, mangrove charcoal producers, honey producers and students (members of the local environmental club). Key informants included the elderly from the village, the head of Nhangau Administrative Post, project managers from NGOs, government officials who participated in the program from the beginning and influential community members. All villages were visited, and 78 people were interviewed in total.

This flexible approach was useful for data validation and triangulation, and also created opportunities for traditionally more reserved groups to speak such as women, youth and illegal cutters (Asante et al., 2017; Nath et al., 2017). Data processing primarily involved interpreting the qualitative information provided by community members to document all mangrove restoration processes and the community-based management program implemented in Nhangau.

3 Results

3.1 Mangrove uses

From the FDGs and individual interviews with the community members, it was demonstrated that mangroves played an important role in the provision of resources for the community (Table 1). These forests are the main source of poles of all sizes such as "laca-laca" (up to 5 cm wide), small poles (5-9 cm wide), medium poles (9-14 wide) and large poles (more than 14 cm wide), which are used for house construction and domestic utensils. The forests also provide fuelwood and wood to produce furniture, doors and window frames. Women also reported medicinal uses of some

TABLE 1 Mangrove goods and services used by the communities at Nhangau.

Mangrove product/service	Uses
Wood resources	Furniture, construction, domestic utensils Firewood and charcoal
Medicine	Stomach ache
Food	Fish, crab, mangrove snail, honey
Ecological services	Coastal protection, temperature regulation, nursery habitat
Other uses	Traditional ceremonies Traditional Christmas meal

mangrove species, such *X. granatum* fruit used for stomach ache, and general use of mangrove species by traditional healers. Food collection is common in and around mangroves forests, and this includes fishing, invertebrate collection (crab *Scylla serrata* and mollusc *Cerithidea decollata* locally known as "mandombe"), and collection of *Sesuvium portulacastrum* for a traditional plant dish only cooked for Christmas (also known as *mpfixiri*). Many fishing products are sold to middle men from Beira town. Mangroves are also used for honey production, which is sold in Beira town. Community members have more than 10 beehives in the mangroves. The honey is commercialized in local markets and fairs with the brand name "Mel de Mangal de Nhangau" (Mangrove Honey from Nhangau) at the price of USD 8 per 0.5L. The communities also reported that mangrove forest provide protection of the coastline, therefore specific restrictions were instated to reinforce protection of seaward mangroves. The community also mentioned that mangrove forests reduce erosion and protect houses from strong winds. It was also mentioned that the mangroves protected properties of the communities living closer to the coastline during cyclone Idai, which made landfall in the area in 2019. Subsequent cyclones and storms (namely Chalane and Eloise in 2020 and 2021, respectively) were less impactful.

3.2 From forest degradation to building community management structures: the history of the mangroves of Nhangau

The Nhangau community divides the last 45 years in two periods. The first period refers to the late 1980 up to 1996, coinciding with the end of the civil war that prompted an increase of unemployed people (mainly former soldiers) that cut and sold mangroves for subsistence. After deforestation the communities experienced a drastic reduction in fish, shrimp and crab stocks, severe coastal erosion, high temperatures, strong winds and whirlwinds (that destroyed many houses) and reduced availability of wood resources, such as poles for house construction and fish. The second period started in 1996 with mangrove planting and re-establishment of some ecological services, such as temperature regulation and shoreline protection from wind and wave erosion. The community also reported an increase in fish stocks and improvement in their lives in general after mangrove plantations because whirlwinds became less frequent and less destructive.

Mangrove restoration was initiated by the local government and intended to address the impacts of forest degradation on the community's social and economic life. Mangrove restoration started in the late 1990's and was primarily carried out by the then Ministry of Agriculture, who was responsible for the management of the mangrove forests in Mozambique; later continued by new entities with the same role namely MICOA (Ministry of Coordination of Environmental Affairs) until 2014, and PD-TADER (Provincial Directorate of Land, Environment and Rural Development) from 2015. Propagules of *R. mucronata*, *B. gymnorhiza* and *C. tagal* and germinating seedlings of *A. marina* were planted directly in the soil without the intervention of a nursery. The selection of sites and species to be planted on each site was based on the community ecological knowledge of the site. No hydrological restoration was carried out, and the system did not seem to require it.

The mangrove planting was conducted by the local community assisted by the PD-TADER, which provided much of the technical capacity. According to key informants, the community was initially organized into a small group dedicated particularly to planting activities. Later on, NGO's (KULIMA and ADEL-Sofala) and civil society (schools, volunteers and others) were also involved, and the government promoted planting campaigns involving several actors (such as local leaders, government representatives and other influential figures) (Table 2). Meanwhile, the community group (assisted by the government and ADEL-Sofala) was converted into the Natural Resources Management Association of Nhangau (NRMC), a registered community association with legal rights and recognition. Currently the NRMC is in charge of all mangrove restoration activities, and the community is working to build a nursery with the collaboration of several partners, such asMozambES project (a partnership between Eduardo Mondlane University, UniLicungo and Lisbon Nova School of Business) and the SWAMP Project supported by the United States Forest Services International Program. Eduardo Mondlane University is also providing technical support for the establishment of the nursery.

All activities of the NRMC were done on a volunteering basis, but government and NGOs provided 2 monthly basic groceries to NRMC members of the main social bodies. They also provided uniforms for the six community rangers and some basic equipment such as gloves and plastic bags for the nursery. No salaries or other monetary incentives were paid.

According to the members of the NRMC and government officials, the propagules were collected in the dense mangrove

TABLE 2 Mangrove restoration history in Nhangau.

Period	Events	Impacts/Outcomes
1996-1997	Agriculture Ministry visits	Pre-planting studies (ecological and socio-economic studies) Initial planting activities with community participation
1997-1998	KULIMA (NGO) interventions	Financial support to the community (boats, fieldwork equipment)
2001	Mangrove restoration in Nhangau becomes permanently part of the annual agenda of MICOA	Annual government funding for replanting activities (field work equipment; 2-monthly basic groceries for nursery workers)
2006/7 – 2016	ADEL-Sofala (NGO) interventions	Improved stoves Alternative and complementary income generating activities 2-monthly basic groceries for NRMC workers
2010	MICOA minister visit to Nhangau mangroves program	Increased national visibility of the program
2016	Extremely high tides (Njalane and Txondja)	Flooding in areas were mangroves had been cleared, highlighting the protective role of mangroves
2016	Legal registration of NRMC and opening of a bank account	NRMC meets legal requirements to apply for funds from the Government and NGO's; and to receive a percentage of fines collected

areas and then transported and planted in the degraded areas during low spring tides. The preferred species for planting were *C. tagal*, *R. mucronata* and *B. gymnorhiza*, which were also more successful given the predominantly muddy conditions in the area. Some *A. marina* was planted particularly on sandier substrates, but with less success.

The community estimated that 500 ha had been planted, however this study only found 10 ha planted between 1996 and 2017 (Figure 3). Non-quantified natural regeneration in degraded sites has also been identified (Figure 4).

The NRMC has representatives from the three villages of the Nhangau Administrative Post: 14 from Njalane, 10 from Nhangau Sede and 10 from Txondja, to ensure that the particular interests of the three sites are represented. Membership is voluntary upon the payment of a joining fee of 50 MZN (USD 0.8) and monthly fee of 10 MZN (0.16 USD). The association aimed at promoting sustainable management of natural resources and local development, coordinate and supervise community projects implemented by partners and promote self-employment within the community. The committee meets ordinarily once a year or extraordinarily on the request of Fiscal Council or 30% of the members. These meetings are the main platform for the community to discuss their concerns and find common ground to solve arising issues. Community members that are not part of the NRMC and

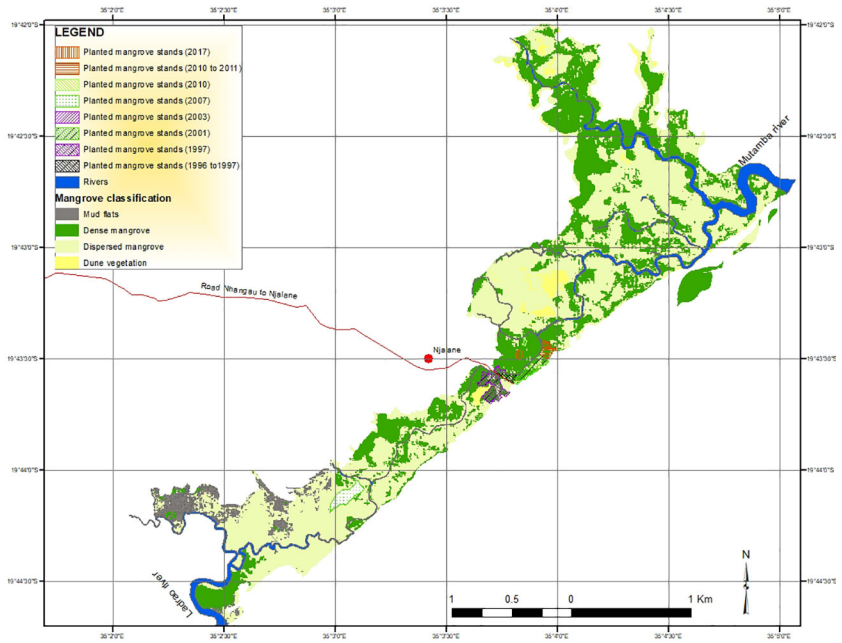

FIGURE 3
Restored mangrove areas and the respective year of plantation.

FIGURE 4
Mangrove restoration facilitated natural regeneration in nearby areas.

that have issues pertaining the mangrove activities can also approach the NRMC members, and if needed, meetings can be organized. The meetings are also used to communicate community concerns to the local authorities and other supporting partners. The structure of the organization is: a general assembly, a fiscal council, a management council (all composed of a president, vice-president and secretary). It also includes an executive council, constituted by a director, coordinator, manager, head of administration; and a financial department, which deals with human resources and finances; and a logistics department. The coordinator and manager are responsible for leading the management, conservation and environmental education department, communication and marketing department, hygiene and calamity department. With this structure, the NRMC intends to provide conservation services to neighbourhood communities, such as providing mangrove propagules and seedlings, training and mangrove restoration. The committee also intends to conduct income generating activities that will benefit the community and support mangrove conservation.

