State-of-the-art in support of Ecosystem-Based Management approaches to address Harmful Algal Blooms, jellyfish outbreaks, invasive species, and decline of top predators

Deliverable 2.2

Co-funded by the European Union

UK Research and Innovation

Grant Agreement no. 101059877

Document Summary

Topic	HORIZON-CL6-2021-BIODIV-01-04
Grant Agreement Number	101059877
Start date of the project	01.09.2022
Project Coordinator	Angel Borja
Work Package	WP2
WP Co-Leader(s)	Nadia Papadopoulou (HCMR) and Michael Elliott (IECS)
Deliverable Title	Technical report on the state-of-the-art in support of Ecosystem-Based Management approaches to address Harmful Algal Blooms, jellyfish outbreaks, invasive species, and decline of top predators.
Deliverable Number	2.2
Deliverable Beneficiary	University of the Aegean
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Dissemination level	PU
Submission date	30 SEPTEMBER 2023

How to cite | Katsanevakis S, Sagarminaga Y, Fortuna CM, Amorim E, Birchenough SNR, Boicenco L, Borrello P, Bosch-Belmar M*, Brasseur S*, Bresnan E, Bueno-Pardo J*, Camp J, Coll M, Claver C, de Angelis R, Doyle T, Ferrer L, Fernández-Corredor E, France J, Fortibuoni T, Franco A, Fraschetti S*, Fumarola LM*, Garcés E, Garcia-Garin O, Giménez J, Holland MM, Jakobsen HH, Jaspers C*, Knudsen SW, Kobos J, Lanzén A, Leone A, Leoni V*, Louzao M, Lynam CP, Magaletti E, Mazaris AD, Machairopoulou M, Montero N, Nikolaou A, Olenin S, Pagou K, Peck MA, Pedrajas A, Piraino S*, Puntila-Dodd R, Raicevich S, Ramírez F, Ransijn J*, Reñé A, Revilla M, Rilov G*, Rodríguez GJ, Russell DJF*, Sampedro N, Sbragaglia V, Serena F, Spada E, Stæhr PAU, Stern R*, Stranga Y, Teixeira H, Tidbury HJ, Tsirintanis K, Tsirtsis G, van Leeuwen A*, Papadopoulou N, Elliott M, Borja A, 2023. GES4SEAS Deliverable 2.2. Technical report on the state-of-the-art in support of Ecosystem-Based Management approaches to address Harmful Algal Blooms, jellyfish outbreaks, invasive species, and decline of top predators. 337 pp.

Acknowledgements: We would like to thank contributions from Dr Irina Makarenko (member of the GES4SEAS' Practitioners Advisory Board – PAB) from the Permanent Secretariat of the Commission on the Protection of the Black Sea Against Pollution for providing information on the current IAS-related policies in the Bucharest Convention, and the EASIN team for providing their latest catalogue of marine IAS (used for the analysis depicted in Table 5).

We also thank Dr Axel Kreutle and Dr Roland Cormier (PAB members) for their valuable insights and comments, and Dr David Reid, Dr Miquel Ortega Cerdà, and Dr Samuli Korpinen for critically reading and reviewing this deliverable.

*ACTNOW participants, contributing to the review papers of this deliverable through a GES4SEAS-ACTNOW collaboration for obtaining synergies and improved outcomes [ACTNOW: European Union's Horizon Europe research and innovation programme HORIZON-CL6-2021-BIODIV-01-04 under grant agreement No 101060072 – "Advancing understanding of cumulative impacts on European marine biodiversity, ecosystem functions and services for human wellbeing"].

GES4SEAS (Achieving Good Environmental Status for maintaining ecosystem services, by assessing integrated impacts of cumulative pressures) project is funded by the European Union under the Horizon Europe program (grant agreement no. 101059877). Views and opinions expressed are however those of the authors only and do not necessarily reflect those of the European Union or UK Research and Innovation. Neither the European Union nor the granting authority can be held responsible for them.

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1. GES4SEAS Project Summary

Human activities at sea (e.g., maritime transport, extraction of living and non-living resources, etc.) and coastal areas (e.g., agriculture, leisure, and recreation, etc.) have expanded considerably, leading to an increased level of pressures and subsequent degradation of ocean health and, ultimately, human health. Single and cumulative impacts of these activities are likely to increase, driven by human demands and enhanced by climate change.

Human activities evolve following socio-economic drivers leading to pressures, which often are studied in isolation from each other even though their impacts on marine ecosystems can interact, making the effects cumulative (e.g., synergistic, antagonistic or a combination). Knowledge on these interactions and their cumulative effects in the marine environment has increased in recent years, but huge challenges remain to be solved. Thus, there is little predictability with which to inform decision-making processes, especially on ecological tipping points, which, if exceeded, could lead to a point of no-return for the system. In this context, an ecosystem-based management (EBM) approach to the management of human activities at sea and on land should ensure that the combined pressure of such activities is kept within levels compatible with the requirements of Good Environmental Status (GES) (within the Marine Strategy Framework Directive – MSFD), against a background of climate change. This means that the capacity of marine and coastal ecosystems to respond to human-induced changes is not compromised, enabling the sustainable use of marine goods and services by present and future generations.

Thus, the main objective of GES4SEAS is to inform and guide marine governance in minimizing human pressures and their impacts on marine biodiversity and ecosystem functioning while maintaining the sustainable delivery of ecosystem services. This will be achieved through developing an innovative and flexible toolbox, tested, validated, demonstrated and upscaled in the context of an adaptive EBM approach. The toolbox will allow competent authorities 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. Ultimately, this will help achieving GES, and support different policies at national, European and global levels (e.g., Birds and Habitats Directives (BHD), Biodiversity Strategy 2030, United Nations Sustainable Development Goals (SDG)).

Stakeholders and the key competent authorities (including national, regional and European levels) are integrated in a Practitioner Advisory Board (PAB) to co-create and validate the toolbox and the EBM approach. This will result in a real problem-solving approach with iterative and incremental development steps.

GES4SEAS will also rely on existing EU and non-EU multi-actor networks to involve and engage with stakeholders. This multi-actor approach will ensure that the research and deliverables are relevant to marine managers all around the world. Lastly, it is important to highlight that the toolbox will be tested and demonstrated at 11 Learning Sites (LSs) covering all European regional seas (and also overseas), and environments. Thus, it is expected that GES4SEAS will achieve Technological and Societal Readiness Levels 6. This will be achieved by the participation of 20 partners, covering the four European regional seas and Canada.

It is expected that GES4SEAS will:

- Operationalise integrative and holistic solutions for EBM based on a software toolbox for analysing, assessing and mapping cumulative pressures, GES and ecosystem services.
- Provide evidence (and training) to key stakeholders of the benefits of using the toolbox that will be developed in GES4SEAS for assessing the environmental status of marine waters and the ecosystem services considering the effects of multiple pressures, so opt for using it.
- Ensure the EBM approach and provide guidelines for the management of Invasive Alien Species (IAS), top predators, jellyfish outbreaks, and Harmful Algal Blooms (HABs).
- Investigate the best ways to obtain thresholds of GES/non-GES status and tipping points (system breaking points) using models.
- Reach and engage a wider society, and specifically young people and educators, on key messages steaming from this project, so GES4SEAS contributes to societal ocean literacy and responsible behaviours.

2. Deliverable 2.2 summary and objectives

The **objective** of Task 2.2 and the related **deliverable D2.2** is to **evaluate the state-of-the-art in support of EBM of four specific problems: IAS, the decline of top predators, jellyfish outbreaks, and HABs**. This task aimed to review the scientific background on drivers-pressures-states-impacts links of these components, their linkages to ecosystem services and societal goods and benefits, including human health and welfare, the existing gaps of knowledge, and the existing experiences on monitoring, predictions and management. Four workshops were organized (IAS, HABs, jellyfish outbreaks, and top predators) in collaboration with our sister project ACTNOW and with the participation of invited international experts to (i) assess existing knowledge and best practices in monitoring, predicting and mitigating these problems, (ii) evaluate the potential of novel methods such as eDNA, metabarcoding, biologgers, and remote sensing, and (iii) compile tools for improved management, to be further developed in T5.2.

This deliverable D2.2 includes comprehensive evaluations of IAS, the decline of top predators, jellyfish outbreaks, and HABs. These evaluations have yielded valuable insights into the challenges faced by marine ecosystems, including the factors driving these challenges, their consequences, areas where knowledge is lacking, and the most advanced methods for monitoring and management.

Biological invasions, resulting from human activities, exert substantial impacts on ecosystems worldwide. **Section 4 focuses on marine 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 EASIN, AquaNIS, and 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 standardisation 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 differences 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 (viii) considering the potential benefits of IAS in ecosystem functioning and services.

The conservation and management of marine ecosystems hinge on a comprehensive understanding of the status and trends of their top predators. **Section 5 delves into the ecological significance of marine top predators**, examining their roles in maintaining ecosystem 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 eDNA analysis. We also evaluate their strengths and limitations in terms of accuracy, spatial coverage, and cost-effectiveness, providing resource managers with essential insights for informed decision-making. Then, 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 EBM is maintaining the ecological balance of marine ecosystems. By examining marine top predators' ecological significance, analysing population trends, discussing monitoring techniques, and outlining effective mitigation strategies, we provide a comprehensive resource for researchers, policymakers, and stakeholders engaged in fostering EBM 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.

Jellyfish (or gelatinous zooplankton) fulfil important ecological roles with significant impacts, yet they are often oversimplified or misunderstood. While jellyfish management has typically focused on local control and mitigation efforts, several current initiatives propose cost-effective monitoring and analyses to include jellyfish in EBM approaches, such as the European MSFD. **Section 6 focuses on impacts, causes, and management strategies for different gelatinous zooplankton groups, along with a review of indicators and monitoring methods applicable to the assessment of jellyfish**. Thereby, this work is envisioned to serve as a practical guide for scientists and policymakers to enhance the assessment and management of outbreak-forming jellyfish across European regional seas, thus contributing to the achievement of GES. Our systematic literature review on the impacts of jellyfish shows an increase in related studies since the early 2000s. Stings were the main cause of human health impacts, with fatal cases reported predominantly in the central Indo-Pacific. Mechanisms of impact on biodiversity included direct predation, modification of trophic flows, competition for resources, and others. Jellyfish also offer benefits, supporting biodiversity, acting as biological regulators, and contributing to sustainable development through food provision and medical applications. Our systematic review on monitoring techniques for jellyfish outlined a variety of implemented techniques, such as nets (the most used technique), continuous plankton recorder, polyp monitoring through visual surveys or cameras, acoustic methods, remote images, citizen science, underwater images, molecular methods, and jelly-falls monitoring. In the context of evolving marine ecosystems and growing recognition of jellyfish's ecological significance, this study highlights the pressing need for enhanced monitoring, assessment, and management of jellyfish populations. Traditional localized management approaches must transition to predictive models to address future jellyfish crises effectively and cost-efficiently. Integrating jellyfish into MSFD requires well-defined criteria, indicators, and thresholds. Understanding outbreak causes and the often-overlooked polyp phase are vital, requiring multidisciplinary research efforts. Ocean literacy campaigns are essential in mitigating the impact of jellyfish outbreaks on public health and various marine activities. Moreover, exploring jellyfish ecosystem services offers opportunities to harness marine resources while mitigating adverse effects, supporting sustainable blue economies.

Marine 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 or seafood trade bans, the multifaceted linkages of HABs with environmental and socio-economic factors require more comprehensive EBM approach tools to support policies. **Section 7 promotes a coordinated understanding and implementation of HABs assessment and management under the MSFD**, targeting the achievement of GES in European marine waters. We introduce two novel tools: GES4HABs 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). Moreover, 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 EBM 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.

The comprehensive reviews on IAS, the decline of top predators, jellyfish outbreaks, and HABs provided insights into these marine ecosystem challenges, including their drivers, impacts, knowledge gaps, and state-of-the-art monitoring and management practices. **Recommendations for these issues highlight the need for holistic, adaptive, and collaborative approaches to safeguard marine ecosystems and their benefits to society, which we consider that could be included in coming MSFD modification.**

3. Introduction

The **fourth outcome indicated in the Horizon Europe proposal call** [HORIZON-CL6-DEC-2021-00-00: Assess and predict integrated impacts of cumulated direct and indirect stressors on coastal and marine biodiversity, ecosystems and their services], in which the project GES4SEAS is included, **aims to identify and interrogate the current EBM approaches and policy measures for activities to reduce pressures to ensure that GES can be achieved thereby enabling the sustainability of coastal and marine ecosystems to deliver services and societal goods and benefits while at the same time being resilient to rapid climate and environmental changes**. In this context, the project delivered on 31st May 2023 Deliverable 2.1 *"Ecosystem management approaches based on a review of the activity-pressures-effects chain towards achieving Good Environmental Status in the Marine Strategy Framework Directive".* This represented the first step towards a proposal and guidelines on EBM for practitioners within the MSFD. Hence, that report provided the background to successive tasks and work packages in the project. In particular, D2.1 firstly presented the current understanding of EBM and the wider principles on which it is based. Secondly, the tools available and as used to test each principle are listed and then described. Thirdly, the report presented conclusions regarding the use of those tools and briefly indicated the way in which they can be combined into a toolbox in order to achieve EBM. These aspects included the way in which EBM is mentioned in international agreements and treaties, regional seas conventions, assessment strategies, EU Directives and national and regional instruments.

Building upon those concepts, tools and approaches, in Task 2.2 (State-of-the-art in support of EBM of specific and increasing problems, such as invasive species, the decline of top predators, jellyfish outbreaks, and HABs) we have focused on the problems derived from those four main issues, by reviewing the scientific background on drivers- pressure-state-impacts links of these components under climate change and socio-economic scenarios, their linkages to ecosystem services and societal goods and benefits including human health and welfare, the existing gaps of knowledge, and the existing experiences on monitoring, predicting and managing these events and their consequences.

Subsequently, Task 5.2 will aim to cover some of the identified gaps by developing, refining, and testing methods to assess and manage invasive species, the decline of top predators, jellyfish outbreaks, and HABs, and developing tools to support EBM. Specifically, Task 5.2 will refine and develop methods, such as: (i) satellite imagery processing and analysis routines to map in all European seas (LS10), the occurrence patterns of phytoplanktonic blooms amd characterize the oceanographic conditions linked to HABs, invasive species distribution, and jellyfish bloom events (T2.2); (ii) configuration/tuning of existing Lagrangian models to simulate and predict transport pathways of these biological components; (iii) molecular techniques (e.g. eDNA) for enhancing monitoring, assessing cause-effect pathways, and identifying key biological components, populations and communities' structures; (iv) improving cumulative impact assessment and mapping in all European seas (LS10) by adapting and expanding the CIMPAL framework (Cumulative IMPacts of invasive ALien species) for assessing the impacts of HABs and jellyfish blooms; (v) utilizing biologging for improving top predators monitoring and management.

It must be highlighted that the topics of invasive species, the decline of top predators, jellyfish outbreaks, and HABs are highly pertinent to the EBM approach. Each of these issues represents significant pressures on marine ecosystems, influencing ecosystem structure, function, and services, which are critical for achieving GES under the MSFD.

- **Invasive Alien Species**: IAS are recognized as one of the major threats to biodiversity globally, impacting ecosystem services and human health. The ecological consequences of IAS include alterations in community structure, nutrient cycling, and food web dynamics, and they can lead to native species local extinctions and ecosystem function changes, which directly affect GES descriptors such as Non-Indigenous Species (D2) following adverse alterations to species groups and broad habitat types, biodiversity (D1) and seafloor integrity (D6).
- **Decline of Top Predators**: Top predators play a crucial role in maintaining the structure and function of marine ecosystems. Their decline, primarily due to overfishing and habitat loss, can lead to trophic cascades, altering ecosystem dynamics and services. Protecting top predators is integral to achieving GES descriptors related to biodiversity (D1) and food webs (D4).
- **Jellyfish Outbreaks**: Jellyfish outbreaks, although natural phenomena, can indicate imbalances in marine ecosystems, resulting from various factors, such as overfishing and climate change. They affect fisheries, tourism, and the structure of marine food webs. Addressing jellyfish blooms is essential for maintaining the balance of marine ecosystems and related services, aligning with descriptors such as food webs (D4) and commercial fish and shellfish (D3).
- **Harmful Algal Blooms**: HABs have increased in frequency and intensity due to various reasons, such as anthropogenic nutrient loading and climate change. They have severe consequences for marine ecosystems, fisheries, and human health through toxin production and hypoxia. Monitoring and managing HABs are crucial for GES descriptors related to eutrophication (D5)

and food webs (D4), while their increased frequency may have consequences on biodiversity (D1), commercial fish and shellfish (D3), and food webs (D4).

Integrating these issues into EBM allows for a more holistic understanding and management of marine ecosystems. Traditional monitoring often focuses on single species or specific parameters, whereas EBM emphasizes the interconnections and cumulative impacts of various pressures. Moreover, enhancing monitoring efforts to include these issues can complement traditional methods by providing early warning signals and more robust data for assessing environmental status and implementing effective management measures. Therefore, integrating these topics into EBM will offer a more complete and adaptive framework for marine conservation and management.

Through the organization of four dedicated workshops, one for each topic, with the collaboration with another project under the same call (ACTNOW), and in liaison with past and ongoing related projects and scientific networks, this D2.2 represents a second important step in moving towards the completion of a proposal and guidance on EBM.

Hence, it is emphasised that the information in the GES4SEAS tasks in WP2 (identifying existing EBM approaches -D2.1-, addressing the four topics mentioned in this report D2.2, and identifying the best options for practical EBM -D2.3-), must result in designing, through consultation, co-creation and iterative processes with WP1 and WP5, *'a practical EBM using risk-based and opportunity assessment management'* (D2.4). Once these concepts and guidelines have been delivered to the Learning Sites (LSs), in WP5, they will be tested, synthesised, and their conclusions, recommendations and lessons learned integrated into an overarching toolbox. This toolbox will then also encompass the tool created and further developed (e.g., with new functions or capabilities) in WP4 ('Linking pressure and status assessment with the capacity to supply ecosystem services into a unifying holistic framework and nested toolbox'). The following task in WP5, Task 5.5 can then make recommendations for improved monitoring, assessment and management for use in areas wider than the LSs integral to the project. In summary, this then creates the links between this task and other WPs of the project thereby highlighting the roadmap to delivering the project vision on the practical implementations of EBM approaches, including a guidance and recommendations from and for practitioners (WP1). **In turn, this achieves the OUTCOME 4 of the call - i.e., EBM approaches and policy measures for activities to reduce pressures and lead to the achievement of GES.** This again in turn enables the sustainability of coastal and marine ecosystems to deliver both ecosystem services and societal goods and benefits and hence allows the areas to be resilient to rapid climate and other environmental changes.

4. Marine Invasive Alien Species (IAS) in Europe: nine years after the IAS Regulation

4.1 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, 2009, 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 EU IAS Regulation as "alien species whose introduction or spread has been found to threaten or adversely impact upon biodiversity and related ecosystem services" (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 socio-economic 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 socio-economic 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 cut-off 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 cut-off date, leading to the use of region-specific temporal thresholds in NIS databases. For example, in Europe and the Americas, the widely accepted cut-off 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 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 MSFD recognizes IAS as a significant pressure on marine ecosystems, negatively affecting environmental status. The MSFD Descriptor 2 indicates that achieving GES requires maintaining NIS species introduced by human activities 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 (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 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 in the list in 2019 (EU, 2019), followed by *Rugulopteryx okamurae* in 2022 (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 centred in Europe but could be considered and adapted elsewhere.

Table 1.International policy context on biological invasions in coastal and marine environments with relevance for European Seas. UNEP: United Nations Environment Programme; MAP: Mediterranean Action Plan; IMO: International Maritime Organization.