3.3 Management measures

Mangrove cut is allowed for community members only. When in need of mangrove poles for construction, for example, a community member must submit a request to the committee, which will indicate a person to accompany the applicant to the mangrove forest and harvest the poles observing sustainable procedures. For instance, in order to protect the coast line against erosion, seaward mangrove cut is prohibited. Communities are also stimulated to cut trees partially, and not the main trunk. Depending on the amount of cut poles, the cutter may be requested to plant a similar amount in a degraded area, or to replace naturally dead plants in planted areas. If a non-authorized person is found with mangrove poles, he/she will either take a penalty from the Committee (if a member of the community), for example working for the committee for several days or paying a fine varying from 0.8 USD to 1.6 USD; or will be handed to the local authorities and prosecuted (if from another community). The community is also allowed to collect fuelwood (wood debris) for domestic consumption only. Mangrove cut in replanted sites and mangrove charcoal production is not allowed in Nhangau, and this goes in accordance with the national legislation. The national legislation also prohibits commercial exploitation of mangrove poles.

The community rangers indicated by the NRMC are also responsible together with the government-employed rangers, to collect a fee from wood loggers and charcoal producers from nearby terrestrial forests (1.0 USD for each bag of charcoal), as commercialization of mangrove poles and charcoal is forbidden by law. Despite this, it is known that mangrove poles and charcoal is produced illegally in Nhangau. When caught by rangers, mangrove poachers are handed to local authorities and charged a fine. The

illegal products are kept by authorities and donated. Twenty per cent of the fees and fines should return to the community and be used in community works. The other sources of income to the NRMC are monthly fees from members, 50% of the fines charged for transgressions reported by the committee and entrance fee (50 USD) charged to students, tourists and other visitors to the Nhangau mangrove restoration area. The NRMC is also providing mangrove restoration services to support conservation activities, such as the construction of the new headquarters of the NRMC.

The management measures at Nhangau can be synthetized in three main components:

i. Reduction of extractive uses

Implemented through the introduction of alternative and complementary income-generating activities (IGA), and alternative sources of domestic firewood. NGOs KULIMA and ADEL-Sofala played a key role in promoting demonstrative alternative IGA such as beekeeping, aquaculture, natural medicine gardens and seedling production. According to our interviews, beekeeping and the natural medicine garden provided complementary source of income to more than 50 people altogether. The NGOs also promoted the production of improved energy-efficient stoves. These stoves are made with local clay, and have a specific structure that slows down firewood burn, therefore lasting longer. This activity was encouraged both as an alternative source of income (stoves were sold within the community and to other areas) and as a means to reduce charcoal consumption. ADEL-Sofala also encouraged the community to plant casuarinas (*Casuarina equisetifolia*) as an alternative source of domestic fuelwood. This project is currently interrupted due to lack of funding to pay salaries to nursery workers and other consumables such as plastic bags.

All actors (government, NGO, NRMC and community in general) agree that mangrove cut has reduced significantly within the community, but they point out that there are illegal cutters from outside the community cutting mangroves in the natural and planted stands. The community struggles to control the invasion of such groups due to the lack of human, material and financial resources.

ii. Continuous awareness and planting

Both government and NGOs were involved in the initial stages of community awareness and in building community capacity on mangrove and environmental related issues. The NRMC invites the community for regular meetings, where people discuss and are informed of the legal procedures for mangrove exploitation and sanctions that are applicable to offenders. Local regulations for mangroves and other natural resources exploitation are also discussed in these meetings (for example mangrove cut near the houses is not allowed) (Table 3). These meetings are also a platform where the community can voice their concerns and discuss the solution to problems that arise.

As a result, the community had a very strong awareness of the importance of mangroves (for example, all interviewees from the community could mention at least three mangrove goods or ecological services), and passes the message to each other and to newcomers. The NRMC coordinates most of the planting and other activities among the community and local schools, with the support of ADEL-Sofala and government institutions, or autonomously.

iii. Law enforcement

The local government works closely with the NRMC and its community rangers for the enforcement of the regulations and procedures, however anyone from the community can denounce offenders. The institutions involved in law enforcement include the Provincial Directorate of Sea, Inland Waters and Fisheries and DP-TADER in collaboration with the coastal police. The authorities have reported the seizure of thousands of mangrove poles and charcoal bags confiscated inside mangrove areas as well as along the road linking Nhangau to Beira town. One of the most relevant actions of the municipal authorities was the dismissal and prosecution in 2017 of the then chief of the Administrative Post of Nhangau, accused by the NRMC of ordering the clearing of 1.5 ha of planted mangrove for personal purposes (Mauricio, personal communication).

According to the decree 12/2002, illegal products and means used for extraction and/or transport must be confiscated by competent entities (including the NRMC) and a fine must be charged. At Nhangau confiscation was applied only to the products. Confiscated products are donated to schools, hospitals, orphanages and other state institutions, or sold by public auction.

However, the implementation of the legislation remains a challenge for the NRMC. Issues include the lack of alternative resources for the community, as one member of the NRMC said herself: “We talk to people about not cutting mangroves, but even us, members of the NRMC, we struggle when we need poles to fix our houses”. The NRMC also struggles to act over people from outside the community. Nhangau is part of Beira municipality and relatively close to it. The demand for poles for house construction from Beira is high, and sometimes involves people with more resources that NRMC. Another member of the community reported episodes were mangrove cutters had cars, boats and even machetes that made her feeling threatened. “What could I have done, as I was alone and had no means to call for help?”, she said.

TABLE 3 Local rules for mangrove exploitation in Nhangau.

Institutional arrangement	Prohibitions		Permissions
	Activities	Sanctions	
National law or regulation	Commercial exploitation of mangrove poles or wood	Fine (167 USD); confiscation of goods and equipment	• Customary exploitation of wood products
	Production of mangrove charcoal		
Local rules	Cutting/ transporting more than 35-40 poles	Fine 0.8 – 1.7 USD or compulsory planting	• Sustainable cut in designated areas • Cut for bridge construction in widened mangrove creeks • Compensatory mangrove replanting for illegal cutters

4 Discussion

The results of this study indicate that 10 ha of mangrove have been replanted in 21 years (average 0.47 ha planted every year) at Nhangau. This reforestation rate is smaller than that of the Limpopo Estuary, where more than 26 ha were replanted between 2010 and 2015 (Bandeira and Balidy, 2016); but similar to that of the Mikoko Pamoja Program in Kenya, where 10 ha have been restored and 0.4 ha are planted every year (Abdalla et al., 2017; Mangrove, 2017). It is significant that the latter is a site where Payment for Ecosystem Services has occurred. Meanwhile additional information is required to fully assess the ecological outcomes of the restoration and management initiatives at Nhangau. For example, satellite images from the region show that mangrove planting has promoted natural regeneration of nearby mangroves in an area that was not estimated by this study. Passive restoration is a process where mangrove planting creates conditions for other parts of the forest to regenerate naturally (Lewis, 2005 ; Corbin and Holl, 2012). It has been documented elsewhere (such as at the Limpopo Estuary in Mozambique, Gazi Bay in Kenya and Pichavaram in India) that this may account for more than 30% of the total recovered area in a forest (Bosire et al., 2003; Selvam et al., 2003; Bandeira and Balidy, 2016). This information is important to assess the outcomes of the management system and to what extent the conservation goals are being met.

When looking at the critical enabling conditions for successful management of natural resources as described by (Agrawal, 2003), one can see that the mangrove management system of Nhangau possesses several key elements of success and that the weaknesses of the model lie in the "External environment" criteria (Figure 5).

There are several positive aspects about the system at Nhangau that have also been seen in successful models across the globe such as Gazi Bay (Kenya), Trang (Thailand) and Lyngayen Gulf (Phillipines) (Table 4). One of the key elements of success is community awareness on the importance of mangroves (Shunula, 2002), in this case possibly highlighted by the impacts experienced after mangrove deforestation in the area. This awareness gave the community a high sense of responsibility reflected in the continuing replanting, self-awareness raising and self-enforcement. The community also feels empowered by the fact that they were able to institute and enforce measures on their resources. These aspects are crucial to achieve community support for mangrove sustainable management and conservation (Shunula, 2002). The fact that mangrove restoration as well as restoration of mangrove ecological services was successful also encouraged the community to engage and maintain sustainable practices of mangrove exploitation.

The external and prolonged assistance provided by the government and NGOs (who worked in partnership) was almost permanent and consisted of technical, financial and moral support to the community, in addition to community training and basic tools for conflict resolution. The lack of alternative IGA is often pointed as one of the main impediments for communities to abandon unsustainable practices of mangrove exploitation (Damastuti and De Groot, 2017). At Nhangau there has been demonstration of various activities, beekeeping and a medicinal garden in particular contributing significantly to the income of several families. There has also been a gradual transfer of responsibilities in the leadership of the mangrove planting, awareness and law enforcement to the communities. However, the communities need more support to increase the number of families working in such activities, and to get involved in new ones. The community expressed interest in aquaculture, for

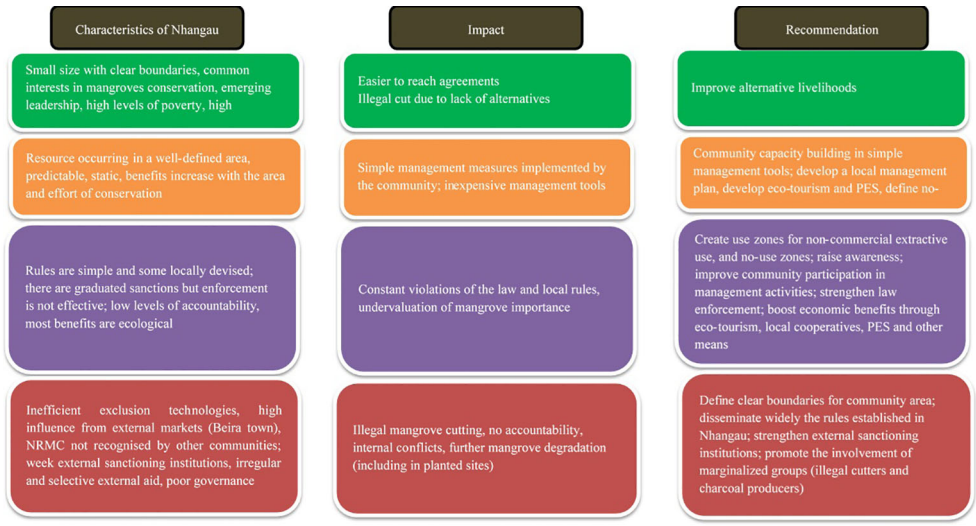

FIGURE 5
Analysis of the critical enabling conditions for natural resources management (Agrawal 2003) and recommendations for improvement for the Nhangau community-based management system. Green: Community characteristics; Orange: Resource characteristics; Purple: Institutional arrangements; Maroon: External environment.