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 minimising, to the extent possible, new introductions of NIS.
OSPAR	**North-east Atlantic**	Endeavour 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-Primary criterion:* Number of NIS newly introduced via human activity into the wild [...] is minimised and where possible reduced to zero. *D2C2-Secondary criterion:* 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-Secondary criterion:* 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. E.g.: *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.

4.2 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 International Maritime Organization Ballast Water Management Convention (IMO-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 analysing 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).

Table 2. Examples of currently active online information systems on marine, brackish, and coastal freshwater alien species relevant for Europe. General biodiversity information systems (e.g., GBIF) and citizen-science initiatives are not included.

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, observations	https://www.artdatabanken.se/
Artsdatabanken	2005	National (Norway) terrestrial, marine, freshwater	Knowledge transfer, outreach, scientific support, identification, 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, species of Union concern, and others). Distribution maps of single or multiple species.	Katsanevakis et al. (2012, 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 Non-native 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, sources, and other)	Costello et al. (2021)

The European Commission launched EASIN in 2012 to support European NIS management policies (Katsanevakis et al., 2012, 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 the scientific literature (Trombetti et al., 2013), through online tools and web services (Fig. 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 (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.

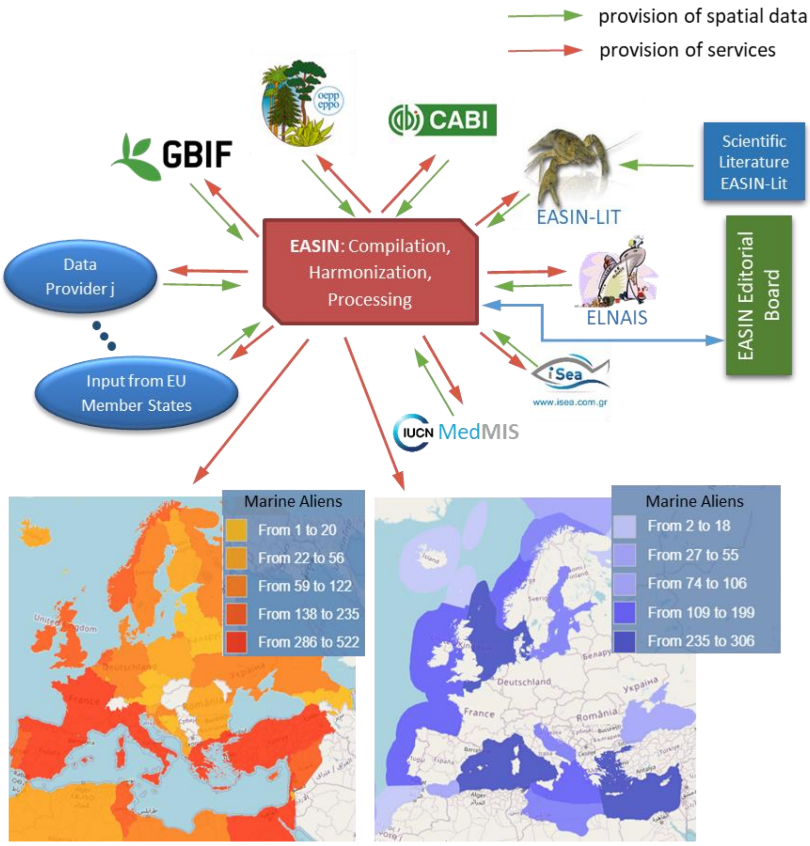


Figure 1. European Alien Species Information Network (EASIN): Schematic of its concept, main elements, and outputs (bottom left: marine alien species by country; bottom right: marine alien species by ecoregion).

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 (Fig. 2). AquaNIS data are regularly updated by the International Council for Exploration of the Seas (ICES) 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 BWMC. Recently, it was equipped with an Early Warning System aimed at preventing the spread of harmful aquatic organisms and pathogens through ballast water.

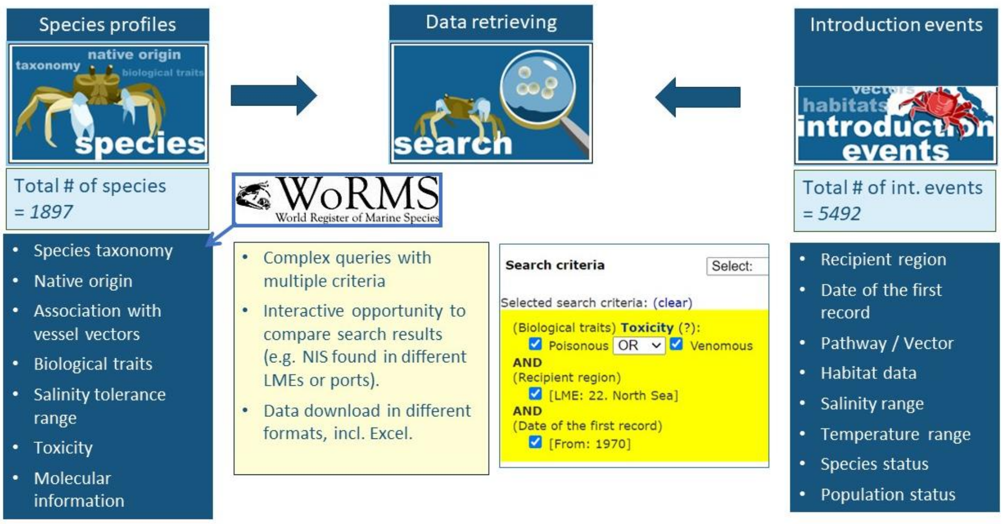


Figure 2. Information system on aquatic non-indigenous and cryptogenic species (AquaNIS) is with a flexible search engine and a built-in comparative analysis tool which makes it practical for management and useful for research.

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 towards the end of a project for generating reports and, occasionally, scholarly papers. However, 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 for 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 three 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 in 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, 2014; Katsanevakis et al., 2012, 2015; Costello et al., 2021):

- Determine the database's intended purposes (e.g., research, management, environmental status assessment, early warning, etc.). 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.

4.3 Monitoring strategies

Monitoring recommendations, including sampling adequacy, coordination and coherence among programmes, 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 current monitoring focus and examples showcasing the potential of novel techniques to enhance the monitoring of marine biological invasions.

4.3.1 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 & 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 RSC's guidelines reflect synergistic top-down and bottom-up approaches to influence and align monitoring efforts at regional and national levels.

Table 3. Brief overview on current efforts by Regional Sea Conventions (RSCs) towards improved monitoring and management of Non-Indigenous Species (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 a 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; 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, 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/MAP 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 the 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 to 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); map areas of non-indigenous species proliferation, among others. In line with BSIMAP the dedicated indicator 'Number of new introduced non-indigenous species (for each 6 years)' must be

	mandatory reported every six years to the Black Sea Commission.

4.3.2 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., EU, 2008; EU, 2014), and information on abundance/biomass of IAS and their impact is required by the MSFD for assessing GES (Stæhr et al., 2023a). National inventories of marine NIS have been compiled and published for several EU countries, e.g., Greece (Zenetos et al., 2018, 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 (Staehr 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 assessment 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).

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. In total, 1671 alien and cryptogenic marine and oligohaline species are reported in the European Seas by EASIN (as of July 2023).

European ecoregions	No of Non-Indigenous Species 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, Madeira	55
Alboran Sea	54
Black Sea	36
North and East Barents Sea	27
White Sea	18
South and West Island	17

4.3.3 Ports 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 five years of implementation in practice (Hewitt and Martin, 2001). The protocol was adopted by the IMO GloBallast programme 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., Pederson et al., 2005; Cohen 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 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 eDNA from IAS across seasons (Knudsen et al., 2022). In the Mediterranean, a study compared eDNA levels inferred from metabarcoding with fishing fleet activity to detect IAS in harbours 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).

4.3.4 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 commonly 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 in 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 becomes relatively more cost-efficient. Conversely, targeted approaches generally exhibit higher sensitivity and specificity, allowing for more accurate estimates of absolute abundance (McColl-Gausden et al., 2023; Sapkota et al., 2023). Both approaches rely on the availability of reference sequence data for successful NIS identification. 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 are 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 at 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 4 April 2023; Bucklin et al., 2021) and a list of all rbcL gene entries from global data repositories (Omonhinmin and Onuselogu, 2022). Out of 2197 NIS in European waters, sequence data for at least one taxonomic marker were available for 1318 species (60%; see Table 5). For 854 species (39%), multiple marker sequences were available.

Table 5. Identified reference sequences per taxonomic marker for Invasive Alien Species (IAS) 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 & Onuselogu, 2022
COI*	1096 (50%)	1069	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	*1318 (60%)*	*1078*	*926*	*493*	*191*	*126*	*49*

Sampling design is critical for comprehensive biodiversity coverage, especially in heterogeneous habitats such as ports (Aglieri et al., 2023; Knudsen et al., 2022). Rey et al. (2020) demonstrated this in the Port of Bilbao and its upstream estuary, where 192 samples were taken from various locations using both 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. Koizol 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.

Sampling design for eDNA monitoring must also consider variation in distribution across time and depth. Different depths harbour 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 night-time 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 (Keeley et al., 2018; Lejzerowicz et al., 2015). 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).

4.3.5 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 colour infrared (IR) photos has been employed for NIS detection in shallow waters since the 1970's (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 *Rugulopteryx 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 modelling 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).

4.3.6 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 JellyWatch Programme initiatives related to jellyfish blooms. These stand out as the most impactful marine citizen science endeavours 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, 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; Knudsen et al., 2023).

Coupling citizen science with eDNA monitoring is a promising approach in both marine (e.g., Agersnap et al., 2022; Tøttrup et al., 2021; 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). However, careful consideration is needed to mitigate the increased risk of sample contamination from unwanted DNA, due to 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).

4.4 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 et al., 2017). Several attempts have been made, mainly using species distribution models (SDMs), to predict favourable 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., 2023b). Additionally, studies have explored factors contributing to successful invasions, such as life-history traits or global invasion history (Vilizzi et al., 2019, 2021; D'Amen et al., 2022, 2023).

When modelling 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 subsequent rapid expansion of the species proved these predictions false (Dimitriadis et al., 2020; Poursanidis et al., 2020, 2022).

Over the past two decades, modelling 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 modelling 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 modelling 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 snorkelling and modelling 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) modelling 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 (*Plotosus 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 harbours 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 *Plotosus lineatus*, a species of EU concern (Peyton et al., 2019, 2020).

4.5 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. Using 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 numbers of introduced species. Interestingly, aquaculture showed a notable decrease in new introductions during 2001 to 2010, attributed to regulatory measures at national and European levels (e.g., ICES, 2005; 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 for 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 Convention on Biological Diversity (CBD) Pathway Classification Framework has become a global standard in recent years (CBD, 2014; Harrower et al., 2018). It consists of six broad categories: Release; Escape; Transport – contaminants; 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' (Fig. 3A). However, when considering only high-impact NIS (as defined in EASIN), species introduced through 'Transport-stowaway' and 'Transport-contaminant' appear to have a relatively greater impact compared to those introduced through 'Corridors' (Fig. 3B).

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, are 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, 2019), fish (Givan et al. 2018), and possibly molluscs (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 Israel coast (photo: G. Ra'anan).

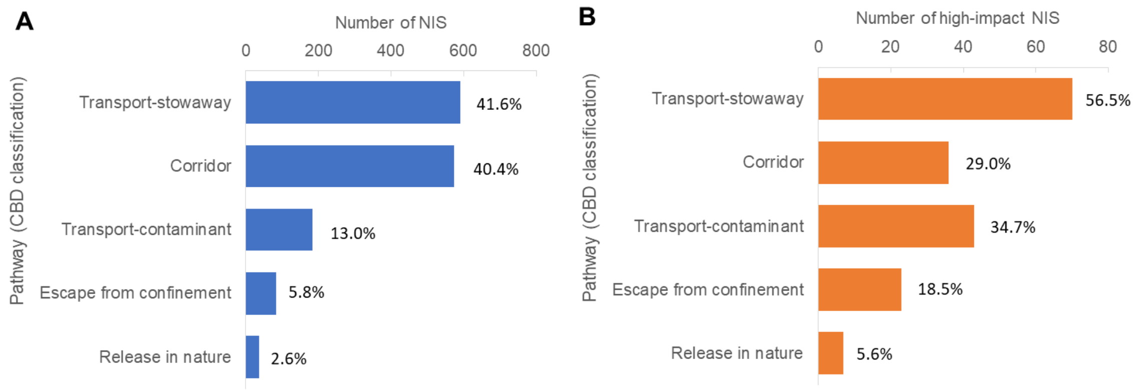


Figure 3. Number of marine Non-Indigenous Species (NIS) (A) and high-impact NIS (B) in European Seas known or likely to be introduced by each of the main pathways, according to the Convention of Biological Diversity (CBD) classification. Percentages add to more than 100% as some species are linked to more than one pathway. High-impact NIS are according to the EASIN classification. Data retrieved from EASIN (22/3/2023).

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 (Fig. 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 (Nunes et al., 2014; Katsanevakis et al., 2014a). 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 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.

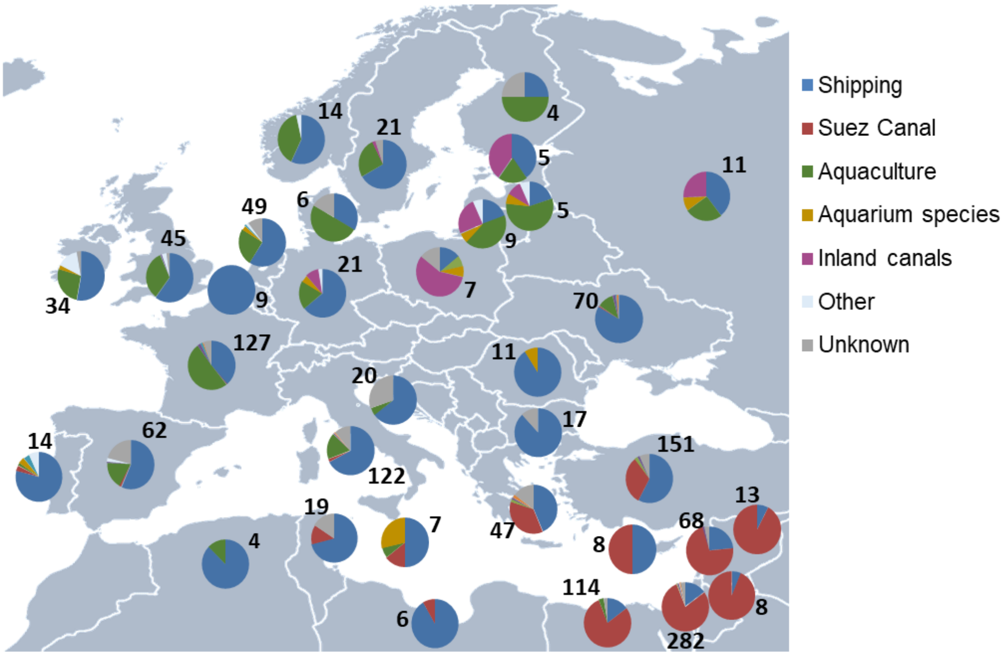


Figure 4. Pathways of introduction for first European records of marine NIS, per recipient country (i.e., countries of initial introduction in Europe). For clarity, data are shown for countries with more than two recorded first introduction events (numbers shown next to the charts). Adapted from Nunes et al. (2014).

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 neighbouring countries accounted for 56% of NIS introductions, 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).

Recreational vessels can substantially contribute to the secondary spread of invasive species, and constitute the largest unregulated vector of NIS secondary spread (Murray et al., 2011). Recreational boats, often moving between marinas and coastal areas, can inadvertently transport NIS mainly via hull fouling, sometimes overpassing oceanographic barriers. The increased mobility and popularity of recreational boating amplify the risk of NIS introduction across various marine environments. Effective management and awareness programs targeting recreational boaters are essential to mitigate this pathway's impact.

4.6 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 positive impacts of alien species; the EICAT+ covered this gap 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 to 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 lifecycle 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, ecosystems 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 (Figs 5, S1, Table S1). Negative impacts on biodiversity were primarily due to competition for resources, followed by the creation of novel habitats and predation (Fig. 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). 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).

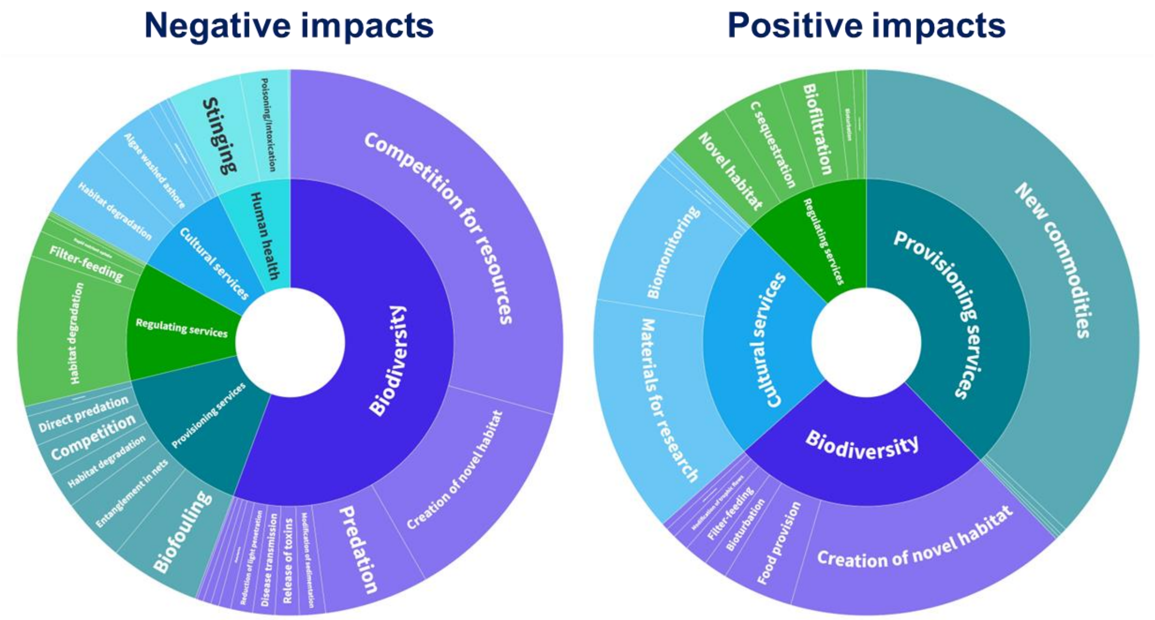


Figure 5. Mechanisms (outer circle)) of Invasive Alien Species (IAS) impacts on biodiversity, ecosystem services and human health (inner circle)) in the Mediterranean Sea (circle compartment size corresponds to sample size). Based on Tsirintanis et al. (2022).

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) (Fig. 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, molluscs and crustaceans have proven a boon for the fisheries and aquaculture sector, especially in the Levantine Sea (e.g., Katsanevakis et al., 2018). Creation of novel habitat is the most important mechanism of positive effects on biodiversity, as alien structural ecosystem engineers provide new habitat and shelter for various species through the formations they create (Katsanevakis et al., 2014b; Guy-Haim et al., 2018; Fig. 5). Cultural services are positively affected through 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 (Fig. 5, Table S1).

Evidence of reported impacts is mostly of medium strength (Fig. 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 modelling to project impact consequences (Fig. 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; Fig. 6).

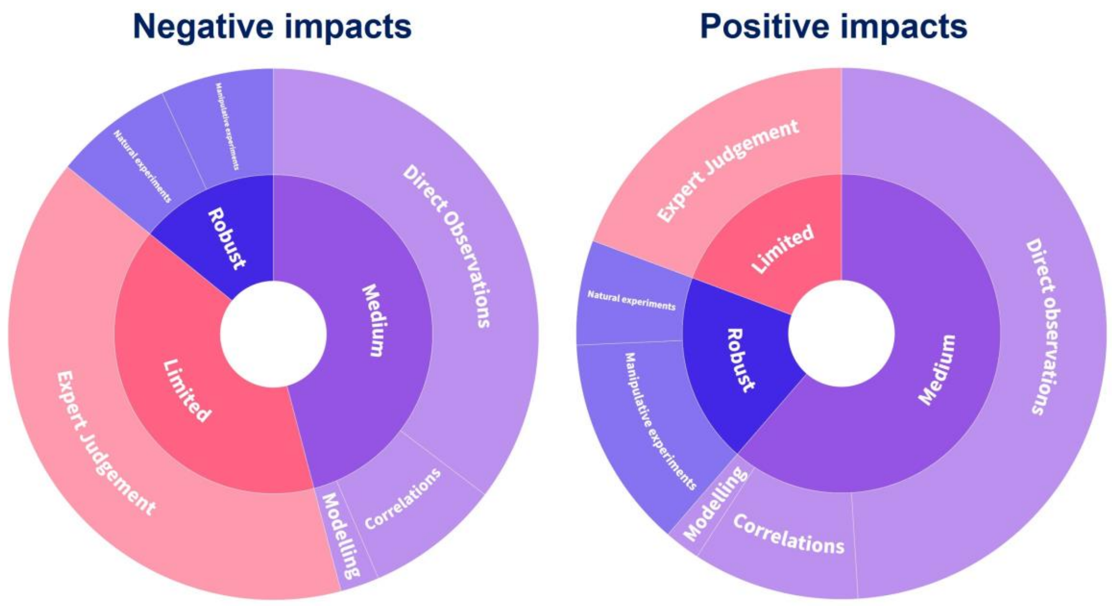


Figure 6. Type of evidence of IAS impacts on biodiversity, ecosystem services and human health in the Mediterranean Sea. Based on Tsirintanis et al. (2022).

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 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 (7 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 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 the 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 towards 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 towards 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).

4.7 Management options – lessons learned from the implementation of management measures

4.7.1 Prevention – pathway management

Prevention of IAS introductions is the first line of defence (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 (Fig. 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 (Fig. 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 considering 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’ (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).

4.7.2 Implemented eradication and control measures for marine IAS (physical, chemical, 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 eleven failed to achieve eradication or control targets (Table S2; Katsanevakis, 2022). These studies mainly focused on macroalgae (10), ascidians (7), and fish (7; 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 sulphate, 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 sulphate to eradicate the mussel *Mytilopsis 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 mitigate 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 *Lagocephalus 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 *Plotosus lineatus* and the alga *Rugulopteryx 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 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 4.7.3) 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; Wotton et al., 2004; Miller et al., 2004; Anderson, 2005; Kleitou et al., 2021), and a good knowledge of the 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).

4.7.3 Management options for established IAS populations

Managing marine IAS is more challenging than terrestrial and freshwater species due to increased functional connectivity of the oceans (Kinlan and Gaines, 2003; Katsanevakis, 2022). Nevertheless, several management measures have been implemented (section 4.7.2; 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 are transformed 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 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).

The "biotic resistance hypothesis," as summarized by Bjarnason et al. (2017), suggests that ecosystems with high native species richness are more resistant to invasions compared to those with lower richness (Elton, 1958; Levine & D'Antonio, 1999; Jeschke, 2014). However, an analysis of 129 studies testing the biotic resistance hypothesis found limited support (Jeschke et al., 2012). Conversely, some studies report a positive correlation between alien and native species richness, leading to the "acceptance hypothesis" (McKinney, 2002; Stohlgren et al., 2003, 2006). Marine Protected Areas (MPAs), while crucial for conservation, are not immune to invasions, as seen in cases like the rabbitfishes in the Mediterranean (Rilov et al., 2018; Giakoumi et al., 2019). Moreover, Caselle et al. (2018) highlighted the complexity of invasion dynamics, showing varying resistance mechanisms in different MPA states. Despite these findings, the influence of biotic interactions and conservation efforts on invasion success remains context-dependent (Giakoumi & Pey, 2017; Caselle et al., 2018; Dimitriadis et al., 2021), necessitating a multifaceted approach to managing invasive species in MPAs, including targeted removal and commercial utilization (Kleitou et al., 2021).

4.8 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 mollusc 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 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 (García-Gómez et al., 2020; Sorte et al., 2010; 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 favourable 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, 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 lifecycle of many IAS, influencing maturation, reproduction, establishment, and persistence (e.g., Teixeria Alves et al., 2021; King 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 (Teixeria 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, 2020). Similarly, Reise et al. (2023) highlighted that some NIS in the Wadden Sea positively contribute to sediment stabilization, mud accretion, and diversifying 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 degrading it.

4.9 Recommendations: How to improve the management of IAS in Europe?

4.9.1 Costs of biological invasions and funding

Global damage and management costs associated with biological invasions have exponentially increased in the last fifty years (Diagne et al., 2020). However, the allocation of economic resources towards 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 in addressing many of the challenges raised in this review.

4.9.2 Inadequate coverage of marine biological invasions by the IAS Regulation.

Currently, only two marine species (*Plotosus lineatus, Rugulopteryx 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, harbouring 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 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).

4.9.3 Learn 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, 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.

4.9.4 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, funding of 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 scientific community.

NIS information systems should be multipurpose, following the principle of "gather data once, utilize it many times". Besides operational usage, these systems should continuously accumulate data for analysis and forecasting. Ideally, this should include not only 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 health.

4.9.5 Improving monitoring and early warning systems

Continued effort to increase the spatial and temporal coverage of marine IAS monitoring, and transboundary cooperation, is 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, 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 has its associated difficulties (Agersnap et al., 2022; Knudsen et al., 2023), and the eDNA metabarcoding itself (Fonseca, 2018) and species-specific eDNA detection is 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 by 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, 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 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).

4.9.6 Improve 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 modelling 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 (Liu et al., 2020; D'Amen and Azzurro, 2020b). As a final note, when selecting modelling approaches (e.g., correlative, mechanistic, process-oriented), a careful consideration of available input data accompanied by rigorous validation is essential (Melo-Merino et al., 2020).

4.9.7 Improve integrated impact assessments - cumulative impacts 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 policy makers 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 towards 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. Policy makers 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.

4.9.8 Assess positive impacts and exploit NIS

NIS have become a permanent component of contemporary ecosystems and their potential benefits on ecosystem services, human well-being and biodiversity should be thoroughly investigated (Schlaepfer et al., 2011; Vimercati et al., 2020, 2022). Many invasion studies are biased towards 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 Figs 5 and S1). Scientists should adopt holistic approaches, considering both 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, 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 safeguarding 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, 2019; De Domenico et al., 2023), alien macroalgae (Misal and Sabale, 2016; Vitale et al., 2018; Cherry et al., 2019; Meinita et al., 2022), and even the poisonous *Lagocephalus sceleratus* (Çavaş et al., 2020).

5. Top predator status and trends: ecological implications, monitoring and mitigation strategies to promote ecosystem-based management

5.1 Introduction

5.1.1 Marine top predators in a changing environment

In the Anthropocene Era, marine predators occupying high trophic levels - including some marine mammal, elasmobranch, large teleost, reptiles and seabird species - have been reported to be rapidly declining worldwide and are generally assessed as threatened or in poor population conservation status (Phillips et al., 2016; Dulvy et al., 2017; Burgess and Becker, 2022; Ferretti et al., 2008; Rodriguez et al., 2019; Peterson et al., 2022). In addition to the issue of increasing extinction risk, top predator populations' fluctuations have been linked to cascading effects in food webs, behavioural modifications in prey communities, and overall losses of ecosystem functions and services (Myers et al., 2007; Heithaus et al., 2008; Estes et al., 2016; Baum and Worm, 2009).

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, 2000; Jackson et al., 2001; Myers and Worm, 2003; Lotze et al., 2006; Halpern et al., 2008; Ryan et al., 2009; Dias et al., 2019; Ripple et al., 2019; Giménez et al., 2022; Juan-Jorda et al., 2022).

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; Mazzoldi et al., 2019). In addition, marine top predators can be used as sentinels of marine ecosystem status (Coll et al., 2019b; Hazen et al., 2019), and changes in their abundance can act as an early warning of decreasing marine health (particularly in less deteriorated systems) 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 GES and informing management actions. For example, 23% of the indicators of the OSPAR 2023 Quality Status Report on the North-East Atlantic targeted top predators.

Given all this, conventional sectoral management and piecemeal governance, focusing on a single species or economic sector (e.g., fisheries), is widely 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; and (iv) management options and tradeoffs costs and effectiveness. This translates into an overall assessment of the costs and benefits of conservation efforts.

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 orcas*), 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, including the potential of novel methods (e.g., environmental DNA metabarcoding, biologgers, and remote sensing); (iii) data needs and modelling capacity for assessing the status and trends of top predators; and (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.

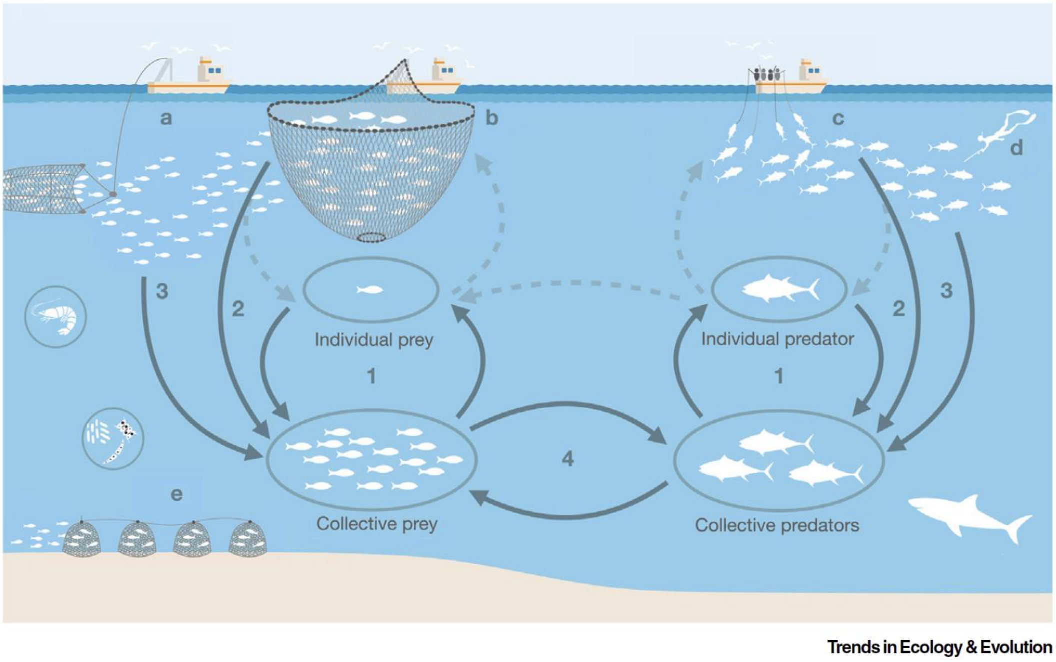
5.1.2 Marine ecosystem and international policy framework

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 their decline (e.g., ACCOBAMS, 2021; Geelhoed et al., 2022). In 1995 the UN CBD identified the 'Ecosystem Approach' as the main framework for biodiversity protection and sustainable use, from which most 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 approach 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 African-Eurasian Migratory Waterbirds, etc.) and regional supranational political and economic inter-governmental entities (e.g., the European Union). Regional commitments and policy tools (e.g., MSFD, EcAp, Maritime Spatial Planning Directive, Integrated Coastal Zone Management protocol, 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).

Examples of species and population recovery or stable decline in the Atlantic and Mediterranean Sea (Boxes 2 and 3) 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.

Box 2 - The recovery of the Atlantic bluefin tuna

A recent example of recovery, following management measures and favourable 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 International Commission for the Conservation of Atlantic Tunas (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 favourable 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 behaviour (Credits: Sbragaglia et al., 2021).

Box 3 - The Mediterranean Sea case

The Mediterranean Sea is a hotspot of both biodiversity (Coll et al., 2010; Serena et al., 2020) 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 to Endangered, recognizing an increasing trend (Karamanlidis and Dendrinos, 2015).

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 and Dendrinos, 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 and Dendrinos, 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 and Dendrinos, 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 behaviour to capitalize on these 'anthropogenic 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 (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 in the 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.

5.1.3 Effects of top predators on the whole marine ecosystem

The decline of marine top predators (e.g., Box 3) 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; Halpern et al., 2020).

There are several key examples of ecological consequences of marine top predator decline or loss. Baum and Worm (2009) conducted a global analysis of large predatory fish declines, such as sharks and tuna, and found that these declines were associated with changes in prey abundance and diversity and shifts in ecosystem structure and function. The decline in shark abundance at coral reefs caused increases in mesopredator densities and changes in their behaviour (Sherman et al., 2020). Similarly, Estes et al. (2009) showed that the decline of sea otters in the Aleutian Islands led to changes in sea urchin behaviour and increased abundance, 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 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 Pace et al. (2017) 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.

5.2 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.

5.2.1 Direct sampling methods to assess trends of top predator distribution and abundance

5.2.1.1 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 ICES (2017, 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).

5.2.1.2 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; Field et al., 2013; Louzao et al., 2011a; 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 of fisheries on top predators (Course et al., 2020), and can be very-cost effective providing valuable data, especially in combination with automated detection software.

5.2.1.3 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; Louzao et al., 2019; Giménez et al., 2018; Waggit et al., 2019) and land-based visual surveys (e.g., Arroyo et al., 2016; den Heyer et al., 2021; IJsseldijk et al., 2021; Gutiérrez-Muñoz et al., 2021). These sampling methods can produce robust absolute or relative abundance estimates (e.g., Hammond et al., 2013, 2021; Authier et al., 2018; Saavedra et al., 2018; García-Barón et al., 2019; ACCOBAMS, 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 moult 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 moult; 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; Westell et al., 2022; Amundin et al., 2022) or active sonars or echosounders detecting species based on their echoes (e.g., Bertrand and Josse, 2000).

5.2.1.4 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; Walker et al., 2012; Tavecchia et al., 2008). Depending on the type of artificial mark, individuals may need recaptures 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 5.3.1.2).

5.2.2 Indirect sampling methods to assess trends of top predator distribution and abundance

5.2.2.1 Biogeochemical markers to inform ecosystem modelling

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 13C/12C (δ13C), 15N/14N (δ15N), and 34S/32S (δ34S) ratio determinations in species tissues, has revolutionized the way we look at wild species' trophic ecology, particularly in marine top predators (Newsome et al., 2010; Bond and Jones, 2009). 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).

5.2.2.2 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, behaviour, trophic and social interactions, and internal state (McConnel 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 behavioural conditions (e.g., Louzao et al., 2011c; Hagihara et al., 2016).

5.2.2.3 Environmental DNA (eDNA)

The eDNA (i.e., the genetic material released to the environment by the organisms inhabiting the ecosystem) is a powerful approach for monitoring marine top predators. DNA traces of top predators can be retrieved by filtering some litters of water so that species present in a water mass can be identified even if they are not visually detected. This is especially useful for the most elusive species, such as deep diving odontocetes or bathypelagic sharks. There are two different approaches that can be used to analyse eDNA: overall community assessments (through metabarcoding) and species-specific detection (through quantitative PCR). The metabarcoding approach allows the simultaneous identification of several taxa using short, conserved DNA fragments (primers) that amplifying the DNA of the taxa of interest. These amplified regions (barcodes) are then high throughput sequenced and the resulting sequence are compared to reference databases. Metabarcoding has been applied to biodiversity studies of cetaceans (e.g., Juhel et al., 2020) and sharks (e.g., Mariani et al., 2021), proving to be effective for rare species.

Species-specific assays are designed to target single (or a few) species and they have been applied to detect presence of some top predators such as harbour porpoises (Foote et al., 2012), angel sharks (Faure et al., 2023) or scalloped hammerhead sharks (Budd et al., 2021). Some studies have even identified intraspecific genetic variability, such as different ecotypes of killer whales (Baker et al., 2018) or haplotypes in bowhead whales (Szèkely et al., 2020). Other studies have focused on prey variability in foraging areas (Berger et al., 2019). eDNA quantification is also possible with species-specific assays and is being applied to fishes (e.g., Knudsen et al., 2019; Shelton et al., 2022) but not to top predators, yet.

Top predators spend most of their time foraging and their behaviour and migrations depend on preys. Thus, understanding prey ecology is important in a climate change and overfishing scenario. Apart from water, DNA can be retrieved from other environmental samples such as soil or faeces. Sampling faeces is specially challenging in the marine ecosystem and has been mostly applied to pinnipeds, which come out of the water and defecate on the ground (e.g., Deagle et al., 2009). Most of the cetacean diet information comes from stomach contents from whaling era (outdated) and strandings (biased); thus, analysis of faecal samples could be the future solution. Some dietary studies have been performed with faeces of some cetaceans such as Bryde's whales (Jarman et al., 2006), killer whales (Ford et al., 2015) and blue whales (De Vos et al., 2018). The combination of water eDNA and faecal eDNA is a powerful approach to understand predator behaviours based on prey shifts (e.g., Carroll et al., 2019). Ecosystem-scale studies are required to contextualize top predator ecological status and eDNA analysis can contribute to megafauna monitoring and to identify fisheries and top predators overlapping areas (Albonetti et al., 2023). Whale faeces are also collected by whale watching vessels worldwide, being a potential application of citizen science.

5.2.2.4 Remote sensing and other digital tools

Remote sensing technologies also provide a non-invasive means for evaluating top predators' presence, distribution, and behaviour. 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 behaviour 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., 2023). The main advantages of emerging digital monitoring are reduced costs and almost real-time data (Lennox et al., 2022).

5.3 Modelling 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 analysed. One dimension in modelling approaches reflects data-driven models directly using monitoring data. Another dimension is based on first-principle assumptions and biological mechanisms. In this section, we review both dimensions and categorize modelling techniques according to their main targets (species, community, and ecosystem).

5.3.1 Population and demographic parameters and models

5.3.1.1 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, 2021; Fortuna et al., 2014; Authier et al., 2018).

5.3.1.2 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, 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).

5.3.1.3 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 ICES, and the General Fisheries Commission for the Mediterranean (GFCM). The age-structured stochastic modelling 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 conducts assessments of cetacean populations rather than of species, which is instead 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 4) 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.

5.3.2 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). This modelling 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; García-Barón et al., 2019; Chavez-Rosales 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).

Box 4 - 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.

5.3.3 Ecosystem modelling: from energy flows to multispecies and food-web interactions

5.3.3.1 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 modelling 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 δ15N 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 modelling TP using only values from the predator, as some amino acids are considered source (i.e., baseline) and others trophic (Bode et al., 2022).

5.3.3.2 Bioenergetic models

Bioenergetics modelling 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; Fortune et al., 2013; Louzao et al., 2014; Jeanniard-du-Dot et al., 2017; Rechsteiner et al., 2013; Winship et al., 2002; 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 centred on predictions of the responses of organisms and populations to novel environmental conditions. Although bioenergetics-based approaches can include mechanistic responses to climate-driven factors, many current modeling approaches highlight limitations in projecting climate change impacts at the population and community levels (Moullec et al., 2022; Erauskin-Extramiana et al., 2023).

5.3.3.3 Multispecies models

Several statistical and mechanistic approaches exist to model multiple species jointly. For example, Joint Species Distribution Models (JSDM) have emerged as a novel analytical framework to 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.