TABLE 4 Factors contributing to success or failure of community-based mangrove management initiatives.

		Where seen
Positive aspects	Clear limits of community area	Trang
	Existence of mangrove reserve area	Trang; Gazi Bay
	High social capital and local autonomy	Trang
	Bottom-up decision making	Surodadi
	Conflict management	Trang
	Community awareness and appropriation	Trang; Gazi Bay; Lingayen Gulf; Surodadi, Limpopo
	Mangrove rehabilitation	Gazi Bay; Surodadi; Limpopo
	Adequate external assistance	Trang; Gazi Bay; Surodadi; Limpopo
	Successful (pilot) livelihood projects	Lingayen Gulf; Surodadi; Limpopo
	Carbon trade and ecotourism	Gazi Bay
	Law enforcement	Lingayen Gulf; Limpopo
Negative aspects	Low community involvement	Mida Creek, Braganca
	Community unequal representativeness	Lingayen Gulf
	Poor relationships between stakeholders	Mida Creek
	Poor local leadership	Bragança
	Lack of financial and technical support	Lingayen Gulf; Kien Giang
	Poaching and poor enforcement	Mida Creek; Kien Giang, Brangança;
	Lack of IGA	Mida Creek; Bragança
	Political conflicts	Bragança
	Legislation conflicts	Bragança
	Poor decision making	Kien Giang

Green and red indicate positive and negative aspects identified at Nhangau respectively.

instance, which would reduce fishing pressure and provide livelihood. High investment is necessary as a starting point, and the community has no means at the moment.

The main negative tipping point in the community-based management system at Nhangau is little law enforcement and compliance, and in this matter, Nhangau represents much of what has been seen elsewhere in the WIO Region and other developing countries (Machava-Antonio et al., 2020). At Nhangau there is both lack (or weak) institutional capacity, and political issues which provide conditions for non-compliance with local laws and regulations, mostly without liability of violators. Nhangau is part of the Beira Municipal District, under the governance of a different party from that of the provincial government, thus many decisions are taken in view of short-term political benefits rather than conservation and long-term well-being of the population. There is a weak follow-up of the cases when seizures are made by the police or other enforcement entities. Offenders are released shortly afterwards and without penalties. The NRMC also lacks the means of policing and authority over outsiders and even some members of their own community. Being located close to a major urban center, Nhangau supplies charcoal and mangrove poles to Beira town. As a result, mangrove wood and pole cutting did not cease and there is an illegal mangrove charcoal market known to the authorities. At the institutional level, there is poor communication between government institutions with overlapping jurisdiction over mangroves (for example provincial directorates of MTA and the Ministry of Sea, Inland Waters and Fisheries – MIMAIP), and weak inter-institutional coordination resulting in redundancy of efforts. Despite being one of the first mangrove rehabilitation sites in Mozambique, the documentation was very poor, and scientific studies on ecology and socio-economy are very scarce. Therefore, the scientific basis for decision making is weak to non-existent, and there is also a risk of repetition of mistakes from the past. In addition, current activities may not be accurately monitored, as demonstrated by the disparity between the area that the community believed to have planted and the area found by this study.

Many local mangrove cutters and charcoal producers claim that their rights are being violated since this type of activity has always been tolerated in the area and that they have no alternative IGA. This position results in non-compliance and people shifting cutting sites to another one where enforcement is less rigorous and also creates a tense environment in the village between the two sides (poachers vs. law enforcers). This situation may be indicative of inadequate consultation before the implementation of management measures (Chen et al., 2005) and could be minimized with a management plan with clear zoning indicating no-use zones and multiple use zones, where mangrove cut is regulated (minimum sizes, rotational cut, closure periods and other adequate measures), as seen at Kenya and Thailand (Sudtongkong and Webb, 2008; Mangrove, 2017). Additionally, it is important to ensure that alternative sources of wood are provided. In this context *Casuarina* species. may not be adequate as it is an exotic species and may alter habitat functionality. Species such as *Thespesia populnea* have been successfully used in other places (Bandeira and Balidy, 2016; Warrier, 2010), but other fast-growing native species may also be considered. No compliance is also often a result of an inadequate management strategy for decision making (top-down vs. bottom up), and inappropriate strategies to encourage community participation (self-mobilized vs. manipulative) (Damastuti and De Groot, 2017).

There is also a need to review the incentives system in ways that the people involved in replanting and management activities feel that it is worth carrying out these activities. Incentives should be diversified, aligned with conservation objectives and satisfactory for the people involved (Dasgupta and Shaw, 2017). Granting additional rights of use of mangrove resources can be a more sustainable form of compensation in the long run instead of

the current system, which is irregular and expensive. The current system also creates friction between the community and members of the NRMC, who are seen as privileged for having additional support from the Government and NGOs. Similar systems produced the same effect at Mida Creek Kenya and other sites (Chen et al., 2005; Damastuti and De Groot, 2017). A fair incentive system and financial sustainability of the community-based management program can also be achieved by harnessing the potential of the region for the development of community and mangrove tourism, taking advantage of the fact that Nhangau is a mandatory pass for Savane beach tourists.

The NRMC lacks financial sustainability due to exiguous membership fees, few visitors and incapacity of the system to deliver their respective percentages on fines and fees. Payment for Ecosystem Services (PES), including the voluntary carbon market, is another potential source of income for community development to be considered (Locatelli et al., 2014).

The community-based management initiative at Nhangau achieved important milestones such as community awareness, engagement and successful restoration. It is certainly also a potential tool for mangrove conservation as demonstrated by the program's outcomes. However, the program is threatened mainly by poor law enforcement, finanacial constraints and alternatives for the community. Community empowerment and more involvement of the local authorities to address mangrove use at several levels (cutters, transporters and final consumers) are necessary. Nhangau is a replicable model for mangrove replantation and community involvement for the rest of the country, however the management component needs improvements before it can be reproduced.

5 Study recommendations

In order to increase the success of the mangrove restoration program at Nhangaau, the following recommendations are made:

- To strengthen the collaboration with the government institutions, in order to ensure that offenses to mangrove regulations are dealt with accordingly. This includes Beira Municipality, the Provincial Directorates of the Ministries of Land and Environment, the Ministry of Sea, Inland Waters and Fisheries, and other relevant entities;
- The reinforce the capacity of surveillance of mangroves, increasing the number of rangers and equipping them with the necessary tools for the job;
- To increase the fee charged over illegal producers of mangrove charcoal and poles, and reinforce other mechanisms for the implementation of local and national legislation on what regards to mangrove management;
- Create and strengthen partnerships with other institutions that can provide technical and scientific support to the program. This includes universities and other relevant research institutions. Such information must be used to support decision making;
- To conduct climate-change vulnerability assessments, in order to ensure that the restored areas will protect the most vulnerable zones; and that restoration efforts will not be nullified by the impacts of climate change;
- To develop a mangrove restoration monitoring program. Such plan shall include mangrove restoration metrics such as survival rates, growth patterns, mangrove mapping and dynamics (including UAVs techniques), community employment indicators as related with mangrove restoration, protection and derived livelihoods
- To produce a mangrove management plan, which should include mangrove zoning, indicating areas for different activities (e.g.: beekeeping, sustainable cut, degraded areas to be restored), and no-take zones. Such plan should also include specific protection measures for the recently restored areas and naturally regenerated areas;
- To work further on the development of a nursery to grow *A. marina*. This species is climate smart and key to create forest resilience, and, as it occurs naturally in the system, it should also be considered for restoration. Direct planting of *A. marina* is challenging, thus the high unsuccess rate that was reported with this species;
- To develop alternative sources of wood, other than *Casuarina* sp, *Thespesia populnea, Hibiscus tiliaceus* and other fast-growing native alternatives must be considered;
- Explore additional options for IGA, e.g.: the medicinal properties of mangrove species. Mangrove species such as *B. gymnorhiza*, *S. alba* and other non-mangrove species are used as source of food in Asian countries. Mangrove fauna species, such as gastropods *C. decollata* and *Terebralia palustris* can also be exploited commercially for food production.

6 Conclusions

This study described and analyzed mangrove co-management experiences at the Nhangau administrative post in central Mozambique. After unsustainable use of mangrove resources had caused several socio-ecological negative impacts, the community, assisted by the local government and NGOs, engaged in several best practice and sustainable management actions for mangrove restoration and conservation, through a successful mangrove restoration and conservation program. The community created a Natural Resources Management Committee, which is responsible for mangrove plantation and oversight of planted and natural areas, law and local regulations enforcement, promoting alternative income generating activities as well as continuous raising awareness. These actions resulted in the rehabilitation of 10 ha of mangrove, increased community awareness, development of (demonstrative) alternative IGA, and development of local procedures for mangrove resources exploitation. Other program outcomes include community empowerment and capacity building,

and the recovery of several ecosystem services with concomitant improvement in community well-being. Law enforcement, more alternative IGA and building robust financial sustainability to the program are the main issues to be targeted to improve the community-based management system at Nhangau. A number of recommendations to improve the restoration program were made, tackling mostly on legislation reinforcement and strengthening the management mechanisms. The study makes a global contribution to the understanding of the interface between community-based mangrove management and the role of stakeholders as well as understanding the factors behind positive and negative outcomes of such initiatives. Future studies at Nhangau should focus on baseline ecological aspects of the forest (forest structure, physico-chemical parameters, regeneration, change detection), including comparisons between replanted sites and natural stands for a better understanding of restoration of ecological services from mangrove and to support decision-making.