5.3.3.4 Mechanistic models

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).

5.3.3.5 Marine ecosystem models (EwE, SNS, Mizer)

Ecological processes and human activities can be explicitly incorporated into process-based marine ecosystem modelling (Fulton, 2010; Tittensor et al., 2018; Peck 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 food web components.

EwE has been widely applied to analyse 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 modelling 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 (Espoir 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 modelling approaches (Coll et al., 2020).

5.4 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 (Saenz-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 unfavourable 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 (followed by other countries), 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 harbour seal population in 1900 (Reijnders, 1992). However, bounties and regular hunting in previous centuries had already decreased the population by 1900 (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.

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 et al., 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; 2022).

5.5 Examples of assessments linked to policy frameworks

5.5.1 Assessment examples

The EU MSFD (Directive 2008/56/EC) and 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) 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 four descriptors: D1 'Biodiversity', D3 'Fishing', D4 'Food webs', and D11 'Energy and Noise'. 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 harbour 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 GES. In contrast, harbor porpoise is often classified as non-GES (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 skates (e.g., *Raja clavata*) and sharks (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 6, 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 6 shows only the 'state' criteria, not 'pressure'; hence fishery-related mortality (D1C1) was excluded.

Table 6. Marine Strategy Framework Directive (MSFD) Descriptor 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). Percentages refer to the proportion of the MSFD assessments reported for each criterion which used the specific indicator.

MSFD Criterion	Indicator for Seabirds	Indicator for Marine Mammals
D1C2 - Population abundance	Abundance (breeding, number of pairs) (32%)	Abundance (number of individuals) (57%)

MSFD Criterion	Indicator for Seabirds	Indicator for Marine Mammals
	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
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%)

MSFD Criterion	Indicator for Seabirds	Indicator for Marine Mammals
		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

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 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 (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 (with the exception of specific countries) to gather 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.

5.5.2 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 (e.g., Fortuna et al., 2018). To complement the use of MPAs and fully harness their strengths, it is crucial to incorporate additional tools into the manager toolkit, such as, for example, Maritime Spatial Planning (MSP) and Other Effective area-based Conservation Measures (OECMs). 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). However, human-wildlife interactions are rarely explicitly addressed in planning and rarely in MSP (García-Barón et al., 2021; Shabtay et al., 2020). The OECMs represent a novel conservation approach distinct from MPAs, as they contribute to conservation goals as a by-product of other management objectives targeting specific human activities (Laffoley et al., 2017).

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 often lacks systematic conservation planning principles, and focus is put on structural characteristics of habitats and iconic species 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 (Afan 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 (Coll et al., 2015; Louzao et al., 2006; 2012). 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).

5.6 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 Text 2. The aim was to identify (i) the concerned threats, (ii) the types of conservation actions applied, (iii) how their performance was assessed, (iv) the factors contributing to their success or failure, and (v) 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 (Figure S2). 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 7A). Over 50% of these success stories occurred in temperate regions of South America, Southern Africa, and the Northern Atlantic (Figures 7B, 8). The country with the most reported success stories was South Africa (18%), followed by Australia (14%), the US (13%), and Brazil (11%) (Figure S3). However, the global distribution of success stories varied by taxon (Figures S4–S7).

Management measures were predominantly local (Figure 7C); 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 (Figure S8). 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 7D).

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 9A). Most population trends for which a trend was available were classified as declining (Figure 9B).

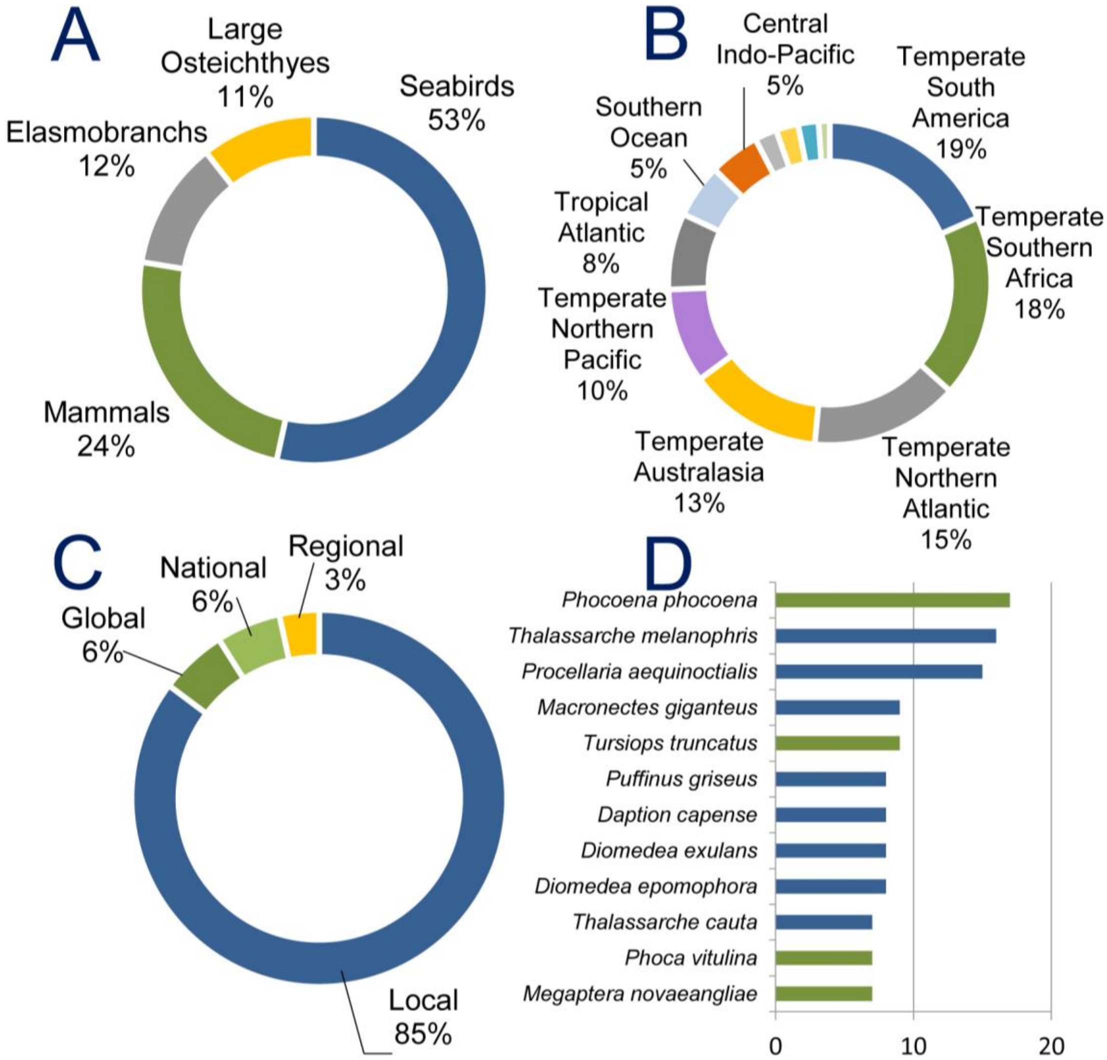


Figure 7. (A) Share of the four taxonomic groups in the success stories retrieved through the systematic review. (B) Distribution of success stories in marine realms (sensu Spalding et al., 2007). (C) The scale of management measures implemented in success stories. (D) Most commonly targeted species by management measures in the reviewed success stories (green: mammals, blue: seabirds).

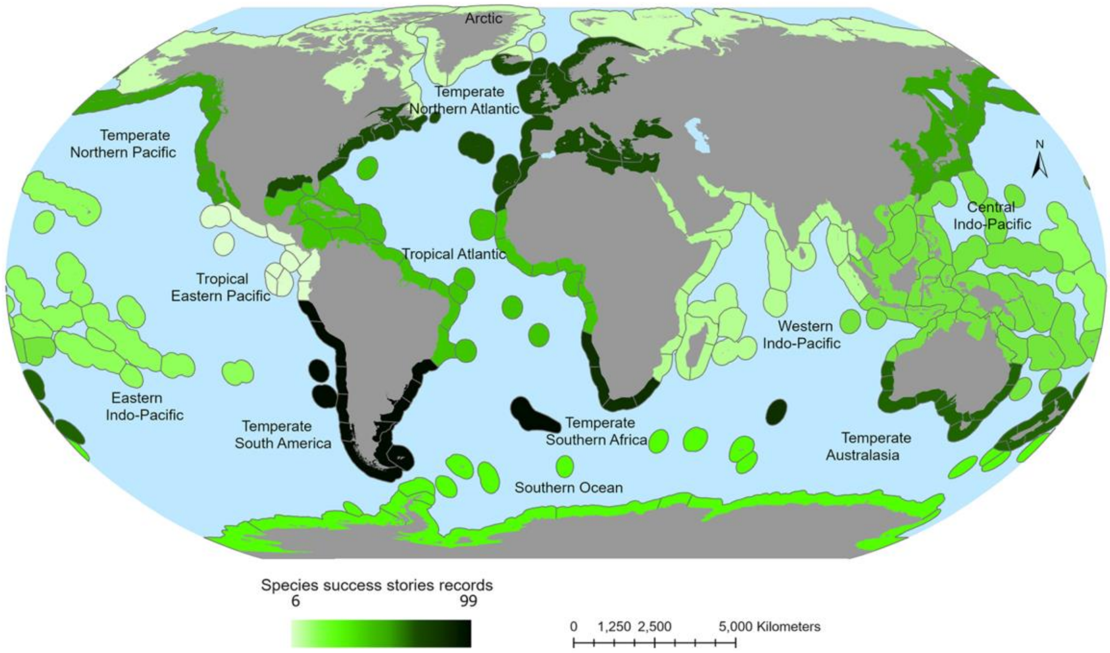


Figure 8. Spatial distribution of success stories in the twelve marine realms, sensu Spalding et al. (2007)

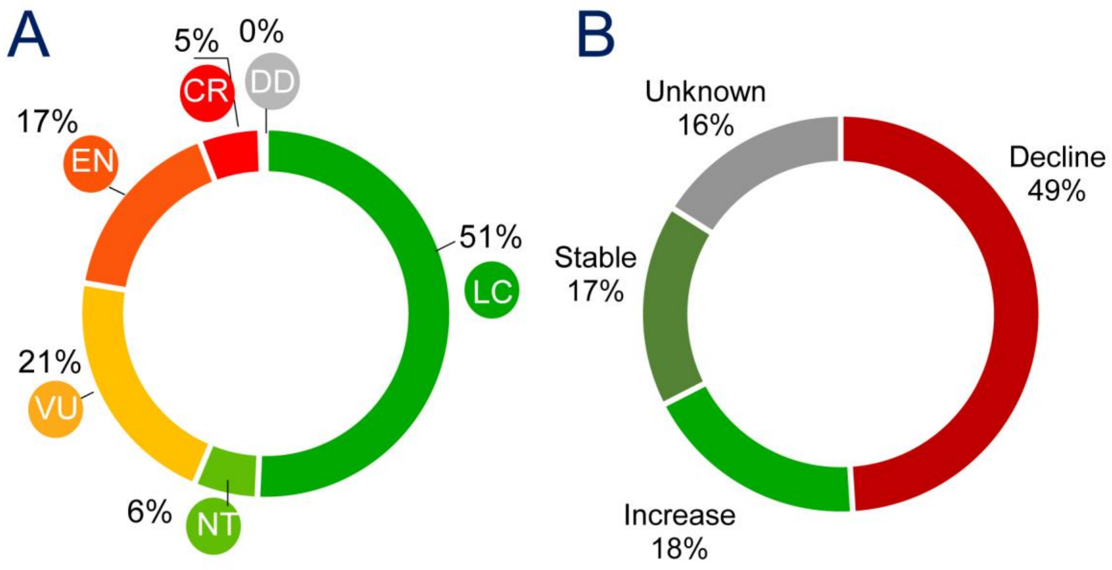


Figure 9. (A) The IUCN Red List categories of the species reported in success stories (CR: Critically Endangered, EN: Endangered, VU: Vulnerable, LC: Least Concern, DD: Data Deficient). (B) The regional population trends of the species reported in success stories according to the IUCN Red Lists assessments.

The most commonly reported management measure was bycatch reduction (57%), followed by the establishment of MPAs (15%) and invasive species management (6%) (Figure 10A). The frequency of the types of management measures in success stories significantly differed by taxonomic group (chi-square test; $p < 0.0001$) (Figure 11). 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 (Figure S9).

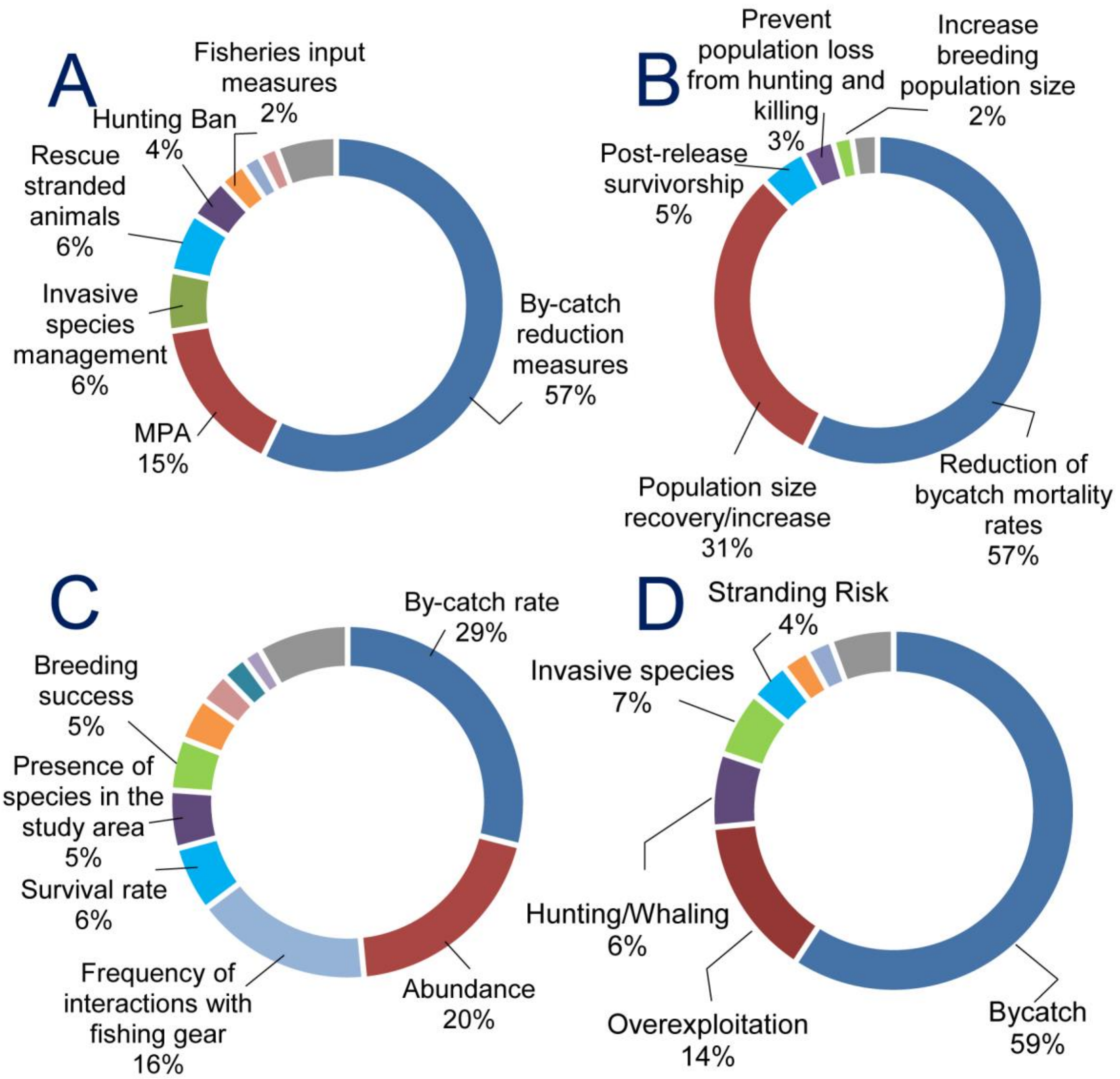


Figure 10. Summary of success stories including (A) share of the management measures, (B) conservation actions targets, (C) indicators of project success, and (D) threat mitigated.

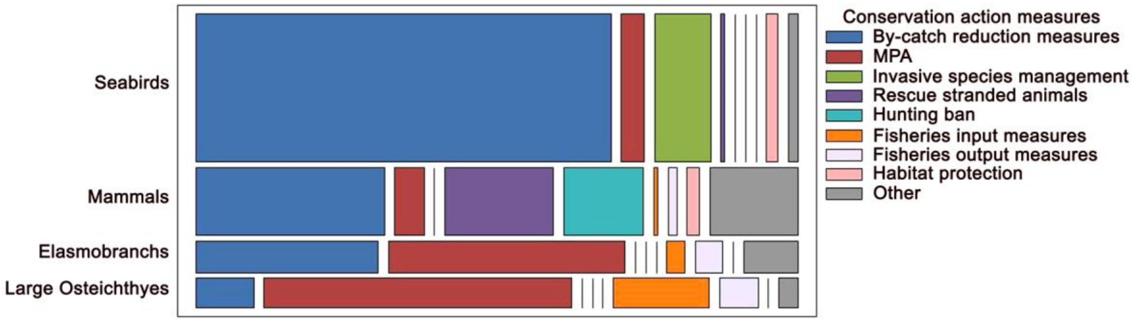


Figure 11. Type of management measures reported in success stories by taxonomic group (Key: the bar size is proportional to the number of success stories)

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 10B).

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 10C). The most common threat reported was bycatch (59%), followed by overexploitation (14%), hunting/whaling (6%), and invasive species (7%).

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 (Figure S10). 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 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 UK 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 (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 success stories as playing a vital role in conservation efforts, ensuring that stakeholders, including local communities and industry sectors, are aware of the importance of sustainable practices (Huang, 2011).

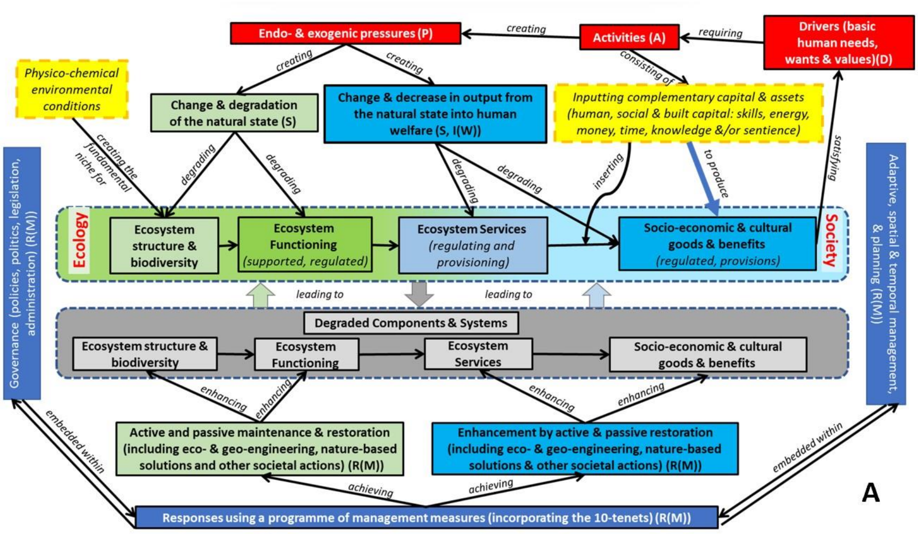
In success stories, the effective establishment and function of MPAs were attributed to a combination of social factors, effective self-enforcement by local stakeholders, good compliance, and widespread support from local communities (Guidetti et al., 2008; Aburto-Oropeza et al., 2011; Jaiteh et al., 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 3) 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.