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 studies involving humans were approved by Nelson Mandela University-Department of Marine Botany. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

FD: Writing – original draft. CM: Conceptualization, Formal analysis, Investigation, Methodology, Resources, Writing – original draft. SB: Conceptualization, Validation, Writing – review & editing. JA: Validation, Writing – review & editing, Funding acquisition. HB: Formal analysis, Writing – original draft.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1337678/full#supplementary-material

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Framing seascape connectivity modeling to prioritize marine conservation effort in China's coastal sea

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Anthropogenic disturbances and climate change are projected to become leading drivers of biodiversity loss and ecological connectivity degradation in marine ecosystems. However, the lack of quantitative understanding for seascape connectivity modeling hinders our ability in providing large-scale marine conservation guidance. By applying well-established theories and tools in landscape connectivity study and marine-specific indicators, we proposed a framework to evaluate the resistance-based seascape connectivity among marine habitats and Marine Protected Areas (MPAs) across China's coastal sea. The spatial vulnerability of marine habitats was further assessed to prioritize conservation effort. Our results showed that 82% of China's coastal seas were covered with middle to high level of resistance for migratory marine species, mainly due to concentrated inshore anthropogenic disturbances such as ship traffic and ocean pollution. With the modeled migration distances of different species guilds from short-range (25 km) to long-range (100 km), the area percentage of connected corridors increased from 12.02% to 44.68% in the study area. Vulnerable areas were identified as high resistance (high exposure) and abundant threatened species (high sensitivity) but with small number of connected corridors (low adaptive capacity), primarily distributed in offshore regions of Yellow Sea and East China Sea. Collectively, inshore regions with high anthropogenic disturbances warrant regulation and mitigation in major coastal cities and ports. While the lack of interconnected networks for offshore regions prioritized efforts to enhance seascape connectivity through the establishment of MPA network. Sensitive species groups require more attention in future marine conservation, including threatened populations, climate refugees of marine species, and species with limited movement ranges. This study highlights the potential of developing seascape connectivity model based on landscape theories, and the importance of seascape connectivity study in guiding evidence-based marine conservation strategies.

KEYWORDS

conservation priority, coastal area, dispersal distance, marine function zone, marine spatial planning, vulnerability assessment, migration

1 Introduction

Global marine ecosystems have been threatened by intensified climate change and anthropogenic disturbances, exacerbating marine biodiversity loss in oceans (Duarte et al., 2020; Dai et al., 2023; Pigot et al., 2023; Saintilan et al., 2023). The IUCN Red List of Threatened Species maintained records of up to 630 endangered marine species by 2020, and 34 marine species were declared extinct (IUCN, 2020). Recognizing the pressing need for marine biodiversity conservation, global initiatives such as the Sustainable Development Goal 14 highlights the significance of preserving marine habitats and biodiversity (Griggs et al., 2013), and the Post-2020 Global Biodiversity Framework emphasizes the imperative need of expanding ocean protection efforts (Erdelen, 2020). Consequently, there has been a growing awareness of the challenges surrounding the protection of global marine ecosystems with scientific guidance (Halpern et al., 2019).

To eliminate the gap between conservation goals and the current status of marine ecosystems, seascape connectivity studies have emerged as valuable tools for providing guidance for effective and scientific marine conservation and management (Virtanen et al., 2020). Seascape connectivity is defined as the spatial linkage across marine ecosystems, which measures potential ecological processes at a seascape scale, including species migration and larval dispersal throughout various seascape structures, and the likelihood of spatial pathways taken by organisms (Treml et al., 2008; Olds et al., 2016; Pittman, 2017). Seascape connectivity studies have been instrumental in informing marine conservation planning across different spatiotemporal scales because the metapopulation persistence of marine organisms is often determined by seascape connectivity through ontogenetic migration and larval dispersal (Olds et al., 2016; Weeks, 2017; Virtanen et al., 2020). Conservation prioritization facilitated by seascape connectivity models empowers decision makers to allocate resources strategically, enhancing the efficacy of marine spatial planning in attaining crucial conservation goals (McLeod et al., 2009; Engelhard et al., 2017). The vulnerability assessment framework, which incorporates exposure, sensitivity, and adaptive capacity, is often used as a comprehensive framework to identify conservation gaps with high ecological risk and to guide socio-ecological management (De Lange et al., 2010; Dudley et al., 2021). Although seascape connectivity quantifies the adaptive capacity and resilience of marine ecosystems, it has yet to be incorporated into the broader framework of vulnerability assessment to provide thorough and multifaceted insights into marine spatial conservation planning (He et al., 2018).

The connectivity of marine ecosystems faces substantial threats primarily driven by climate change and anthropogenic disturbances. Global warming has led to severe changes and anomalies in ultraviolet (UV) radiation, ocean acidification, and sea surface temperature, predominantly attributed to human influence (Abadie et al., 2018; Barneche et al., 2021). Specifically, in China's coastal sea for the past 40 years, the sea surface temperature (SST) of offshore China has increased by 0.16 °C/decade and accelerate to 0.45 °C/decade (1.88%/decade) over the past decade, which is almost twice the warming rate of the global mean SST (Qi et al., 2019; Tang et al., 2020). These environmental stresses threaten a rich variety of key biogenic habitats (i.e., mangroves, seagrass, coral reefs, and salt marshes) distributed along and off the coast. In addition to climate change, 59% of global marine ecosystems are directly threatened by human activities, including fishing efforts, ship traffic, and land- or aquatic-sourced pollution (Halpern et al., 2019). In connectivity studies, these factors are listed as resistances that hinder the movement of marine organisms among ecosystems and increase the physiological costs associated with migration through a particular environment (Zeller et al., 2012). While landscape connectivity studies have widely applied the quantification of resistance as organisms move through landscape patches (Dickson et al., 2017; Hilty et al., 2020), these climatic or anthropogenic resistances may be interpreted with different sources and functions in the context of seascape connectivity modeling. This necessitates a thorough examination of migration resistance in marine ecosystems using resistance-based connectivity modeling to advance seascape connectivity-based conservation efforts.

Seascape core patches in marine conservation networks play a pivotal role in the ontogenetic migration of marine organisms (Kong et al., 2021). Marine Protected Areas (MPAs), as a type of core patch, are designed as specialized areas for the conservation of marine resources, environment, and biodiversity. MPAs contribute to seascape-scale conservation by safeguarding critical habitats within the local ecosystem and acting as effective components of the broader marine network (McLeod et al., 2009). MPAs have been widely recognized as effective tools to restore and preserve marine biodiversity, especially in coastal exclusive economic zones (EEZs), where invaluable biodiversity is heavily affected by anthropogenic disturbances (Sala et al., 2021). In addition, the key natural habitats of mangroves, salt marshes, seagrass, and coral reefs in marine systems also play critical roles as biofilters, nurseries, and foraging sites to improve species ontogenetic migration and seascape connectivity (Mumby et al., 2004; Olds et al., 2013; Olson et al., 2019). The larval dispersal of marine species may rely heavily on nursery habitats to supply juvenile populations, depending on the proximity and area of the connected network of MPAs and key habitats (Weeks, 2017). In addition to acting as potential core patches in connecting neighboring habitats, MPAs and key habitats maintain the function of mitigating resistance along migration corridors (Jacob et al., 2020), especially in filtering coastal pollution, providing alternative habitats near marine exploitation, and enhancing population resilience against fishing efforts (Wallentinus and Nyberg, 2007; Game et al., 2009; Ling et al., 2009). The interconnected networks of MPAs and key habitats are efficient in maintaining and restoring marine biodiversity and ecosystem resilience to disturbances (Swadling et al., 2019). Although previous research on connectivity modeling has acknowledged the positive impacts of MPAs and key habitats (Galpern et al., 2011; Zeller et al., 2012; Cecino et al., 2021), the contributions and responses of core marine habitats in framing seascape connectivity models are still not well addressed.

Here, we modeled resistance-based seascape connectivity based on landscape theories and tools and assessed the vulnerability of

marine ecosystems to identify priorities in marine conservation planning. We integrated the positive effects of MPAs and key habitats as offset factors in resistance modeling in China's coastal seas. The resistance-based seascape connectivity of marine species guilds with different migration distances was projected. Additionally, by integrating resistance and connectivity maps with the distribution of threatened marine species, we identified vulnerable areas following the vulnerability assessment framework. Areas with high levels of resistance (exposure) and threatened species distribution (sensitivity) but not well connected by corridors (low adaptive capacity) were identified as vulnerable areas in marine conservation, with critical implications for prioritizing marine conservation efforts.

2 Materials and methods

2.1 Study area

China's coastal sea is of great significance for marine biodiversity preservation and serves as a critical zone for supporting the lifecycle of global marine species. This region consists of four parts: Bohai Sea, Yellow Sea, East China Sea, and South China Sea. However, this coastal region also experiences high levels of anthropogenic disturbance from both terrestrial pollution and marine human activities. According to the Ministry of Ecology Environment of China in 2018, 43% of the monitored land-sourced sewage outfalls failed to meet national standards, such as major pollutants of total phosphorus, ammonia nitrogen, and suspended matter. Extensive anthropogenic disturbance has become the major challenge in China's coastal sea, including ship traffic, fishing efforts, and nearshore pollution, exacerbating the degradation of coastal ecosystems and the loss of seascape connectivity and resilience. In addition to human disturbances, climatic effects exert great pressure on marine species in the coastal seas of China. In this region, over 250 MPAs were established to provide additional protection to 9.3% of China's coastal sea. In this study, we used the spatial extent of the Marine Function Zone (MFZ) of China's coastal sea as our study area to model resistance-based seascape connectivity, which is the near-coast sea crucial to natural resources, biodiversity protection, and marine socio-economic development (Lu et al., 2015).

2.2 Mapping resistance and offset factors

With reference to well-established theories and methods of landscape connectivity, our methodology is provided in three parts (Figure 1): (1) estimating the resistance surface using anthropogenic and climatic disturbances, as well as offset effects of key habitats and MPAs based on patch sizes. The landscape change datasets were substituted with marine function zones to serve the essential function of regulating various seascape types within the marine environment. The proposed framework is the first to incorporate posititve influence of key habitats and MPAs in resistance modeling. Connectivity analysis was performed using the Linkage Mapper Tool, leveraging graph theory and least-cost theory to accurately measure the spatial arrangement of corridors and the degree of permeability within the landscape (McRae and Kavanagh, 2011; Mitchell et al., 2013); and (3) assessing spatial vulnerability from the three aspects of exposure (represented by resistance), sensitivity (threatened species distribution), and adaptive capacity (connected corridors) (Pacifici et al., 2015).

Based on landscape connectivity studies and the characteristics of marine ecosystems, we selected a series of indicators to model human disturbances and climate change (Table 1) and identified potential core patches in the connectivity network. Resembling land use and cover change in terrestrial connectivity modeling, the MFZ (Supplementary Figure 1) was used to specify the domain function of nearshore marine area for the usage and regulation based on environmental, biological, and social-economic conditions (Lu et al., 2015). The main types of MFZ included protected and reserved areas, recreation, tourism, fishing, industry, mining, shipping, and reclamation (Supplementary Table 1). The spatial

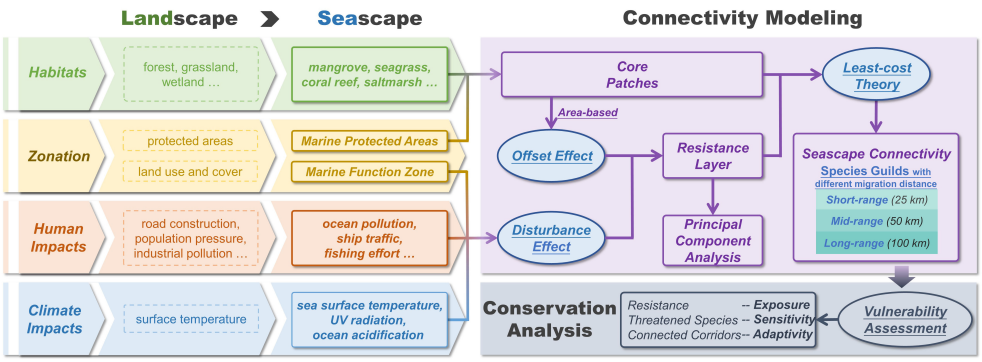

FIGURE 1
Framing seascape connectivity modeling and conservation analysis. The datasets used in the marine system were selected based on the landscape system into four categories. They were further transformed to calculate the disturbance and offset effects in marine ecosystems. Least-cost theory from landscape modeling was applied to seascape connectivity for species guilds with different migration distances (25 km, 50 km, and 100 km). Vulnerability assessments regarding resistance-based connectivity and threatened species were performed using modeling results to prioritize conservation efforts.

TABLE 1 Spatial datasets used in seascape connectivity modeling.

Types	Factor/Objectives	Resolution	Data Sources
Marine Protected Area	Marine Protected Areas in China	Vector	MNR, 2011
Habitats	Distribution of Mangrove in China	Vector	Zhang et al. (2022)
	Global Distribution of Saltmarsh	Vector	UNEP, 2015
	Global Distribution of Seagrasses	Vector	UNEP, 2020
	Global Distribution of Coral Reefs	Vector	UNEP, 2018
Species Distribution	IUCN Red List of Threatened Marine Species	Vector	Brooks et al. (2016)
Climate Change	Sea Surface Temperature Anomalies	1 km	Halpern et al. (2015)
	Ultraviolet Anomalies	1 km	Halpern et al. (2015)
	Ocean Acidification	1 km	Halpern et al. (2015)
Human Disturbance	Ship Traffic	0.05°	Shipfinder, 2020
	Fishing Effort	0.05°	Shipfinder, 2020
	Marine Function Zone in China	Vector	MNR, 2011
	Reclamation	Vector	Sajjad et al. (2018)
	Ocean Pollution	1 km	Halpern et al. (2015)
	Inorganic Pollution	1 km	Halpern et al. (2015)
	Invasive Species	1 km	Halpern et al. (2015)

MNR, Ministry of Natural Resource of China; UNEP, United Nations Environment Programme.

extent of the MFZ and MPA of China's coastal sea was extracted from spatial planning by the Ministry of Natural Resource of China in 2011, and we also included the updated reclamation zones from a previous study (Sajjad et al., 2018). Salt marsh, coral reef, and seagrass distributions were derived from the global dataset of the United Nations Environment Programme (UNEP, data.unep-wcmc.org/datasets). Mangrove distribution in China was interpreted on a finer scale from remote sensing images in a previous study in coastal East Asia (Zhang et al., 2022).

While road construction and population distribution are prominent factors influencing land ecosystem connectivity (Li et al., 2019), this study utilized ship traffic and fishing efforts to quantify human influences in marine ecosystems (Chen et al., 2022), which generate underwater noise, oil spills, and turbidity that hinder marine species movement and lifecycle (Jonsson et al., 2021). In addition, we included spatial datasets of marine- and land-based pollution potentially resulting from wastewater, which has detrimental effects on marine wildlife migration (Lott, 2022). The shipping density distribution was derived from Automatic Identification System datasets with a 1 km × 1 km resolution in Shipfinder (www.shipxy.com). Fishing effort is represented by the density of fishing ships, and ship traffic is represented by the total density of passenger ships, cargo ships, tankers, and high-speed crafts.

Climatic factors, such as ocean acidification, SST anomalies, and UV radiation anomalies, were also included, which could result in habitat loss and food web alteration in large-scale marine environments and negatively impact species migration and resilience (Berkström et al., 2020). These changes in environmental conditions may hinder marine species movement in local regions, resulting in a range shift in native species (Morelli et al., 2017; Pinsky et al., 2020).The preprocessed datasets (Table 1) were used as inputs to generate the resistance layers and core patches. Ocean pollution, land-sourced inorganic pollution, invasive species risk, and climate change indicators were derived from Halpern et al. (2015) at a resolution of 1 km × 1 km. All the geospatial datasets were scaled to a resolution of 1 km. Spatial analysis and preprocessing were performed using ArcMap 10.4.1.

Mapping resistance from anthropogenic disturbance and climate change is informative for understanding exposure to marine species, and it is the crucial first step in advancing Euclidean distance to resistance distance for functional connectivity modeling with detailed spatial information (Magris et al., 2014; Halpern et al., 2019; Keeley et al., 2021). Here, we adopted a resistance scoring system from landscape connectivity studies to normalize the resistance factors with equal weights, with higher scores representing greater resistance (Theobald, 2010; Li et al., 2019; Trew et al., 2019). Human-induced resistance factors, such as ocean pollution, risk of invasive species, ship traffic, and fishing effort, were divided into five levels based on their percentiles and assigned a resistance score from 1 to 5 (i.e., the highest 20% of the factor was assigned a value of 5, while the 20% lowest was assigned a value of 1) (Supplementary Table 2). Marine climate change factors, such as ultraviolet radiation anomalies, ocean acidification, and SST anomalies, were scored using the same statistical approach to evaluate the impact of climate change. We implemented a scoring system ranging from 1 to 5 for different types of areas within the MFZ. This scoring was derived from expert evaluations of the key functions of the areas, distinguishing between natural and unnatural attributes and assigning scores accordingly. The methodology involved referencing the expert assignment approach utilized in quantifying the effect of different land-use covers within landscape connectivity studies. (Theobald, 2010). As a destructive coastal redevelopment in China, the constructed reclamation area in the MFZ was considered to have the highest level of resistance to species (scored as 5), while aquaculture and fishing zones scored as 3 and tourism zones scored as 1 with the least impact (Supplementary Table 1). Although different species may exhibit varying responses to the aforementioned disturbances, the selected resistance indicators significantly impact a broad spectrum of marine species and imply a seascape-scale resistance

spatial pattern (Doney et al., 2011; Pinsky et al., 2019). The overall resistance score ranged from 0 to 40, ranking from low (0–15), middle (16–29), to high resistance (30–40).

To reveal how resistance was offset by MPAs and key habitats, we calculated the difference in resistance with or without offset factors. Such mitigation effects of core patches on disturbances are positively correlated with their size (Bruno and Kennedy, 2000; Mitchell et al., 2013; Edgar et al., 2014; Shinomiya et al., 2017). Therefore, we assigned an offset score ranging from −1 to −5 (negative as in resistance score for mitigation) based on the level of patch size (with the largest 20% patches in this study scored as −5, while the smallest 20% patches scored as −1 in offsetting resistance, etc.). The overall resistance layer was the accumulation of the scored indicators of anthropogenic disturbance, climate change, and offset factors, with equal weights for each factor. Principal Component Analysis (PCA) was applied to illustrate the contribution and relationship of each indicator in the study area.

2.3 Modeling seascape connectivity

To account for variability in migration distances among marine species (Caldwell and Gergel, 2013), we mapped seascape connectivity at different migration distances based on species guilds with different traits. Resistance-based connectivity modeling developed in landscape ecology utilizes the least-cost path (LCP) to indicate the best possible migration corridors, which is calculated as the path with the least cumulative resistance connecting core patches (Carroll et al., 2012). By adjusting the longest LCP modeled as the migration distance, we were able to investigate how marine species guilds with different migration distances exhibit different spatial patterns of seascape connectivity. Core patches, including MPAs and key natural habitats, were used as connecting nodes in the modeled network to determine the pathways of marine species migration.

The migration distances of many common marine fishes, invertebrates, and their larvae generally range from 10 km to 100 km (Palumbi, 2004). Within this range, we conducted a series of connectivity modeling at different migration distances (Supplementary Figure 3) using the Linkage Mapper Tool (Kavanagh et al., 2012; Cecino et al., 2021). Among these, three representative species guilds were selected (25 km, 50 km, and 100 km) to present the spatial distribution of seascape connectivity. These three selected distances represent the major marine species guilds as short-range (25 km) and mid-range (50 km) species, including *Rhynchobatus immaculatus*, *Odontaspis ferox*, and *Squatina formosa*, and pelagic long-range (100 km) species, including whales, sharks, and tuna. In addition to the LCPs identified by the Linkage Mapper Tool, it also generates a map of rank-based connectivity metrics across the spatial extent, comprising the spatial aggregation of alternative migration pathways based on the prioritization of lower cumulative resistance. The connectivity metrics modeled in this study were derived from multiple habitat types and least-cost distances across a resistance map; specifically, lower connectivity metrics indicate a higher priority for species migration in such a path. These paths are characterized by lower cumulative resistance costs that species encounter when moving across seascape patches. The best paths were identified as LCPs with a connectivity metric value of 0 (i.e., the first path to choose with the least resistance). The actively connected areas, considered as connected corridors, were identified based on ranked connectivity metrics ranging from 0 to 200,000, representing the first 200,000 paths prioritized by species for migration among patches.