5.7 The way forward - recommendations

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 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) 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 (Fig. 12A), 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 Fig. 12A). Fig. 12B lists all elements of the DAPSI(W)R(M) matrix that are deemed relevant to top predators, according to our analysis.



Drivers	Commerce (transport, shipping)	
	Food provision	
	Safety	
	Production of goods	
	Tourism and Recreation	
	Off-shore wind farms	
Activities	Aquaculture	
	Commercial fisheries	
	Hunting	
	Recreational diving	
	Recreational fisheries	
	Shipping	
	Touristic development of the coastal zones	
	Heavy industries (incl. Plastics industry)	
Pressures (endo- & exogenic)	Bycatch	
	Chemical contamination	
	Climate Change	
	Deliberate killing	
	Habitat degradation	
	Invasive Species	
	Marine litter	
	Overexploitation	
	Parasite infections	
	Ship collisions	(?)
	Energy-originated pressure (i.e., underwater noise, electromagnetic fields)	
State	Loss of ecosystem functioning (e.g., ocean nourishment, carbon sequestration, cultural and recreational services)	
	Population decline	
	Range reduction/fragmentation	
Impact (Welfare)	Disruption of the food chain	
	Economic damages to the fishing industry	
	Loss of ecosystem services (e.g., ocean nourishment, carbon sequestration, cultural and recreational services)	
Response (Measures)	Antiparasitic treatment	
	Bans: hunting, finning, fishing (no-take/no-entry zones, ban on gears)	
	Bycatch reduction measures	
	Ecosystem-based fisheries management	
	Ecotourism promotion	
	Habitat restoration	
	Invasive species management	
	Reintroductions/translocations	
	Rescue plans for stranded individuals	
	Restoration of reproduction habitats	
	Area-based conservation tools (MPAs, FRAs and OECMs networks)	
	Vessel restrictions	(?)

B

Figure 12. (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 top predators, according to this review.

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 (Lotze et al., 2011; Jackson et al., 2001; Worm et al., 2006). Rebuilding and restoring efforts can be successful (e.g., Bowen and Iverson, 2020) but may require sustained conservation measures and robust EBM 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. The proposed EU Restoration Law (European Parliament 2023) recognizes the need to restore specific top predator populations in its preamble: "It is important that restoration measures are also put in place for the habitats of certain marine species, such as sharks and rays, that for example, fall within the scope of the Convention on the Conservation of Migratory Species of Wild Animals or of the European Regional Sea Conventions' lists of endangered and threatened species, but outside the scope of Directive 92/43/EEC, as they have an important function in the ecosystem."

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 7. We need to highlight that in many countries, most of these recommendations have become common practice; however, scaling-up is what is still missing for a large-scale positive outcome at global population level.

Table 7. 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 • Fishery stakeholders	⇨ Reduction of human-induced mortality leads to recovery of top-predator population and species ⇨ Meet RFMOs and single stakeholders declared sustainability objectives
	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 necessary stakeholders, but preserving the concept of science-based management	• EU funding agencies • National and regional authorities	⇨ Scale-up data collection and improve our knowledge and understanding on top 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

5.7.1 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 2 and 3). 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 Fig. S8). 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.

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 4) 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 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 modelling 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) and the potential ecological benefit on the concerned species.

5.7.2 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 modelling 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, including Local Ecological Knowledge (Sáenz-Arroyo et al., 2005; Maynou et al., 2011; Coll et al., 2014), incorporating novel approaches can greatly enhance our knowledge, particularly when combined with established techniques (Ramos et al., 2009; Louzao 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 behaviour 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-Bregu et al., 2022; Valsecchi et al., 2023), or the consideration of publicly available information sourced from digital media (e.g., Sbragaglia et al., 2023), 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 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.

6. Management of jellyfish outbreaks to achieve Good Environmental Status

6.1 Introduction

Jellyfish have long been associated with stinging risks to bathers and adverse impacts on other socioeconomic activities at sea (Bosch-Belmar et al., 2021b; Lee et al., 2023). However, recent recognition of their significance as important components of marine biodiversity highlights their ecological roles and contribution to the provision of various ecosystem services and benefits to humans (Graham et al., 2014; Culhane et al., 2019), to the extent that a few species receive protection in specific regions in response to the requirements of the Convention on Biological Diversity (e.g., *Haliclystus auricula, Calvadosia campanulata, C. cruxmelitensis*) (United Kingdom, 2006).

The term "jellyfish" collectively encompasses gelatinous zooplankton from diverse taxonomic groups, including Cnidaria (true jellyfish: the planktonic life stages of Hydrozoa, Scyphozoa and Cubozoa), Ctenophora (comb jellyfish), and pelagic tunicates (e.g., larvaceans, salps) (Boero, 2013; Jaspers et al., 2023) (Fig. 13). Many cnidarian jellyfish species undergo complex life cycles, often including coexisting benthic (polyp) and pelagic (medusae) morphs (Russell, 1953, 1970).

Jellyfish impacts typically result from sudden increases in the abundance of populations, which can lead to a mass occurrence at various spatial scales (from localized patches of few meters to swarms detectable for kilometres). This may be due to a high reproductive and developmental potential, for which several medusozoan jellyfish are renowned (e.g., *Aurelia* spp.). Most reported jellyfish mass occurrences are known for a relatively small number of scyphozoan species, but several hydrozoans – due to their complex pelago-benthic life cycles – are also known to release large numbers of small-sized and hardly noticeable free-swimming medusae. Overall, a limited number of cnidarian jellyfish taxa exhibit high biological potential for rapid population growth, mostly in a restricted number of genera of Rhizostomeae and Semaeostomae scyphozoans (Hamner and Dawson, 2009; Fernández-Alías et al., 2021; Leoni, 2022). In other cases, highly venomous species (e.g., *Chironex fleckeri, Physalia physalis*) can exert considerable impacts by a few individuals (e.g., Lippmann et al., 2011; Cegolon et al., 2013).

Local short-term jellyfish concentrations may form in particular environments, due to passive drifting or active behaviour of individuals (Hamner and Dawson, 2009). These accumulations should be referred to as "aggregations" (mostly driven by passive drifting) or "swarms" (mostly driven by active behaviour). In turn, a monospecific mass proliferation due to demographic change is usually referred to as "outbreak", referable to the outbreak-forming potential of a minority of gelatinous taxa characterized by sexual and asexual reproduction. Only those outbreak-forming species have the potential to become invasive (either native or non-indigenous) in a certain habitat (Valéry et al., 2008). In contrast, "blooms" is a term widely attributable to pulses of both primary and secondary production, and it is often applied to describe episodic, multi-specific assemblages of diverse phytoplankton and zooplankton taxa.

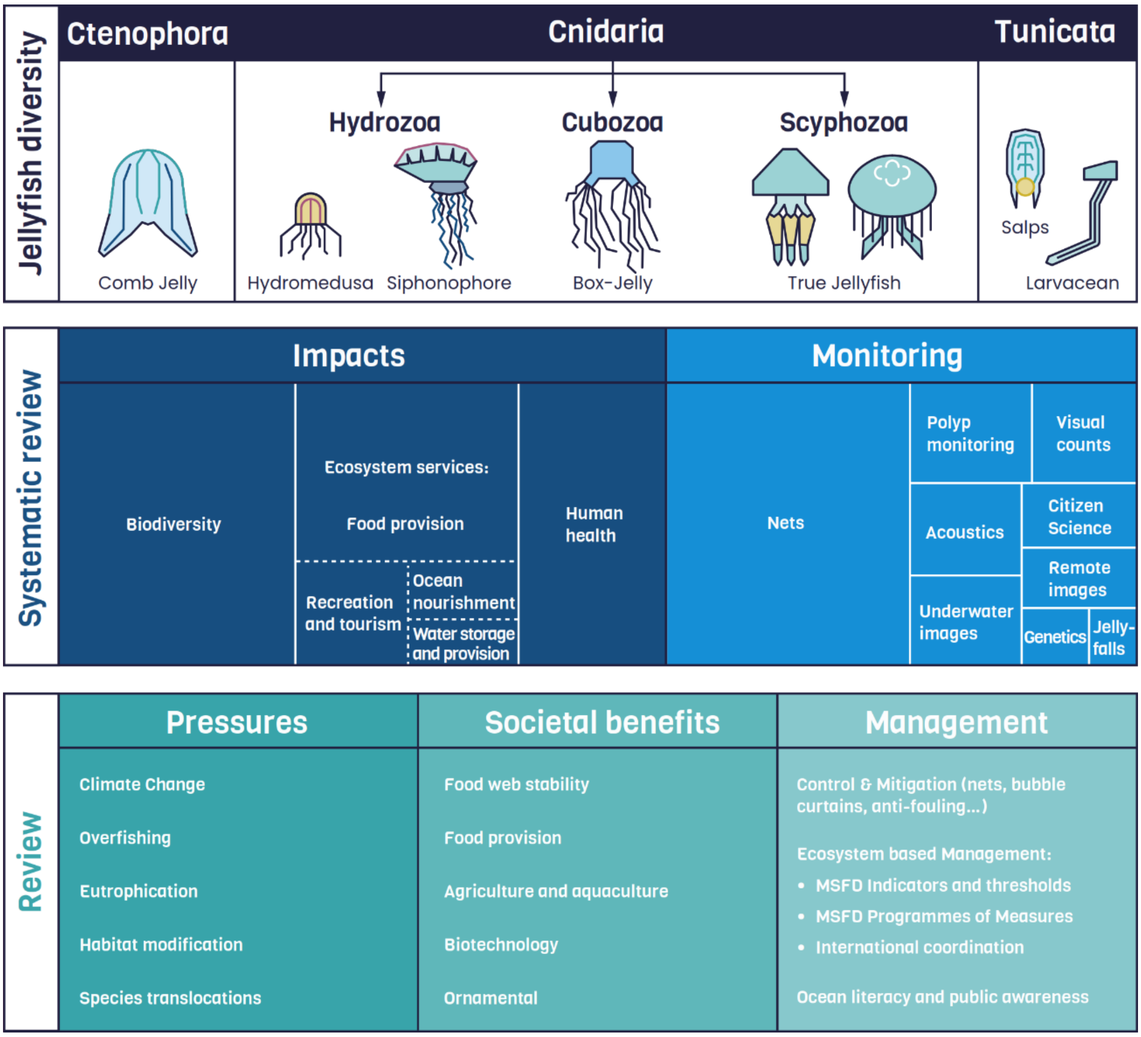


Figure 13. Overview of the different aspects related to jellyfish covered by this study

Gelatinous zooplankters exhibit prompt responses to environmental changes and are sensitive to various human-related pressures, such as climate change, pollution, and overfishing (Mills, 2001; Purcell et al., 2007; Richardson et al., 2009). These sudden shifts in jellyfish population dynamics can have significant impacts on marine biodiversity, food webs, and ecosystems, as well as on human health and human activities at sea, with relevant socio-economic consequences. Therefore, their presence, absence, or population dynamics in a region can offer valuable insights into the ecological quality status and trophic regimes of marine ecosystems.

Despite their importance, the ecological roles of jellyfish are often grossly oversimplified or misunderstood, and jellyfish remain poorly monitored compared to other zooplankton groups (Templeman et al., 2021). Currently, jellyfish management is mainly focused on responsive control and mitigation of local impacts (Dong, 2019) and few resources are allocated to regular monitoring of jellyfish populations by managers due to an assumption of their uncontrollable nature (Aubert et al., 2018). However, as marine ecosystems continue to change due to advancing ocean warming and human activities, paralleled by a concurrent increase in abundance and frequencies of jellyfish records in coastal waters (Brotz and Pauly, 2012; Lee et al., 2023), research and assessment of gelatinous zooplankton has become essential in supporting EBM strategies. These strategies aim to anticipate and manage jellyfish outbreaks, rather than merely reacting to emergencies at higher costs and societal impacts (Brodeur et al., 2016). Recognizing the need for jellyfish research, the United States first mandated their study through the Jellyfish Control Act of 1966.

In Europe, the MSFD (European Commission, 2008) marked a significant milestone in adopting an ecosystem-based management approach for the sustainable supply of marine goods and services across Europe. The initial MSFD's objective was to achieve GES in European seas by 2020 (now, by 2026) (European Commission, 2020). Implemented through a six-year adaptive management cycle, the MSFD includes assessing the status of the marine environment and its essential features, analysing 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) and establishing environmental targets and associated indicators (Art. 10 MSFD) are essential, leading 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 the assessment of the abundance and distribution of key taxa with fast turnover rates, i.e., rapidly responding to environmental changes, as early warning indicators of the food web functioning (Rogers et al., 2010).

However, despite some dedicated project funding calls (e.g., FP7 Oceans of Tomorrow: FP7-OCEAN-2010-2), jellyfish were nearly 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 analysis techniques as well as assessment strategies and tools that can foster the inclusion of jellyfish information in the MSFD assessments (Magliozzi et al., 2021).

In this context, our study includes reviews of the main impacts, pressures and management options currently described in the literature along with current and upcoming monitoring methods and indicators applicable to jellyfish assessments (Fig. 13). This study seeks to contextualize these findings within the MSFD implementation framework, offering practical information to policymakers for the ecosystem-based assessment and management of jellyfish in European coastal and oceanic areas. For the needs of this study, we consider any pelagic or benthic life stage of “gelatinous” taxa such as cnidarians, ctenophores, pelagic tunicates (hereinafter collectively referred to as “jellyfish”) that has or may have the potential to affect biodiversity and ecosystem services, either positively or negatively.

6.2 Methods

The organization of this work included a one-day face-to-face workshop and several successive virtual meetings. The review method includes (i) a traditional literature review based on comprehensive, critical, and objective analysis of the current knowledge for pressures, indicators, and management sections and (ii) three systematic literature reviews following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al., 2009), conducted for the impacts and monitoring techniques sections.

The detailed criteria used in the systematic reviews are the following ones:

For the impacts review, 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 2,337 and 1,322 articles from Scopus and Web of Science online databases, respectively (Fig. S11). Screening of additional publications identified within the references of assessed articles or reviews was carried out (n = 149 articles). Following the removal of duplicate entries, a total of 2,548 articles remained for the initial screening stage. Four reviewers assessed the articles for eligibility for inclusion in the second-stage screening, based on the titles and abstracts. To ensure inter-rater reliability, the reviewers independently evaluated a randomly selected sample of 50 retrieved articles, subsequently discussing any discrepancies. This validation process occurred during two virtual meetings involving all participant reviewers. Due to this process, 301 articles were selected for the second-stage screening. 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. Ultimately, 211 articles were included for data extraction.

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 (based on Katsanevakis et al., 2014b) (Table S5), (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) (Table S6), and (7) any indication of benefits from jellyfish.

For the monitoring efforts systematic review, 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 database, covering peer-reviewed literature from 2008 (year of the MSFD publication) to 20th April 2023. The initial search yielded 1,077 and 645 articles from Scopus and Web of Science online databases, respectively (Fig. S12). Screening of additional publications identified by experts was carried out (n = 5 articles). Following the removal of duplicate entries, a total of 1,126 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 selection criteria applied included the mention of gelatinous zooplankton identification techniques, the use or development of monitoring tools, and the specific languages (English, Spanish, Italian, Portuguese, Greek, or French). Each reviewer independently evaluated a third of the total number of 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. Due to this process, 267 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, 200 articles were included for data extraction.

An additional search was performed specifically for monitoring focused on jellyfish 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 290 (Scopus) and

177 (Web of Science) papers published from 2008 to 19th June 2023 was reduced to 297 after removing duplicates (Fig. S13). These papers were consecutively screened by title, abstract and full text by three reviewers, resulting in 69 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, 68 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 finally 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) jellyfish species considered, (6) monitoring objectives, and (7) results related to stressors present in the area of jellyfish proliferation, predictions, geographical or phenological changes, abundance/biomass (and units used), outbreak periodicity, and shifts in species composition. All figures were created using the open-source software R 3.6.0 (R Core Team, 2020) and the `ggplot2´ package (Wickham, 2016).

6.3 Impacts of jellyfish outbreaks

The systematic review of articles related to the impacts of jellyfish revealed that most of the studies were conducted in the temperate Northern Atlantic region (57%), followed by the temperate northern Pacific (13%), the central Indo-Pacific (7%), the temperate South America (6%), and the western Indo-Pacific (5%) (Fig. 14A), with very few studies in other regions (less than 5%). Also, after the early 2000s studies about negative jellyfish impacts increased (Fig. 14B). Most of the studies reviewed focused on jellyfish's impacts on biodiversity, food provision, or human health (Fig. 14C). The term "biodiversity" is used in line 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). Fewer studies addressed impacts on recreation and tourism, ocean nourishment and water storage.

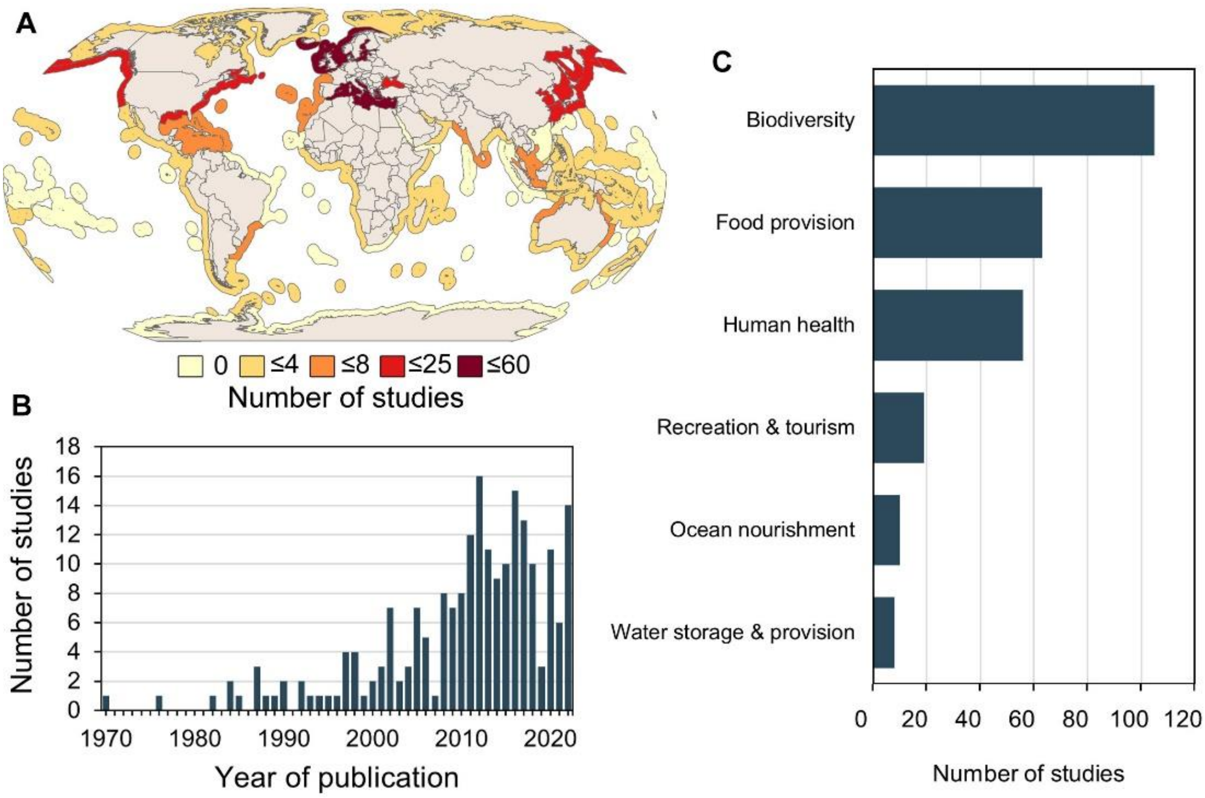


Figure 14: (A) Spatial distribution of studies investigating negative impacts of jellyfish on biodiversity, ecosystem services and human health, (B) number of studies published per year investigating jellyfish impacts, and (C) number of studies investigating jellyfish impacts on biodiversity, ecosystem services categories (food provision, recreation and tourism, water storage and provision, and ocean nourishment) and human health.