2.4 Identifying conservation priority areas based on vulnerability assessment

The identification of conservation priorities in marine ecosystems was based on the vulnerability assessment framework; the resistance map represents exposure magnitude, the spatial distribution of threatened marine species included in the IUCN Red List to represents sensitivity, and a layer of connected corridor numbers to indicates adaptive capacity. The conservation status of the threatened species was classified by IUCN using criteria such as decline rate, distribution area, population size, and distribution fragmentation (IUCN, 2020). These threatened marine species populations, including critically endangered (CR), endangered (EN), and vulnerable (VU) species, are particularly sensitive to both anthropogenic disturbances and climate change (Crozier et al., 2021; O'Hara et al., 2021), making it imperative to maintain a highly connected network for their resilience. The number of threatened species in each area was used as an indicator of the sensitivity and level of conservation demands in that region.

To specify seascape connectivity with different migration abilities, we quantified the spatial distribution of the number of connected corridors throughout the eight species guilds (Supplementary Figure 3), ranging from 0 to 8. Areas with low corridor numbers indicate that only species with long dispersal distances (usually 100 km–150 km) can reach those places, whereas these corridors are not accessible by short-range and mid-range species. Given the significant heterogeneity of biodiversity distribution and connectivity across the four seas in China, we classified the values of threatened species number and corridor number into three levels (low, mid, and high) according to the percentile intervals in each region. For instance, this categorization identified pixels with the highest 33.3% of species numbers in a giving sea as high number of threatened species.

Vulnerable areas were identified as regions characterized by high levels of human-induced and climatic disturbances, as well as the abundance of threatened marine species, but lacking sufficient connected corridors. Based on these three aspects of vulnerability, we categorized four categories with critical conservation implications: (1) highly vulnerable (mid-to-high exposure and sensitivity with low adaptability), (2) vulnerable (mid-to-high exposure and sensitivity with mid-level adaptability), (3) slightly vulnerable (high exposure, sensitivity, and adaptability), and (4) protected (low exposure and sensitivity with mid-to-high adaptability). We then calculated the percentage of area in each category across the four regions.

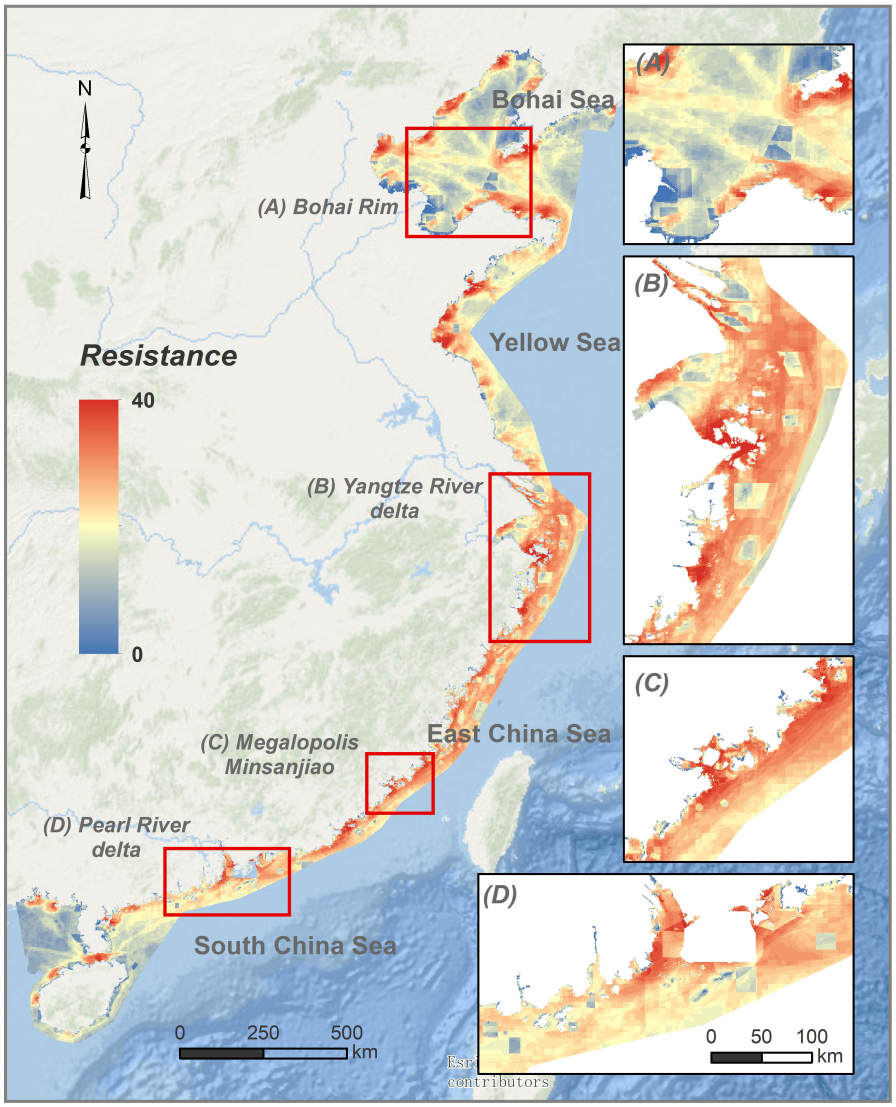

FIGURE 2
Distribution of the overall resistance across China's coastal seas. The high value of resistance in red represents a high level of disturbance to marine species' migration. Four major economic zones were zoomed in to show more regional details: Bohai Rim **(A)**; Yangtze River Delta **(B)**; Megalopolis Minsanjiao **(C)**; and Pearl River Delta **(D)**.

3 Results

3.1 Spatial distribution of resistance

Most of the study area was covered by low to middle resistance, and areas with high resistance were scattered with small patches (Figure 2). Approximately 78.18% of the study area was covered by middle resistance (between 16 and 30), 18.54% of the study area had low resistance (<15), and only 3.28% was covered by high resistance (between 31 and 40). Incorporating the offset effect of MPAs and key habitats into resistance quantification significantly lowered the total resistance within these core patches by an average decrease of 27.88% and a total resistance decrease of 2.14% in the whole study area (p <0.05). The resistance offset effect is especially significant in the East China Sea and South China Sea, where total resistance is high, but many MPAs and key habitats exist. This indicates the effectiveness of protected areas in mitigating anthropogenic or climatic disturbances. The reduced resistance prioritizes the connected pathways to be modeled within or close to these patches in regions such as the Yellow Sea, East China Sea, and South China Sea. The resistance score was distributed with a high-to-low gradient change from the inshore to offshore areas in China's coastal sea. High resistance was mainly identified in the inshore area along the coastline, but the offshore regions of the Bohai Sea and South China Sea had relatively low resistance. The overall resistance varies spatially across the four seas, where the East China Sea and Yellow Sea are covered with higher resistance than the Bohai Sea and South China Sea.

Among all the resistance factors, ship traffic, fishing efforts, and ocean pollution were identified as the key factors. This result was substantiated by examining the relationships between the total resistance distribution on PCA, which revealed cosine similarities

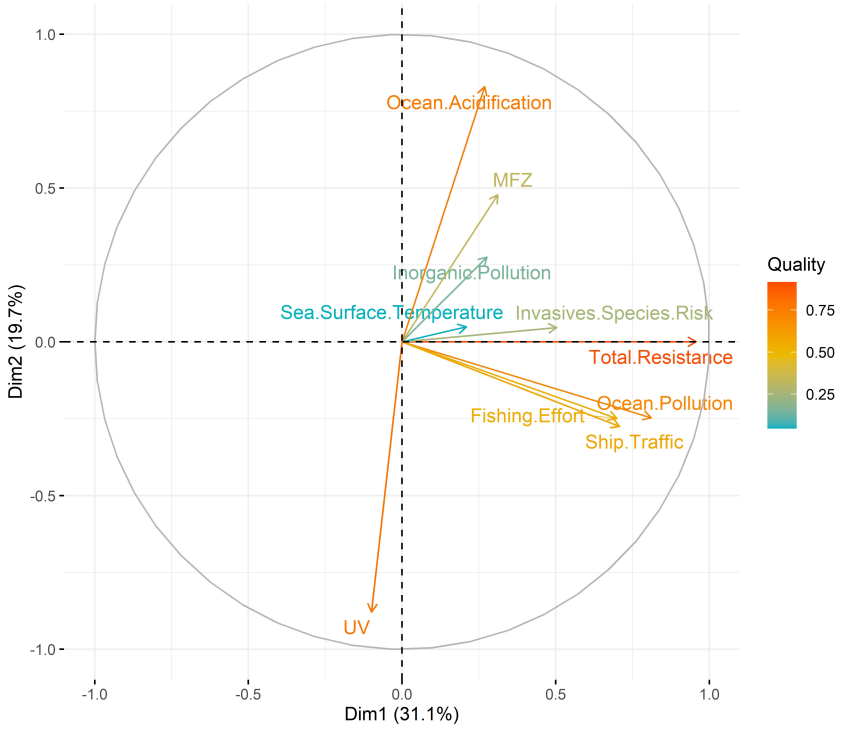

FIGURE 3
Contribution of different resistance factors in the study area (China's coastal sea) based on Principal Component Analysis (PCA). Arrows of resistance distributed close to each other are positively correlated, whereas orthogonal arrows are not correlated. The length and color of each arrow represent the quality of this indicator for the first two key components (Dim1 and Dim2). The correlation between the two variables was stronger when the angle between the arrows was smaller.

of 0.93, 0.95, and 0.96, respectively (Figure 3). The high values of these anthropogenic resistances are spread across the East China Sea and part of the Bohai Sea. Most anthropogenic disturbance indicators, including inorganic pollution and invasive species, are distributed along the coastline as point-source resistance. High resistance values were concentrated in major coastal cities (Shanghai and Yangtze River Delta; Shenzhen and Pearl River Delta) and ports (Tianjin Port and Bohai Rim; Xiamen Port and Megalopolis Minsanjiao), which are regions with intensive coastal development of industry and harbors in the inshore areas.

Climate change indicators, on the other hand, were less related to the spatial patterns of overall resistance (Figure 3), although they showed a latitudinal gradient across China's coastal sea (Supplementary Figure 2C). Ultraviolet anomalies had significant impacts on resistance at higher latitudes (Bohai Sea), whereas ocean acidification appeared to be more severe at lower latitudes (South China Sea).

3.2 Seascape connectivity in different migration distances

The number of LCPs and the area covered by connected corridors increased substantially with higher modeled distances for species migration ability (Figure 4, Supplementary Figure 3), indicating a changing pattern of seascape connectivity from local to broader scales corresponding to different marine species guilds. The number of LCPs in the study area increased from 504 at 25 km, 749 at 50 km, to 924 at 100 km. The percentage of connected corridor areas in the study area (with connectivity metrics ranging from 0 to 200,000) varied from 12% at 25 km, to 26% at 50 km, and reached 44% at 100 km (Figure 4).

Spatially, connectivity for short-range species (within a distance of 25 km), the actively connected networks were sparsely distributed in small fragmented areas. Linkages between inshore and offshore seas were not established, whereas connections mostly appeared among inshore habitats. The number and area of corridors for mid-range species (50 km) were higher than those for short-range species, especially in economic development zones with relatively higher human disturbances (Yangtze River Delta, Megalopolis Minsanjiao, and Pearl River Delta). However, only a part of the offshore core patches in these regions was incorporated into their connectivity network. Corridors for long-range species (100 km) covered the highest proportion of the coastline in both inshore and offshore areas, but the connectivity gaps in the Bohai Sea and Yellow Sea were apparent compared to those in the southern part of China's coastal sea.

3.3 Vulnerability assessment

Across China's coastal sea, our results showed that 18.5% of the total area was identified as highly vulnerable, while an additional 24.0% was categorized as vulnerable. These vulnerable areas are

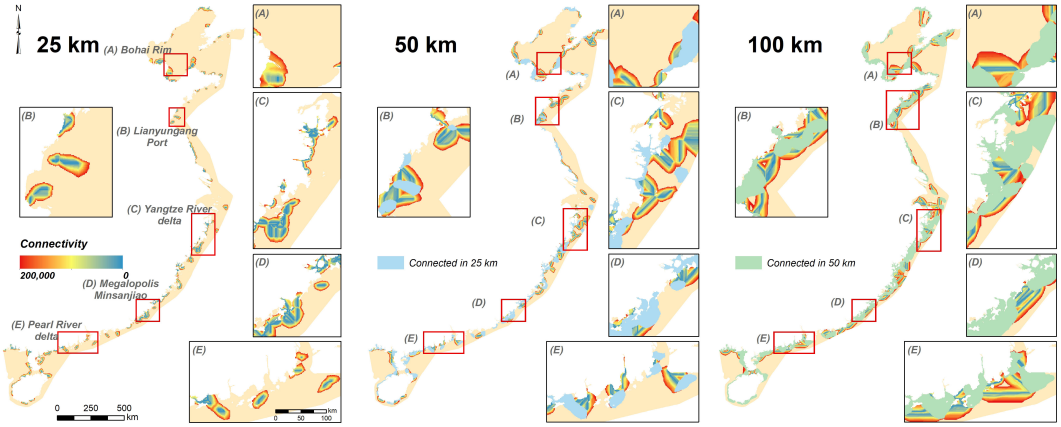

FIGURE 4
Seascape connectivity of China's coastal sea for species guilds with different migration distances, including short-range (25 km), mid-range (50 km), and long-range (100 km) species. With the least-cost path (rank-based connectivity metric of 0) in the center, the actively connected areas (rank-based connectivity metrics of 0 to 200,000) surrounded are the corridors prioritized by organisms while moving across patches with minimal cumulative resistance. Panels on the side of each map were detailed connectivity maps for major coastal economic zones, including Bohai Rim **(A)**, Lianyungang Port **(B)**, Yangtze River Delta **(C)**, Megalopolis Minsanjiao **(D)**, and Pearl River Delta **(E)**.

mainly distributed in the southern Bohai Sea and offshore areas of the Yellow Sea and East China Sea. In contrast, only 4.1% of the study area was categorized as protected, mainly in the inshore region of the northern Bohai Sea and western South China Sea. Among the four regions studied, the Bohai Sea had the highest percentage of highly vulnerable areas, accounting for 23.7% of its total area, where a large number of threatened marine species and high resistance scores were present, but a small number of corridors were shown to support such biodiversity. South China Sea has the largest area under protection, accounting for 9.4% of the region. The Yellow Sea has the smallest proportion of areas in all vulnerable categories combined, with 40.7% of the areas classified in the three vulnerable categories and 4.4% in the protected category. The East China Sea exhibited the largest areas in the three vulnerable categories combined, with 46.5% covering almost half of the region, primarily in offshore areas.

4 Discussion

4.1 Framing resistance-based seascape connectivity

Globally, marine ecosystems are facing increasing threats from both anthropogenic disturbances and climate change, endangering the invaluable biodiversity and lifecycles of marine species (Doney et al., 2011; Griggs et al., 2013; Hilborn, 2016; Halpern et al., 2017). There is a pressing need to assess resilience and vulnerability in marine ecosystems on a seascape scale to guide large-scale marine conservation efforts with ample scientific evidence (Chin et al., 2010; Pacifici et al., 2015). In this study, we framed a seascape connectivity model to provide implications for marine conservation implications. Connectivity modeling, coupled with marine species distribution, allows us to examine the spatial patterns of vulnerability in coastal regions (Wilson et al., 2020).

Threats to marine ecosystems are especially intense in coastal seas, where heavy human activities occur, including coastal urban pollution, ship traffic, and exploitation of marine resources (Montefalcone et al., 2010; Puritz and Toonen, 2011). In China's coastal sea, marine biodiversity is exposed to high levels of anthropogenic disturbances and climate change impacts with the rapid coastal economic development of China (Jiao et al., 2015; Xu et al., 2016), raising concerns about regional seascape vulnerability. Human activities have challenged seascape resilience at a regional scale, with a concentrated distribution in major economic zones. Specifically, the inshore regions of major coastal metropolises and ports in China are exposed to concentrated and intensive human disturbances, such as the Bohai Rim, Yangtze River Delta, and Pearl River Delta (Figure 2). In 2019, four of the major ports in these coastal regions were listed in the top five global busiest ports according to data collected from Lloyd's list, illustrating the high impact of the world's most concentrated shipping business on coastal ecosystems. In addition, large-scale reclamation and ocean pollution along China's coastline have also been identified as key factors contributing to the overall seascape resistance (Ma et al., 2014; Jiao et al., 2015). In contrast, climate change impacts are less concentrated and drastic compared to heavy human disturbances in China's coastal seas. For instance, even with high levels of SST anomalies, the Yellow Sea has a rather low resistance value with lower anthropogenic disturbances (Figure 2) (Xu et al., 2018). As anthropogenic effects had the highest contribution to determining the spatial patterns of overall resistance (Figure 3), the key to reducing resistance to seascape connectivity is to restrict and mitigate concentrated human activity along China's coastline, especially in inshore areas due to the development of major ports and coastal cities. Enlarging or proliferating connected core patches (key habitats and MPAs) are of great help in lowering the exposure to human impacts and enhancing the adaptive capacity to disturbances at the local scale, as shown in the mitigation effect provided by these core patches in our model (Figure 2). However,

the gradual but large-scale impact of climate change should not be overlooked because it requires long-term commitment, particularly for high-emission countries, to battle the critical global impact and consequences even beyond current measurement (Chin et al., 2010; Beier, 2012; Magris et al., 2014).

Connectivity is often modeled as a practical way to quantify the adaptive capacity of ecosystems in the face of anthropogenic and climatic exposures (Grober-Dunsmore et al., 2009; Ortodossi et al., 2019; Virtanen et al., 2020). Marine species tend to migrate and adjust their distribution ranges in response to environmental stress or as part of their natural life cycle (Berkstrom et al., 2013). Climate refugee (or range-shifters) of marine species, which describe species forced to shift their ranges due to climate change impact, may significantly rely on connected corridors and habitat resources to maintain their population integrity (Ashcroft, 2010; Pimentel et al., 2014; Noll, 2018). Therefore, preserving connectivity on a seascape scale is critical for marine ecosystem resilience (Mellin et al., 2016; Li et al., 2019). Areas connected with corridors, especially for multiple species guilds, indicate a greater capacity for species with a variety of traits to access suitable and abundant marine habitats, shelters, and resources to migrate to complete lifecycle processes or avoid stress. We found that short- and mid-range marine species (including *R. immaculatus*, *O. ferox*, and *S. formosa*) showed connected corridors only in the inshore regions of China's coastal sea (Figure 4), which are more likely to be restrained from offshore movement because of the lack of core patches and connected corridors for these species. Even with abundant habitat resources, the inshore region is highly concentrated with shipping and pollution (Figure 2), which serve both as environmental stress and resistance that impedes movement (Zeller et al., 2012). Therefore, the loss of inshore habitats under high stress levels could potentially have catastrophic effects on short- to mid-range species whose lifecycles are closely tied to these habitats, including reproduction, shelter, access to food (Hitt et al., 2011; Olds et al., 2013; Abadie et al., 2018), and lack of alternative corridors to migrate. In contrast, pelagic long-range species (≥100 km, e.g., whales, sharks, and tuna) can redistribute their movement pathways through offshore areas in an extended spatial range (Figure 4). Corridors for these species are distributed across the inshore and offshore coastal seas; thus, alternative pathways in such connectivity networks may ease the local losses of connectivity due to disturbances. Therefore, in addition to the mitigation and regulation of human impacts in the concentrated inshore region, it is important to highlight the need to ensure that short- and mid-range marine species have ample protection and support with an interconnected network for movement. Emphasis should be placed on offshore areas that may not be actively connected and utilized because of the lack of existing core patches, especially in the Bohai Sea and Yellow Sea with large corridor gaps. Ensuring the implementation of the critical attributes outlined by Edgar et al. (2014) for successful MPAs holds promise for restoring and conserving fish abundance and biomass, particularly in regions where MPAs are lacking. The establishment of a larger, interconnected network of MPAs can potentially enhance population sustainability not only within protected sites but also by creating a spillover effect on neighboring non-reserve areas (Kininmonth et al., 2011; Edgar et al., 2014). The design considerations for MPA locations and sizes based on connectivity principles should be tailored to site-specific conservation objectives and account for their relevant spatiotemporal scales (Balbar and Metaxas, 2019). At local or regional scales, establishing small but abundant patches may also effectively enhance connectivity and conserve the population if they are placed in proximity within the connected network (Weeks, 2017; Wintle et al., 2019). In essence, applying MPA networks as an effective tool to promote connectivity in offshore regions and to preserve critical inshore habitats is imperative to safeguard seascape connectivity and resilience, particularly under high exposure.