Impacts on biodiversity and ecosystem services were investigated mostly in the northern hemisphere, especially in the northern European Seas and the Mediterranean Sea (Fig. 15A, B). Human health impacts, though less frequently reported, were found along most temperate and tropical coasts (Fig. 15C). Stings were the primary cause of human health impacts, and only three articles identified jellyfish as potential vectors of pathogens (Basso et al., 2019; Stabili et al., 2020, 2022). Fatal cases were reported mainly in the central Indo-Pacific (Fig. 15C) and involved mainly box jellyfish (class Cubozoa), such as *C. fleckeri* (Currie and Jacups, 2005), but also scyphozoans, such as *Nemopilema nomurai* (Fenner and Williamson, 1996; Kim et al., 2018). Fewer reports were reported from the Atlantic coasts (Fenner and Williamson, 1996).

Among the species frequently cited for impacting biodiversity, *Mnemiopsis leidyi* (n = 28 articles), *Aurelia aurita* (n = 19) and *Pelagia noctiluca* (n = 10) were most prominent. For ecosystem services impacts, 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), and *C. fleckeri* (n = 6). A detailed enumeration of the reported species associated with different adverse impacts is included in Table S7. However, taxa known to be formed by a complex of cryptic species have often been misidentified and typically referred always to as a single, most popular species (e.g., the moon jellyfish *A. aurita*).

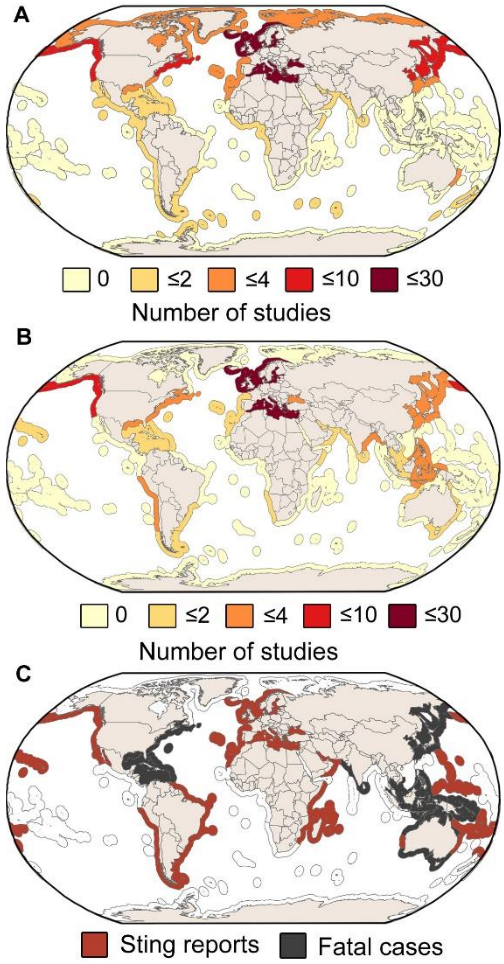


Figure 15: Spatial distribution of studies investigating jellyfish impacts on (A) biodiversity and (B) ecosystem services. (C) Marine provinces where stinging events were reported from the retrieved studies and fatal cases.

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; Jaspers et al., 2020; Stabili et al., 2022), reduction of light penetration (Zaitsev, 1992; Stoner et al., 2014), behavioural changes of species in order to avoid jellyfish (Carr and Pitt, 2008; Chittenden et al., 2018), and envenomation (Helmholz et al., 2010) (Fig. 16A). "Modification of trophic flows" as a mechanism of impact on biodiversity refers to the ability of jellyfish to indirectly induce changes to the community and trophic relations, thus potentially affecting ecosystem functioning through trophic cascades (Dinasquet et al., 2012a; Tiselius and Møller, 2017). Such modifications may occur through predation (Schneider and Behrends, 1998; Dinasquet et al., 2012a; West et al., 2009a), jellyfish decay (Tinta et al., 2012; Chelsky et al., 2016) and mucus and nutrient excretion (West et al., 2009b; Condon et al., 2011; Dinasquet et al., 2012b; Manzari et al., 2015; Marques et al., 2021). Most studies investigating impacts on biodiversity drew conclusions primarily from non-experimental correlations, followed by manipulative experiments and expert judgment, direct observations, and modelling (Fig. 16B). Hence, for a substantial portion of the reported impacts the strength of evidence was low.

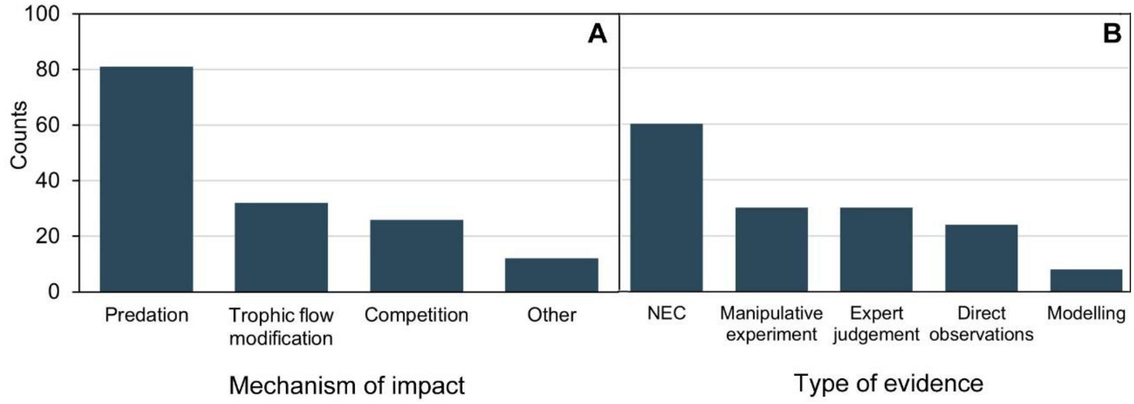


Figure 16: (A) Counts of the reported mechanisms of impacts of jellyfish on biodiversity. "Other" includes reduction of light penetration, disease transmission, envenomation and behavioral changes to other species. (B) Counts of type of evidence for the reported impacts of jellyfish on biodiversity. "NEC" stands for non-experimental based correlations.

Jellyfish impacts on biodiversity were predominantly categorized as moderate in magnitude (n = 77 impact reports), where moderate refers to induced population declines in other species but without altering the community structure or the biotic and abiotic parameters of the environment (Blackburn et al., 2014). The body of knowledge is replete with evidence of jellyfish species effectively preying on various planktonic organisms, including copepods, pteropods, rotifers, cladocerans, chaetognaths, hydromedusae, fish larvae and eggs, consequently leading to reduced population abundances (Fraser, 1970; Burrell and Van Engel, 1976; Møller and Riisgård, 2007; Wang et al., 2020; Budiša et al., 2021).

Minor impacts were also prevalent (n = 43) and pertained to instances in which jellyfish could compromise the fitness of individuals, albeit without clear indications of driving population declines (Brodeur et al., 2008; Shoji et al., 2009; Helmholz et al., 2010; Tilves et al., 2018a; Basso et al., 2019). Minimal impacts were infrequently reported in the literature (n = 11). This category encompasses species that are exerting negligible detrimental effects on the ecosystem (Drits et al., 1992; Møller and Riisgård, 2007; Marques et al., 2021). The under-representation of this category may be due to publication bias, as non-significant results are less likely to be published (Jennions and Møller, 2002).

Jellyfish are classified as having major impacts (n = 21) when they result in the local extinction of at least one prey species. During outbreak phases, jellyfish can significantly diminish the density of prey populations, yet typically the species and the community can recover after the wane of the jellyfish outbreak (Zaitsev, 1992; Uye et al., 2003; West et al., 2009a; Yilmaz, 2015). “Massive” impacts have not been documented for jellyfish species. According to Blackburn et al. (2014), for an impact to be classified as massive, it necessitates the local extinction of at least one species and the subsequent induction of irreversible changes within the community. However, non-indigenous gelatinous zooplankton organisms can have a significant impact on food web structure and functioning (Tiselius and Møller, 2017; Van Walraven et al., 2017; Jaspers et al., 2018), with documented shifts in community structure from mesozooplankton to microbial loop-dominated food webs (e.g., Riisgård et al., 2012).

Conversely, jellyfish can also offer significant benefits to humanity and contribute to sustainable development (Doyle et al., 2014; Leone et al., 2015). They can help to support biodiversity as they are an important food source for various species, including top predators and threatened species like sea turtles and fish (Cardona et al., 2012; Jarman et al., 2013; Mianzan et al., 2014; Smith et al., 2016). Moreover, some species can act as biological regulators of invasive species, for instance, *Beroe ovata* played a major role controlling the population of *M. leidyi* in the Black Sea (Finenko et al., 2003). Additionally, certain jellyfish species 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., 2018b). In the Mar Menor lagoon, an ecosystem under significant stress, jellyfish may play a role in maintaining water quality through a top-down process and preventing dystrophic crises. Their selective feeding prevents the proliferation of large phytoplankton cells while allowing smaller phytoplankton to thrive. Consequently, this activity shapes the composition of both zooplankton and phytoplankton communities differently from what would be expected under eutrophicated conditions without the control exerted by jellyfish (Pérez-Ruzafa et al., 2002, 2019; Fernández-Alías et al., 2022).

Jellyfish provide other ecosystem services, including food provision for human consumption. For millennia, jellyfish have been consumed in Asia and in some areas are considered delicacies (Omori and Nakano, 2001; Brotz and Pauly, 2017; Syazwan et al., 2020). Recently, there has been growing interest also in Western countries regarding jellyfish as a sustainable food option and at least 15 species have the potential to support jellyfish fisheries in Europe (Brotz, 2016; Brotz et al., 2017; Leone et al., 2019; Bleve et al., 2019; Youssef et al., 2019; Duarte et al., 2022; Edelist et al., 2021; Raposo et al., 2022). The target species are particularly large-sized Rhizostomeae, with low stinging potential and high population density in recurring annual blooms, such as *Rhizostoma pulmo*. In the framework of the Horizon 2020 GoJelly project (2018-2021) new jellyfish processing were tested and developed, overcoming the limitations of traditional Asian processes and resulting in new patented jellyfish foods

(Bleve et al., 2019, 2021; Leone et al., 2021; Ramires et al., 2022a, b). In the absence of significant consumption, jellyfish are so far labelled as a "novel food" under the current European Regulation (EU Regulation 2015/2283), however, the scientific assessments of quality and safety carried out on different Mediterranean species, including non-native species such as *Rhopilema nomadica*, and the globalization of the food markets, will probably allow an opening to the exploitation of jellyfish for human food uses in Western Countries. This will raise the issue of massive taking of single species for commercial purposes in the Mediterranean Sea. In principle, commercial harvesting can potentially contribute to the control of jellyfish outbreaks; however, ecological considerations and potential impacts on the pelagic food-webs, including outbreaks of other non-targeted jellyfish, should be carefully considered before providing incentives for such fisheries (Gibbons et al., 2016; Hays et al., 2018).

Jellyfish focal harvesting or jellyfish as by-catch may also offer novel resources to diverse industries and economic activities. For instance, they can support sustainable agriculture used as organic fertilizers (Emadodin et al., 2020), as insecticide products (Yu et al., 2005, 2014), or as feedstock for terrestrial animals and for aquaculture (Duarte et al., 2022).

Notably, jellyfish provide important biomaterial for medical applications and research (Widdowson et al., 2018; Ahn et al., 2018; Rastian 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, which he uncovered by studying *P. physalis*. From the serendipitous discovery of green fluorescent protein (GFP) in the crystal jellyfish *Aequorea victoria*, in 1962, by Shimomura et al. (1962), the biotechnological potential of cnidarians started to attract the attention of researchers for their well-documented ability to produce powerful toxins and venoms (Turk and Kem, 2009). However, further research has demonstrated that bioactive compounds produced by the biochemical biodiversity of cnidarians are more than toxins and venoms. Bioactive compounds from various jellyfish species have been examined for their antioxidant, anticancer, antihypertensive, and antimicrobial properties, suggesting potential use in the pharmaceutical sector (Ranasinghe et al., 2022). Furthermore, in the fields of biotechnology and biomedicine, utilizing jellyfish biomass has been explored for designing cell-scaffold devices to address nonhealing skin wounds, a significant socio-economic challenge in recent decades (Nudelman et al., 2019; Fernández-Cervantes et al., 2020). Structural proteins such as collagen, abundant in some thick-bodied species, produce, by hydrolysis, antioxidant and anti-inflammatory peptides (De Domenico et al., 2019), while zooxanthellate jellyfish such as *Cotylorhiza tuberculata* and *Cassiopea andromeda* holobionts represent a source of powerful antioxidant and cancer-preventive compounds coming also from the endosymbiotic zooxanthellae (De Domenico et al., 2023; De Rinaldis et al., 2021; Leone et al., 2013).

Jellyfish may also offer other provisional services, such as contributing to the aquarium trade (Duarte et al., 2022), serving as bait for fishermen (Mianzan et al., 2014), and more recently jellyfish material is proposed as a potential alternative for replacing fossil-based plastics (Steinberger et al., 2019). In recent years, several studies described some vital regulatory ecosystem services provided by jellyfish. Further, pelagic tunicates, such as salps (Décima et al., 2023) and larvaceans (Jaspers et al., 2023) have a significant capacity to fuel carbon sequestration, highlighting their crucial role in carbon export amidst the ongoing climate crisis. Moreover, it has been proposed that jellyfish mucus might be used as bio-flocculation material for trapping and sequestrating plastic micro- and nanoparticles from contaminated waters of factories where microplastic is produced (Patwa et al., 2015; Lengar et al., 2021).

6.4 Potential pressures causing jellyfish outbreaks

Attributing jellyfish outbreaks to specific causes, whether natural or anthropogenic, is often challenging and accompanied by uncertainty (Lee et al., 2023). Despite public perceptions of a global upsurge in jellyfish outbreaks often linked to climate change, this claim lacks substantiation due to the lack of reference baselines and limited long-term gelatinous zooplankton data (Condon et al., 2012). This perception bias is evident in media reports, as localized gelatinous zooplankton outbreaks, which were historically documented, are portrayed as novel phenomena (e.g., fish kills in the British Isles by *P. noctiluca* outbreaks).

Increases in jellyfish populations appear often to be influenced by a combination of human activities, which might interact synergistically to trigger outbreaks of certain jellyfish species (Richardson et al., 2009). The evidence suggests that factors such as species translocations, overfishing, eutrophication, climate change, and habitat modification and degradation could contribute to the proliferation of jellyfish, particularly in coastal areas (Table 8). For example, the *M. leidyi* invasion in the Black Sea began with its introduction through ballast waters. The subsequent population explosion was likely propelled by several interconnected factors, including diminished predation due to overfishing-inducing declines in predatory populations (Daskalov et al., 2007), climate variation (Oguz et al., 2008), and eutrophication (Oguz, 2005).

Jellyfish have a range of attributes that enable them to thrive in disturbed marine ecosystems, including a broad diet (Purcell, 1992; Nagata et al., 2015; Lilley et al., 2009; Fleming et al., 2015), rapid growth rates (Marques et al., 2015; Jaspers et al., 2023), tolerance of harsh conditions (Purcell, 2012) and 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). These attributes allow jellyfish to capitalize on ecological opportunities presented by anthropogenic activities. Various human-related causes of jellyfish outbreaks have been reported in the literature (Table 8).

Table 8: Potential causes (pressures) of jellyfish outbreaks reported in the literature.

Cause of jellyfish outbreaks	**Natural / anthropogenic**	**References (non-exhaustive)**
Eutrophication	anthropogenic	Parsons and Lalli (2002), Richardson et al. (2009), Dong et al. (2010)
Climate change	anthropogenic	Mills et al. (2001), Purcell (2005), Purcell et al. (2007), Dong et al. (2010), Feng et al. (2015), Decker et al. (2023)
Climate variation	natural	
Power plants' thermal effluents	anthropogenic	Purcell et al. (2007)
Turbidity	Anthropogenic/natural	Purcell et al. (2007)
Hypoxia	Anthropogenic/natural	Purcell et al. (2007), Shoji et al. (2010)
Fisheries' induced decline of predators	anthropogenic	Purcell and Arai (2001), Purcell et al. (2007), Daskalov et al. (2007), Richardson et al. (2009), Dong et al. (2010)
Fisheries' induced decline of competitors	anthropogenic	Lynam et al. (2006), Richardson et al. (2009), Roux et al. (2013)
Marine structures offering substrate for polyps	anthropogenic	Lo et al. (2008), Duarte et al. (2013)
Changes in hydrological regimes due to dams and other constructions	anthropogenic	Xian et al. (2005), Purcell et al. (2007)
Releases to enhance jellyfish fisheries	anthropogenic	Purcell et al. (2007)
Introductions of alien jellyfish	anthropogenic	Daskalov et al. (2007), Graham and Bayha (2007), Katsanevakis et al. (2014), Edelist et al. (2020), Tsirintanis et al. (2022)
Nutrient variations	Anthropogenic/natural	Chen and Hong (2012)

(i) Overfishing has led to the removal of millions of tons of marine life globally, potentially creating ecological space for jellyfish to thrive. The decline of fish populations, which compete with jellyfish for zooplankton prey or predate on them, has allowed jellyfish to exploit available resources more effectively and has led to jellyfish outbreaks (Lynam et al., 2006; Richardson et al., 2009).

(ii) Eutrophication. Changes in the food web due to nutrient enrichment can create conditions that are more suitable for jellyfish than for fish, promoting their growth and survival (Parsons and Lalli, 2002). Furthermore, jellyfish are reported to be more competitive than other metazoans under hypoxic conditions (Purcell et al., 2001; Purcell, 2012).

(iii) Climate change, with its associated sea surface warming, altered water column stratification, and increased climate variability, can also influence jellyfish populations (Lee et al., 2023; Jaspers et al., 2023). Increased sea surface temperatures (SST) can create more favourable conditions for jellyfish by favouring their prey and/or accelerating their growth (see Purcell, 2005). Recently, a review on the most significant environmental features promoting scyphozoan jellyfish mass proliferation (Fernández-Alías et al., 2021) unveiled that larger scyphozoans living in temperate, shallow waters have higher outbreak-forming potential, with SST as the main environmental factor regulating the onset of population outbreaks, and food availability, boosted by bottom-up eutrophication, is key to sustain large biomass outbreaks.

Moreover, 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. 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 seas (such as the Suez Canal) has introduced new jellyfish to areas where their natural predators may be absent. These introductions have led to outbreaks of non-indigenous jellyfish and impacts in the invaded regions, e.g., *M. leidyi* in the Black Sea and *R. nomadica* in the eastern Mediterranean Sea (Katsanevakis et al., 2014b; Tsirintanis et al., 2022).

(iv) Habitat modification, such as an increase in suitable benthic habitat, either natural or artificial, could contribute to the proliferation of jellyfish polyps. Certain human activities, such as coastal development and the construction of marine structures, could create additional substrates for polyp attachment and growth (Duarte et al., 2013).

A critical review by Pitt et al. (2018) contended that there was weak evidence that anthropogenic stressors may trigger jellyfish outbreaks, because such claims (a) were mostly based on two highly invasive taxa (*A. aurita* and *M. leidyi*), (b) relied on correlative investigations that cannot establish causation, and (c) frequently referred to reviews that presented mainly circumstantial evidence and other reviews (Duarte et al., 2015). However, the diversity of the "*Aurelia* spp." complex has been recently highlighted (Scorrano et al., 2017), clarifying that most articles on *A. aurita* blooms actually were most probably referring to many diverse *Aurelia* species (nearly 30 molecular species; see Lawley et al., 2021; Moura et al., 2023), all of them most probably retaining the biological potential of massive proliferation, as suggested by Fernández-Alías et al. (2021). Also, by reviewing available evidence of jellyfish mass proliferations and environmental characteristics, the same authors (Fernández-Alías et al., 2021) raised the number of outbreak-forming scyphozoan species from 31 to 55, suggesting that additional species might be added, with temperature and food availability as key factors leading to jellyfish outbreaks.

Further, invasive hydrozoan jellyfish species such as *Blackfordia virginica* (Marques et al., 2017), *Maeotias marginata* or *Nemopsis bachei* (Nowaczyk et al., 2016) may attain very high abundances, posing significant ecosystem impacts in invaded habitats. This suggests we are still far from understanding the true number of non-indigenous jellyfish species that cause problems due to a lack of monitoring activities and identification bias. Also, the increasing frequency and abundance of *N. nomurai* outbreaks in the Sea of Japan (Uye, 2008), the prolonged sexual reproduction of *P. noctiluca* (Milisenda et al., 2018) and the westward geographical expansion of non-indigenous jellyfish taxa such as, e.g., *R. nomadica* (Deidun et al., 2011; Dror and Angel, 2023) and *C. andromeda* (Mammone et al., 2021) across the Mediterranean Sea, or the multiple invasions of European seas by *M. leidyi* (Jaspers et al., 2021) witness human-driven changes in marine ecosystems are drivers of jellyfish joyride at least in some critical marine subregions (Richardson et al., 2009). Overall, the unceasing and expanding increase of human uses of the marine ecosystems and maritime domain suggests that regardless of global increases of jellyfish populations, jellyfish-human interactions are and will be on the rise, particularly in coastal waters (Gibbons and Richardson, 2013).

6.5 Management measures and strategies

Currently, jellyfish management strategies primarily focus on controlling and mitigating adverse impacts locally (Lucas et al., 2014; Dong, 2019). Economic analyses have shown that investing in mitigation and protective measures can lead to reductions in the revenue losses of the affected coastal and marine activities (Ghermandi et al., 2015). Ecosystem-based strategies including jellyfish components are merely inexistent although their potential to better anticipate and manage adverse impacts or benefits of jellyfish outbreaks, rather than merely reacting to jellyfish outbreaks (Brodeur et al., 2016).

Some of these control management actions used nowadays are listed below.

Jellyfish cutters are used by Japanese fishers to remove aggregated jellyfish. While effective for concentrated patches, this method is limited by the vast geographical range of jellyfish distribution (Lucas et al., 2014). In Korea, Kim et al. (2013) developed a remotely controlled floating vehicle claimed to be effective in grinding large amounts of jellyfish at sea surface, minimizing jellyfish impacts.

However, cutting and/or grinding jellyfish raises two major issues. First, cutters or grinders do not affect jellyfish distributed at sub-surface depths. Second, these methods do not consider the powerful regenerative property of cnidarian jellyfish, such as *Aurelia coerulea*, able to produce new polyps even by few cell debris (He et al., 2015). Overall, cutting jellyfish may lead to enhancing, instead of reducing, the number of jellyfish in coastal areas. Also, jellyfish-excluding devices like the Jellyfish Excluder for Towed fishing gear (Matsushita and Honda, 2006) have been developed to prevent jellyfish from entering nets, reducing damage to fisheries.

Anti-jellyfish nets have assumed great significance to secure economic development of coastal communities. First adopted in Australia to protect beachgoers against envenomation from lethal cubozoans, these nets are purposefully designed to create enclosed areas for safe swimming in the coastal water and maintain tourism appeal. Throughout the Mediterranean, outbreaks of the mauve stinger *P. noctiluca* prompted the adoption of net-enclosed areas to foster a sense of security and protect beachgoers. Following early experiences in the French Riviera and the Elba Island, several anti-jellyfish nets of various sizes were set up and tested in the framework of the MED-JELLYRISK project (2012-2015) at various popular Mediterranean beach tourist destinations in Italy, Spain, Tunisia and Malta (Piraino et al., 2016). The effectiveness of those nets was monitored through visual jellyfish counting at both inner and outer sides of net-enclosed areas ranging 1,000-3,000 m^2, and the general public's perception of the net enclosures was also evaluated through targeted questionnaires distributed on the beaches. A recent study by Ruiz-Frau (2023) on tourists' holiday destination choices and expectations about anti-jellyfish mitigation measures highlighted that (a) the adoption of anti-jellyfish nets can be effective to reduce the loss of tourists from popular beach destinations by 83% and (b) most respondents declared their willingness to pay up to €12.4 per visit to the beach for anti-jellyfish countermeasures, including enclosure nets, first aid hotspots and warning flags, informative panels on species identification, and availability of procedures to adopt in case of jellyfish stings. However, the effectiveness of nets –whose design, material and installation procedures are mostly standardized by patents– can be severely affected by environmental conditions such as currents, tides, and wind: small waves can cause the entrance of surface jellyfish into the protected areas, or big waves and rough sea (Douglas' sea-grade 3 or more) may eventually dislodge or damage the nets. Therefore, monitoring and maintenance of the nets is crucial, even requiring rapid intervention to remove the nets when required.

In this context, public education and awareness (e.g., ocean literacy) on different jellyfish species and their associated risks play a significant role in mitigating the impacts of jellyfish outbreaks on public health and tourism (Gershwin et al., 2010; Lucas et al., 2014), for example helping locals and tourists adopt safer behaviours and use protective clothing. Collaborative citizen science approaches involving trained personnel, volunteers, social networks and media can also help to gather data for these applications and enhance public engagement (e.g., Pikesley et al., 2014; Dobson et al., 2023).

Operational early warning systems (EWS) based on hydrodynamic models and real-time observations are being developed to inform coastal users about potential jellyfish presence, enabling them to make informed decisions regarding beach activities (Marambio et al., 2021) or predict the outbreak intensity for certain noxious species for fisheries, such as *N. nomurai* (Uye, 2008; Lucas et al., 2014). In the latter case, through monitoring juvenile medusae from ships of opportunity, researchers have developed forecasts for *N. nomurai* outbreaks, allowing Japanese fishers to prepare countermeasures. Other cases involve species such as *Cyanea purpurea*, *R. pulmo*, *Phacellophora camtschatica, Agalma okeni*, *A. aurita, Phyllorhiza punctata*, and *Rhopilema esculentum*, in China (Gao et al., 2023). Remote sensing techniques also have the potential to be used in early warning detection systems. Methods using unmanned aerial vehicles (UAVs) allied with high resolution imagery and effective image analysis algorithms have been developed (Aznar et al., 2017; Mcilwaine and Casado, 2021). UAVs currently offer the best platform providing images for an early warning detection system, due to a combination of ease of access to technology and its deployment, low relative cost and very high-resolution data (Mcilwaine and Casado, 2021). Moreover, early warning systems may benefit from recent scientific advancements such as deep learning technology for the detection of jellyfish species (Han et al., 2022; Zhang et al., 2023) and eDNA-based methods for detecting rare but life-threatening species (Bolte et al., 2021).

Other innovative solutions like protective covers, mesh screens, and bubble screens are being explored in the aquaculture industry to safeguard fish production, and in power stations and desalination plants to protect the cooling and pumping systems from jellyfish infestations (Verner, 1984; Lucas et al., 2014). Bubble curtains are not a new idea (Ratcliff, 2004) but their practical application has only recently been tested. Bubble curtains consist of a perforated tube that encircles the lower perimeter of a fish farm or fish pen. Air is continuously pumped through the tube and the resulting curtain of bubbles generates an upward current that can trap jellyfish and bring them to the surface, where they are deflected horizontally away from the farm. Haberlin et al. (2021) carried out field trials on large scyphozoans and found mixed results. A bubble curtain that had a high air flow and a linear design (~10 m of tubing) deflected large compass jellyfish (*Chrysaora hysoscella*); however, a much larger bubble curtain with a circular design (800 m circumference) did not impact the abundance of hydromedusae on either side of the curtain. Haberlin et al. (2021) also carried out experiments in a flume tank using silicone jellyfish which showed that bubbles can be effective barriers to jellyfish in calm conditions and when jellyfish were located at the surface. But when stronger currents and turbulence were introduced, they disrupted the integrity of the curtain and reduced its efficiency.

Chemical compounds used for antifouling ship paints to inhibit polyp settlement and attachment in aquaculture facilities and other man-made structures (Guenther et al., 2009, 2010; Feng et al., 2017, 2022) or introducing natural polyp predators, like nudibranchs, to habitat areas can also help control some jellyfish populations (Hernroth and Gröndahl, 1985; Hoover et al., 2012). These approaches could potentially reduce recruitment to the medusa stage and mitigate the frequency and intensity of jellyfish outbreaks.

Although technological advances and increasingly effective tools and approaches are likely to emerge to control and mitigate jellyfish impacts, EBM approaches (like MSFD) are needed to integrate the multifaceted linkages between jellyfish and different ecosystem components and ecosystem services to potentially reduce outbreaks of harmful jellyfish species and preserve biodiversity and marine ecosystem services (Richardson et al., 2009; Bastardie et al., 2021; Edelist et al., 2021).

6.6 Indicators to include jellyfish in the MSFD's assessments

The MSFD is an EBM approach adopted by the European Commission to attain GES across European Seas. GES is not intended to reflect pristine status but acknowledges that there have been changes to ecosystems encompassing natural variability, climate change, human activities and their impacts, as well as the limits of ecosystem resilience and recovery capacities (Claussen et al., 2011). Furthermore, GES allows for sustainable activities in the present and future (Borja et al., 2013).

To assess GES in practice, eleven thematic descriptors and associated criteria have been agreed to be assessed (European Commission, 2017). The implementation of the MSFD requires that EU member states or Regional Sea Conventions determine indicators and associated thresholds that are considered 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).

As jellyfish have been considered minimally in the 2012 and 2018 reporting cycles, an initial assessment would be required to (i) define appropriate indicators and associated thresholds for different jellyfish taxa and areas, (ii) differentiate between anthropogenic and natural factors driving jellyfish outbreaks ("pressures"), (iii) identify impacts and services of jellyfish in the ecosystem, and (iv) devise relevant management actions to mitigate/prevent their harmful effects where practical. Such analysis is pivotal to designing and implementing effective monitoring programs that aid jellyfish-related assessments and establish a robust scientific foundation for crafting efficient management strategies to attain GES. Jellyfish are relevant to several MSFD descriptors (D) and criteria including, among others, biodiversity (D1), non-indigenous species (D2), food webs (D4) and eutrophication (D5) (Table 9).

Furthermore, jellyfish are frequently regarded as indicators of marine ecosystem health, making them pivotal for evaluating the ecological conditions of marine waters (Schrope, 2012; Lee et al., 2023). Gelatinous zooplankton can thus serve as valuable indicators for assessing changing oceanographic conditions, offering diagnostic insights to aid the interpretation of changes in other state indicators across the food web, including higher and lower trophic levels (Bedford et al., 2018).

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 jellyfish or the frequency of occurrence of their aggregations). However, to understand why jellyfish are changing 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, if possible, indicators of direct pressure(s) favouring jellyfish (e.g., provision of man-made habitat; Duarte et al., 2013) would be useful to develop mitigation measures and identify risk of expansion (Foster et al., 2016). Similarly, a measure of jellyfish as a pressure and their impacts on the ecosystem (e.g., losses in fisheries, aquaculture, or energy generation) would be useful to inform management 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).

Table 9: Marine Strategy Framework Directive (MSFD) descriptors and jellyfish relevance.

MSFD Descriptors	Relevance of jellyfish
D1-Biological diversity is maintained. The quality and occurrence of habitats and the distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions.	Jellyfish can have significant impacts on the diversity, distribution, and abundance of marine species, populations and communities in pelagic and benthic habitats. All these alterations can negatively impact pelagic habitats (D1C6) but also species groups of birds, mammals, reptiles, fish and cephalopods, thus potentially involving D1C2 (“Species abundances”), D1C3 (“populations structures”, D1C4 (“Species distribution patterns”) and D1C5 (“Habitats extent and condition”).
D2-Non-indigenous species introduced by human activities are at levels that do not adversely alter the ecosystems.	Some jellyfish species can be introduced/established in new areas creating alterations in the biodiversity structure
D3-Populations of all commercially exploited fish and shellfish are within safe biological limits, exhibiting a population age and size distribution that is indicative of a healthy stock.	JELLYFISH may affect the recruitment of several commercially exploited (wild and farmed) species. D3C2 (“Spawning stock biomass”).
D4-All elements of the marine food webs, to the extent that they are known, occur at	JELLYFISH may play key roles in the structure and function of food webs during their outbreaks. It is necessary to identify changes in population status potentially affecting food web structure and

normal abundance and diversity and levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity.	species or groups with fast turnover rates that will respond quickly to ecosystem change and are useful as early warning indicators. Any of the D4 criteria could be relevant: D4C1 (Diversity of the trophic guild), D4C2 (The balance of abundance between trophic guilds), D4C3(Size distribution between individuals and the trophic guild), and D4C4 (Productivity of trophic guild)
D5 - Human-induced eutrophication is minimized, especially adverse effects thereof, such as losses in biodiversity, ecosystem degradation, harmful algae outbreaks and oxygen deficiency in bottom waters.	JELLYFISH can be involved in eutrophication problems due to changes in the food web due to nutrient enrichment that creates more suitable conditions for jellyfish growth and survival. Jellyfish are also reported to be more competitive in hypoxic condition. Further, the massive jellyfish falls can potentiate bottom oxygen depletion and impact the benthic macrophytes and macrofauna. Thus, potentially relevant criteria include Input of nutrients (D5C1), chlorophyll-a (D5C2), depth of photic limit (D5C4), concentration of dissolved oxygen (D5C5), Abundance of opportunistic macroalgae (D5C6), The species composition and abundance of benthic macrophytes (D5C7), and the species composition and abundance of benthic macrofauna (D5C8).
D6 - Sea-floor integrity is at a level that ensures that the structure and functions of the ecosystems are safeguarded and benthic ecosystems, in particular, are not adversely affected.	Alterations in sea floor integrity due to human interventions such as coastal infrastructures, subsea mining and dumping, fish bottom trawling, dredging, change of riverine sediment inputs due to damming or irrigation, etc. may potentiate polyp settlement (increasing habitats extent). If a linkage of JELLYFISH with sea floor alteration is identified in the assessment units, the relevant D6 criteria may also be required.
D7 - Permanent alteration of hydrographical conditions does not adversely affect marine ecosystems.	Different human activities (e.g., land claim, barrages, sea defenses, ports, wind farms, oil rigs, pipelines, heat, and brine outfalls, etc.) causing permanent alterations of hydrographic conditions like temperature and salinity changes, residence time, stratification, and distribution of turbidity and heat plumes may affect the risk of jellyfish outbreaks. In these cases, D7C1 criterion for the spatial extent and distribution of permanent alteration of hydrographical conditions or D7C2 criterion for the spatial extent of each benthic habitat type adversely affected by to permanent alteration of hydrographical conditions might be added in the assessment.
D8 - Concentrations of contaminants are at levels not giving rise to pollution effects.	n/a
D9 - Contaminants in fish and other seafood for human consumption do not exceed levels established by Community legislation or other relevant standards.	Only relevant if jellyfish fisheries were set up for human food provision.
D10 -Properties and quantities of marine litter do not cause harm to the coastal and marine environment.	Jellyfish ingestion of macro and micro plastic items may represent a significant vector for trophic transference of marine litter to the marine food web. D10C3: The amount of litter and micro-litter ingested by marine animals is at a level that does not adversely affect the health of the species concerned. D10C4: The number of individuals of each species which are adversely affected due to litter, such as by entanglement, other types of injury or mortality, or health effects.
D11 - Introduction of energy, including underwater noise, is at levels that do not adversely affect the marine environment.	linkages not known.

Here, we summarize a subset of indicators considered in current biodiversity assessments (including OSPAR, Holland et al., 2023a; HELCOM, 2018; and Black Sea Commission, BSC, 2019) and potential alternatives. OSPAR's Intermediate Assessment and HELCOM's coreset of indicators were delivered to assist contracting parties when reporting to the MSFD and to deliver the North-East Atlantic Environment Strategy and The Baltic Sea Action Plan respectively. The Black Sea Commission report on change in the "State of Gelatinous Plankton" within their assessment "Chapter 1: State and Dynamics of the Black Sea Ecosystem" (BSC, 2019).

While OSPAR, BSC and HELCOM have each developed indicators for non-indigenous species, only the BCS mentions jellyfish explicitly, given the well-documented roles of *B. ovata* and *M. leidyi* in the region, even though *M. leidyi* was first documented in the North Sea and Baltic Sea in 2005/2006 (as reviewed in Jaspers et al., 2018). In fact, HELCOM (2018) noted that jellyfish were an important group missing from the indicator: “Trends in arrival of new non-indigenous species” (HELCOM, 2018). Hence, although non-indigenous species indicators do exist, they have not been used to inform on change in jellyfish within ecosystems yet. Given that an aim of marine management is to avoid the spread of non-indigenous species, metrics based on easily distinguished features of marinas and coastal areas could be used as a proxy to assess risk of invasion of non-indigenous species – including jellyfish, as has been done for the hydroid *Cordylophora caspia* that has so far been detected in three marinas in Northern Ireland (Foster et al., 2016).

Although jellyfish do not feature in either the OSPAR or HELCOM regional assessments of biodiversity, metrics for jellyfish have been proposed by OSPAR as part of the indicator “Changes in Phytoplankton and Zooplankton Communities” (Holland et al., 2023a). This indicator is used within assessments of pelagic habitats (for D1) and food webs (D4), but assessments are supported by very little monitoring data on jellyfish, with all species of Cnidaria and Ctenophora currently grouped together as “Gelatinous zooplankton”. Data for these groups were available to OSPAR (2017) from a single sampling site within the western Channel (“L4”, Atkinson et al., 2021) but this was improved for OSPARs Quality Status Report 2023 (Holland et al., 2023a) where additional data were made available for a station off north-western Scotland (Loch Ewe), which indicated a declining trend in abundance (Fig. 17), a station off eastern Scotland (Stonehaven), and Swedish data for the Kattegat and Norwegian Trench in the eastern North Sea. However, these jellyfish data were insufficient to support additional analyses to determine key environmental pressures (Holland et al., 2023a, b).