4.2 Prioritizing seascape conservation efforts through vulnerability assessment

Building on the modeling of resistance-based seascape connectivity, we further applied the vulnerability assessment framework to explicitly prioritize marine conservation efforts in China's coastal seas (He et al., 2018). Vulnerable areas were identified as regions characterized by high levels of human-induced and climatic disturbances, as well as the abundance of threatened marine species but lacking sufficient connected corridors. The identified vulnerability may significantly increase the risk of a higher local extinction rate, loss of critical ecological functions, and reduced ecosystem resilience to disturbances (Etter et al., 2011; Kininmonth et al., 2011; Pacifici et al., 2015; Sajjad et al., 2018). The areas highlighted in red in Figure 5 are primarily located in offshore regions, particularly in the offshore Yellow Sea and East China Sea, where the absence of well-established MPAs and key habitats creates significant conservation gaps for locally threatened species. These regions overlap with the high risk of coastal natural hazards, which may continue to intensify under climate change scenarios (Sajjad et al., 2018). This risk underscores the crucial importance of conserving these vulnerable regions as they are susceptible to potential catastrophic events that could significantly disrupt marine populations (Dulvy et al., 2003). A small proportion of the study area (4.1%) was identified as protected areas, mainly situated within a connected network of core patches or contained within these patches. Only 10.1% of the study area is safeguarded by the current MPA and key habitats. The sustainable development goals and "30 × 30" target of the global biodiversity framework highlight the importance of effective conservation in halting biodiversity loss and conserving key habitats (Shen et al., 2023). This leads to a large gap of 19.9% in the coverage of biodiversity conservation targets in China's coastal sea. The identified areas with high vulnerability in the four regions can be further prioritized as potential conservation zones to increase total coverage. The spatial conservation gaps identified in our study underscore the urgency to expand the MPA network and establish offshore support systems for the preservation of threatened marine species.

Notably, we found that the Yellow Sea suffered the greatest exposure to SST anomalies (Supplementary Figure 2), creating potential marine climate refugees seeking a suitable range shift.

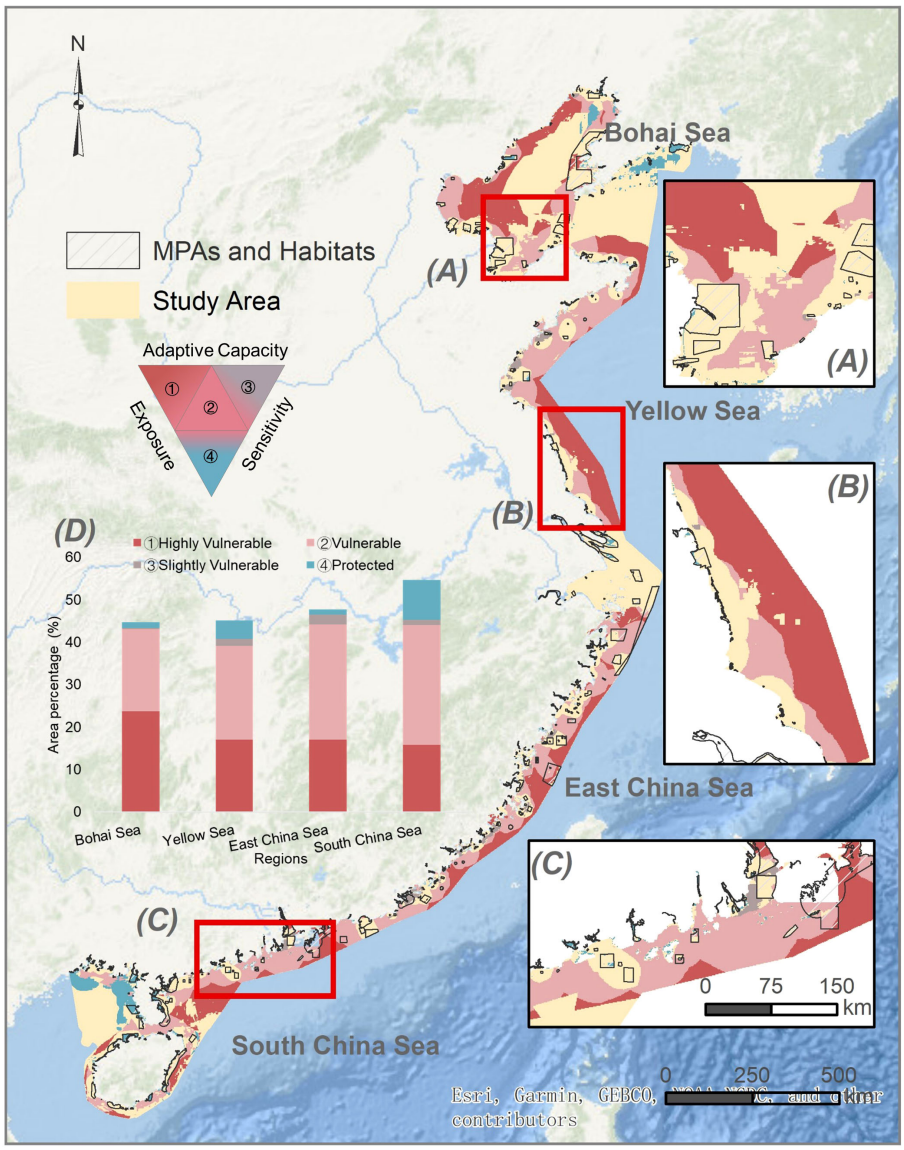

FIGURE 5
Vulnerability map of China's coastal sea, assessed in terms of exposure (resistance), sensitivity (threatened marine species), and adaptive capacity (number of corridors). The right panels show a detailed view of the Bohai Rim **(A)**, Yellow Sea **(B)**, and Pearl River Delta **(C)**. The left panel **(D)** show the area percentages of the four categories in the four seas: ①Highly Vulnerable, ②Vulnerable, ③Slightly Vulnerable, and ④Protected.

However, offshore regions with a high number of threatened species are left unconnected and unprotected because of insufficient MPA networks. Intensifying marine heat waves caused by climate change has substantially reduced the supporting capacity and resilience of marginal coral reefs, which act as thermal refugia in the South China Sea (Mo et al., 2022). Climate change-induced range shifts of species could significantly alter community structure, and such shifting may be much faster in marine environments due to fewer physical barriers than in terrestrial ecosystems (Wallingford et al., 2020). The tropicalization of foundation species, such as the poleward expansion of mangroves, could rapidly replace salt marsh habitats and critically impact coastal ecosystem structure and function (Osland et al., 2022). Sensitive marine species groups that can be disproportionately affected by conservation gaps include climate refugees outpaced by changes in native habitats, threatened species with vulnerable populations, and/or short-to-mid-range species with limited corridors for migration (Wilson et al., 2020; Hermoso et al., 2021). Climate refugee marine species have been shown to have significantly greater diversity in patches with greater connectivity and protection of climate change refugia (Morelli et al., 2017); therefore, prioritizing strategies to enhance seascape connectivity is crucial for climate-adaptive conservation efforts targeting these sensitive species groups (Littlefield et al., 2019). Strategies to support marine ecosystem connectivity and resilience may include the establishment of MPA networks, habitat restoration initiatives, and identification and improvement of key migration routes (McLeod et al., 2009; Wallace et al., 2010; Fraschetti et al., 2021).

We identified marine conservation priorities along the coastal sea of China by applying the proposed seascape connectivity framework and vulnerability assessments. Our results showed that inshore regions of China's coastal sea concentrate on both high levels of anthropogenic disturbances and connected corridors, while offshore regions often lack sufficient interconnected networks to protect sensitive threatened species. Consequently, marine conservation efforts in inshore regions should prioritize the regulation and mitigation of human impact in major coastal cities and ports such as Bohai Rim, Xiamen Port, Lianyungang Port, and Pearl River Delta. Offshore conservation efforts should be directed toward enhancing seascape connectivity, providing connected corridors, and facilitating species movement. The combined strategy of conservation and marine spatial planning should prioritize species groups that are particularly sensitive to environmental stress, including threatened populations, climate refugees of marine species, and short-to-mid-range species. Collectively, this study underscores the potential of applying existing tools and theories from landscape connectivity studies and marine-specific indicators in functional connectivity modeling at a seascape scale. Furthermore, our results highlight the important role of seascape connectivity modeling in prioritizing spatial marine conservation strategies, thereby providing valuable insights for evidence-based marine conservation efforts. The proposed modeling framework introduces uncertainties regarding how the impact of resistance factors might change with varying water depths and how populations of marine species might respond to the identified potential corridors. Further research is necessary to address these uncertainties and enhance the understanding of their influence within the framework.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

YK: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. YXL: Validation, Visualization, Writing – review & editing, Conceptualization. ZC: Validation, Visualization, Writing – review & editing. XZ: Formal analysis, Software. YL: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – review & editing, Software.

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Conflict of interest

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

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1322001/full#supplementary-material

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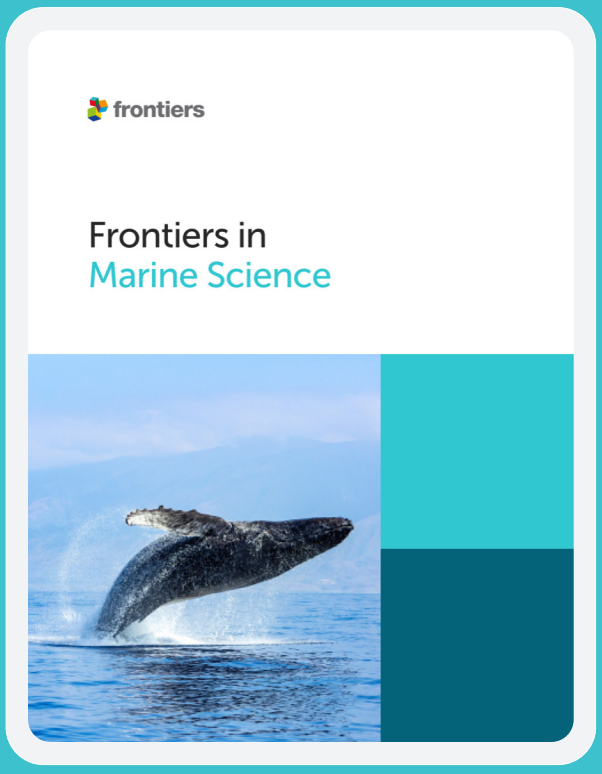

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