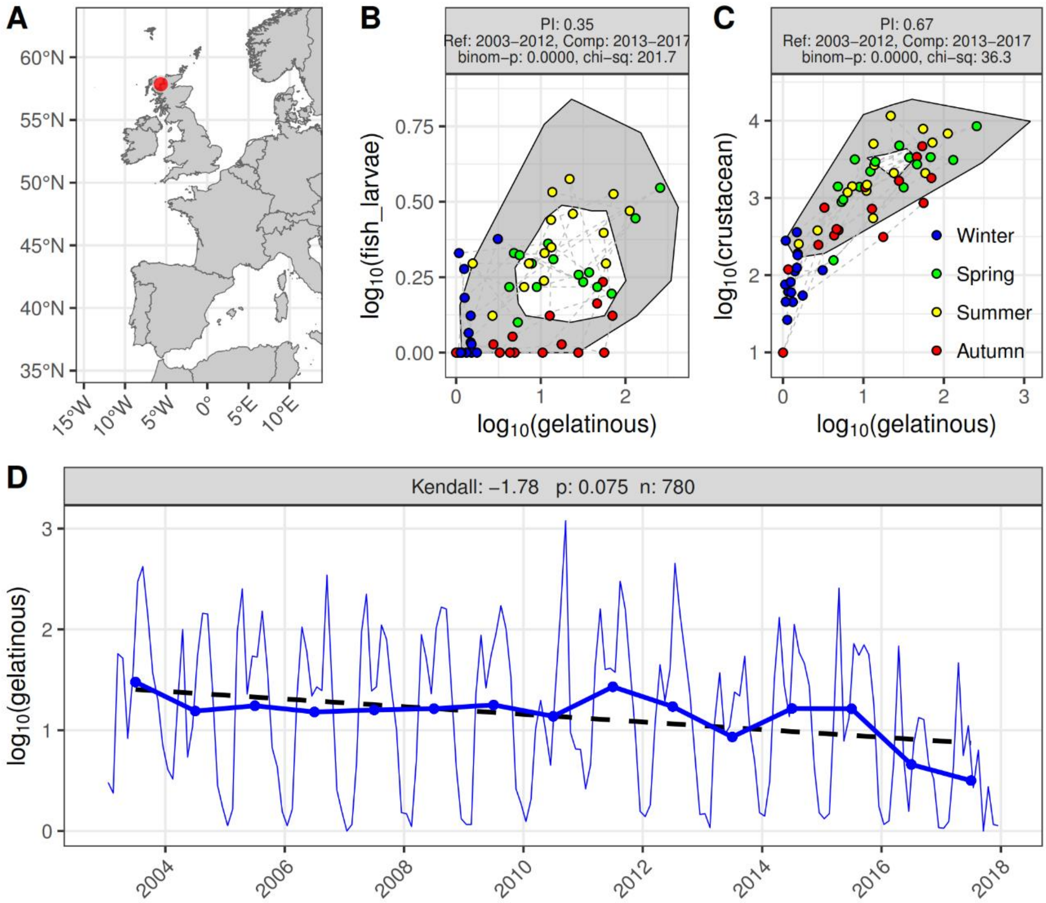


Figure 17: *A) Location of Loch Ewe Site from the Scottish Coastal Observatory. B) paired monthly observations of lifeform abundances: B) gelatinous zooplankton versus fish larvae/eggs, C) gelatinous zooplankton versus crustacean zooplankton, D) Interannual decreases of gelatinous zooplankton. (Marine Scotland Science, 2018 and Wells et al., 2022).*

The OSPAR indicator is assessed using a methodology based on the Phytoplankton Community Index approach of Tett et al. (2008). The indicator relies on the concept of “lifeforms”, 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, then the ratios of specific pairs of lifeforms are evaluated as indicators of energy or mass flow through trophic pathways in marine food webs (McQuatters-Gollop et al., 2019; Holland et al., 2023a,b). For jellyfish, two lifeform pairs indices are considered currently: 1) Gelatinous zooplankton versus fish larvae/eggs and 2) Crustaceans versus gelatinous zooplankton. In each case, jellyfish are considered as a predator (of crustacean plankton and of fish eggs and larvae) directing energy away from fish populations. However, jellyfish outbreaks may also result from (rather than cause) ecosystem degradation, and metrics of jellyfish abundance have been proposed as a potential indicator of ecosystem instability (Lynam et al., 2011).

We consider the following to be potentially useful additional indicators for jellyfish:

Pressure indicators driving change in jellyfish:

- • Indicators of water-mass dynamics (e.g., Ndah et al., 2022)
- • Provision of man-made 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 jellyfish:

- • Estimation of seasonal onset of jellyfish aggregations at sea as an early warning indicator of climate effects on the marine environment (van Walraven et al., 2013, 2015)
- • Frequency of occurrence of gelatinous zooplankton in stomach contents samples of predators (e.g., Smith et al., 2016)
- • Zooplankton Mean Size and Total Stock (Pitois et al., 2021)
- • Polyp presence and abundance in coastal habitats (lagoons, marinas) (e.g., van Walraven et al., 2016).

Impact indicators due to jellyfish outbreaks:

- • Frequency of occurrence of jellyfish supporting dependent predators (Witt et al., 2007)
- • Economic losses in fisheries (e.g., Uye, 2008; Quiñones et al., 2013)
- • Economic losses in aquaculture (e.g., Doyle et al., 2008)
- • Economic losses in desalination or energy coastal installations (e.g., Abdul Azis et al., 2000)
- • Social impact indicators, such as beach closures and loss of tourism (Ghermandi et al., 2015; Kennerley et al., 2022).

The selection of jellyfish-related indicators 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), accumulated uncertainties (Racault et al., 2014), and the potential for pan-European intercomparison and harmonization (European Commission, 2017). These requisites will heavily rely on the monitoring programs and methods to be defined and implemented for the assessment process.

6.7 Current monitoring programs and techniques and new alternatives.

Monitoring programs and techniques hold a vital role in supplying the required information for the MSFD assessment. 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 adding the benefits achieved from efficient management (Nygård et al., 2016). Furthermore, the coordination and complementation of data from different monitoring programs like those 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. For instance, some fisheries surveys dedicate sampling during the night-time to monitor gelatinous zooplankton (e.g., Køhler et al., 2022) although it would be preferable to adapt the monitoring schema (spatial and temporal extensions and resolutions, periodicity, sampling and analysis methods) to the purpose of the jellyfish assessment (identification of species, biomass and abundance estimation, seasonal patterns, trends, etc.).

Presently there are increasing efforts towards cost-effective and innovative monitoring approaches to enhance research on jellyfish and foster their integration into the MSFD assessment and management framework (Magliozzi et al., 2021). Towards that direction, the findings of our global review on monitoring programs and methodologies for jellyfish provide useful insights and are described hereafter.

Conventional jellyfish monitoring often relies on visual inspections where skilled observers manually identify and count jellyfish. Although trained observers can individually count jellyfish at specific locations, this method is labour-intensive, time-consuming, and prone to biases. Additionally, trawl nets are commonly used to collect jellyfish specimens (Brodeur et al., 2016; Aubert et al., 2018). This technique is suitable for detecting prominent jellyfish species (specifically non-siphonophore hydrozoans, scyphozoans, cubozoans, and some ctenophores). However, it can be highly detrimental when studying delicate organisms like siphonophores, small ctenophores, and pelagic tunicates due to their fragility. If implemented, slower and shorter net sampling could prevent the deterioration of samples. A major limitation in many studies is the lack of high-frequency sampling survey programs sustained over time which is a prerequisite required to capture seasonal changes in abundance and the timing of outbreaks (Køhler et al., 2022). For surveys conducted annually (e.g., many fisheries surveys) the assumption of consistent sampling across the seasonal cycle may lead to misinterpretation due to changes in phenology, as highlighted by Van Walraven et al. (2015). Jellyfish have been historically overlooked in national and international marine scientific surveys, often neglected in favour of the economically important commercial fish species or the more simple and cost-effective sampling of smaller zooplankton. While these programs are increasingly multidisciplinary and claim to follow an ecosystem approach, ship time is rarely allocated to specific jellyfish sampling, specimens are collected as by-catch (e.g., Pitois et al., 2019), and jellyfish specialists are rarely on board to sample, identify, and preserve the specimens. The increasing importance of jellyfish for society and science makes them a crucial part of national and international sampling programs (Lynam et al., 2011; Miloslavich et al., 2018; Prieto, 2018).

Technological advancements have introduced new techniques for monitoring jellyfish outbreaks, including sampling approaches more suitable to study these fragile animals:

- **Nets.** WP2 and Bongo nets are the most widely used jellyfish monitoring tools. They are particularly suited for small, abundant hydromedusae, scyphozoan ephyra and calycophoran siphonophores. Different sampling gears provide complementary insights in jellyfish 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, routine fishery trawl surveys have been proposed as a cost-effective approach to support jellyfish monitoring (Aubert et al., 2018). Even though not routinely conducted, night-time ichthyoplankton work conducted during fisheries trawl surveys represent another cost-effective sampling alternative for jellyfish. Here, ichthyoplankton sampling gear such as MIK-nets can be used to quantitatively assess the gelatinous macrozooplankton community (Aubert et al., 2018; Køhler et al., 2022). However, nets have the disadvantage of underestimating fragile gelatinous organisms that may break during collection. Differing water volumes processed per net can introduce biases, either destroying fragile ctenophores or siphonophores when large volumes are processed or underestimating true abundances if species are present in very low abundances and low water volumes are processed. Alternatives are to use multiple opening and closing nets, such as MOCNESS or MultiNets to sample discrete depth strata where jellyfish are known to accumulate (e.g., Haraldson et al., 2013).
- Another available surface monitoring method is the **Continuous Plankton Recorder** (CPR). During a tow, plankton enters the CPR through its mouth and is trapped between the filtering and the covering silk bands. The two bands of silk are then progressively wound up on a spool located in a tank filled with a fixing solution (Lynam et al., 2011). CPR can detect outbreaks of both meroplanktonic and holoplanktonic hydrozoans and scyphozoans. Outbreaks of the scyphomedusa *P. noctiluca*, recorded by the CPR off Ireland in October 2007, were confirmed by net tows (Licandro et al., 2010), suggesting that CPR can provide reliable information for identifying regions and periods favourable for jellyfish outbreaks. The main limitation of this technique is the inability to preserve the gelatinous plankton morphology, except for rigid calycophoran siphonophores (Gibbons and Richardson, 2009). This limits the taxonomic identification at species level so that CPR data are typically recorded as presence of "coelenterates" and siphonophores. However, preserved samples can be used for re-analysis

and genetic studies. Moreover, 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 jellyfish monitoring method. Despite their crucial role in jellyfish outbreak development, polyps remain the least known stage in the jellyfish life cycle; field investigations of this stage have only recently gained attention. These research efforts encompass density estimations, ephyrae production, and the identification of suitable substrates (e.g., Miyake et al., 2002, van Walraven et al., 2016). Monitoring of this benthic stage is usually carried out through visual surveys by SCUBA divers or by employing underwater cameras for recording (Table 4).
- **Visual counts:** Although jellyfish monitoring based on visual observations from a ship or ranks as the fourth most frequently reported method in the review, this approach is inherently biased towards species of detectable size and relatively straightforward taxonomic identification, making it inadequate for providing reliable information on the abundance and composition of jellyfish populations across oceans. However, for certain remarkable (dangerous or visually striking) species, visual counts during beach surveillance and cleanup activities, or during boat tours (such as whale watching, birdwatching, and coastal tours) can serve to manage bathing 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 as ground truth dataset complementing other monitoring techniques.
- **Acoustic methods:** Underwater acoustic devices like single-beam and multibeam echosounders, scanning sonars and, hydrophones, have already been used in several studies for detecting jellyfish 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 gelatinous zooplankton 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 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 jellyfish aggregations from previous recorded acoustic cruises for fish abundance assessment could prove 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 for equipment investment, mission planning, sensor integration, and deployment. 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).
- **Remote images:** Satellite imagery, aerial photography, and videorecording from piloted aircraft, drones, UAVs, and ROVs are increasingly employed for cost-effective jellyfish monitoring.

Whereas drones, UAVs, and ROVs may include optical sensors with sufficient resolution for jellyfish identification and counting, aerial and satellite platforms should be equipped with very high resolution or hyperspectral sensors to be effective in jellyfish monitoring. Moreover, customized signal processing algorithms need be developed to enable the detection and/or counting of jellyfish 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 in conjunction with other techniques to provide environmental data that can be incorporated into jellyfish 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. In addition, drones are cost-effective and easy to handle due to their small size, requiring minimal training for flying (Hamel et al., 2021). However, their usage is constrained by factors like flight duration, local flight operation regulations, and environmental conditions such as rain and wind speed (Mcilwaine et al., 2022). Remote images 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 jellyfish in the water column (Churnside et al., 2016).
- **Citizen science:** Active participation from the public in collecting jellyfish data offers a valuable opportunity to cover larger coastal areas that would be costly 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 needed for scientific studies. In addition, data collection often suffers from spatial bias (more data from popular sites) and time bias (typically occurring during a short-time period, e.g., summer). Therefore, it is advisable to sustain these programs over time and not restrict them to summer seasons and short-term projects.
- **Underwater images and automatic count systems:** Underwater photography and video recording systems (Cillari et al., 2022) on ROVs can facilitate quantitative evaluations from long-lasting and spatially extensive surveys. However, they are commonly perceived as foreign objects by the local fauna, potentially causing bias due to species escaping behaviour. 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 jellyfish, 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**: With the advancement of DNA barcoding, mitochondrial and nuclear DNA and RNA facilitate species detection, including jellyfish (Créach et al., 2022).

Quantitative real-time PCR (qPCR) has also been used to identify jellyfish by tracing eDNA (Bayha and Graham, 2009; Marques et al., 2019). This emerging method enables the analysis of water and sediment samples to detect specific jellyfish cells released into the environment through excretion (Minamoto et al., 2017, Ogata et al., 2021). Depending on the monitoring objectives, this technique may have limitations related to sampling and preservation procedures, but it offers several advantages, increasing the likelihood of species detection and, in some cases, reducing the time and costs compared to other monitoring and sampling methods. Moreover, marine eDNA is preserved for only one day in water, whereas it can persist for at least one year in sediments and could therefore be useful to reconstruct past occurrences (Ogata et al., 2021). Furthermore, these techniques can be applied to analyse the gut content of potential jellyfish 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 jellyfish carcasses have been conducted using various techniques, including sediment traps, photography and video systems, and trawling nets (Lebrato et al., 2012; Dunlop et al., 2018).

Among the analyzed records, most jellyfish monitoring publications were found in Europe, Asia, and the United States (Fig. 18). At the Marine Realms level (Fig. 19), Temperate North Atlantic emerged as the most studied, with the most diversified sampling techniques, followed by the Temperate North Pacific. In Temperate South America, Temperate Australasia, Tropical Eastern Pacific, and Temperate South Africa, nets have been the unique method used to monitor jellyfish outbreaks. Nets were the predominant monitoring method in all Marine Realms, except for the Eastern Indo-Pacific, where citizen science was the only method recorded. Polyp monitoring has only been conducted in the Temperate Northern Atlantic, Temperate Northern Pacific, Central Indo-Pacific, and the Arctic.

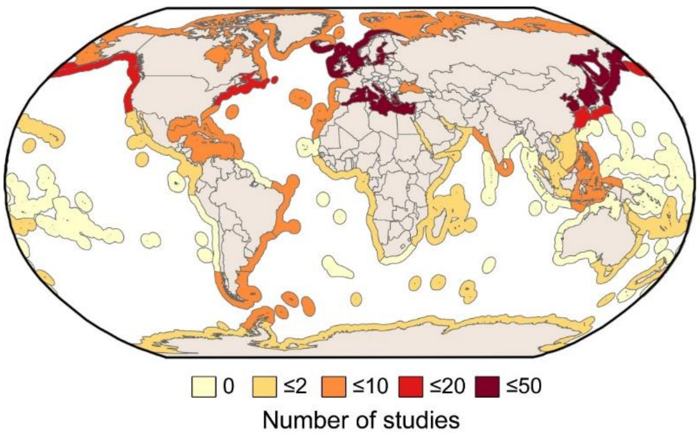


Figure 18: *Spatial distribution of studies on jellyfish outbreaks (n=200) and polyp monitoring (n=19) published between 2008-2023.*

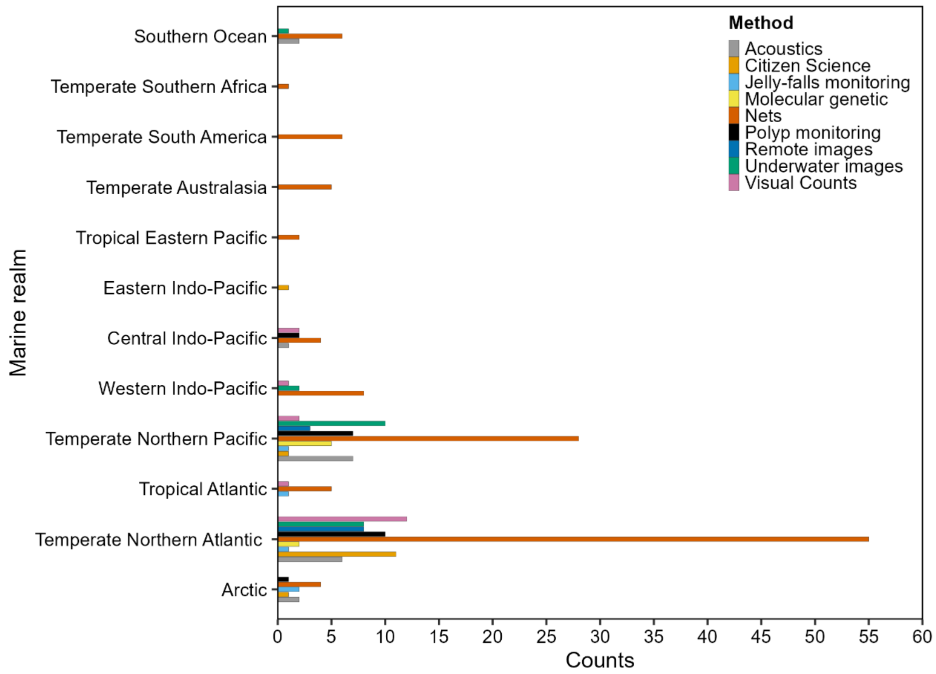


Figure 19: *Types of monitoring methods used to monitor jellyfish outbreaks and polyps across each Marine Realm, published between 2008-2023.*

Most studies have focused on outbreaks caused by cnidarians (Fig. 20). The four most commonly implemented methods for this group, in decreasing order of frequency, were nets, underwater images, acoustics, and visual counts. For Ctenophora, the most used monitoring techniques were nets, underwater images, and citizen science, whilst for Tunicates, nets and underwater images were the most commonly employed. Nets, underwater images, visual counts, and citizen science have been implemented to monitor all the three considered taxa (Cnidaria, Ctenophora and Tunicata). Acoustics, remote images, molecular methods, and jelly-falls have been implemented only for Cnidaria and Tunicata (Fig. 20).

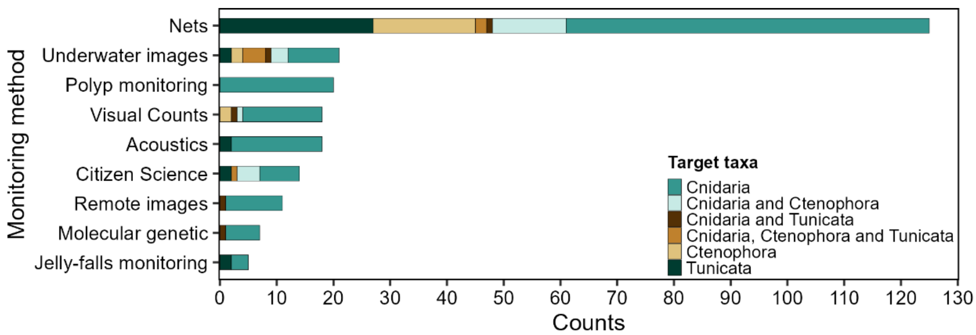


Figure 20: *Jellyfish outbreaks and polyp monitoring studies sorted by target taxa based on the methodology used, published between 2008-2023.*

The temporal distribution of studies (Fig. 21), both in the pelagic and benthic stages, shows an increase from 2008 to 2022. Nets are the most employed method. A notable change occurred in 2021-2022 when there was a notable increase in publications related to citizen science.

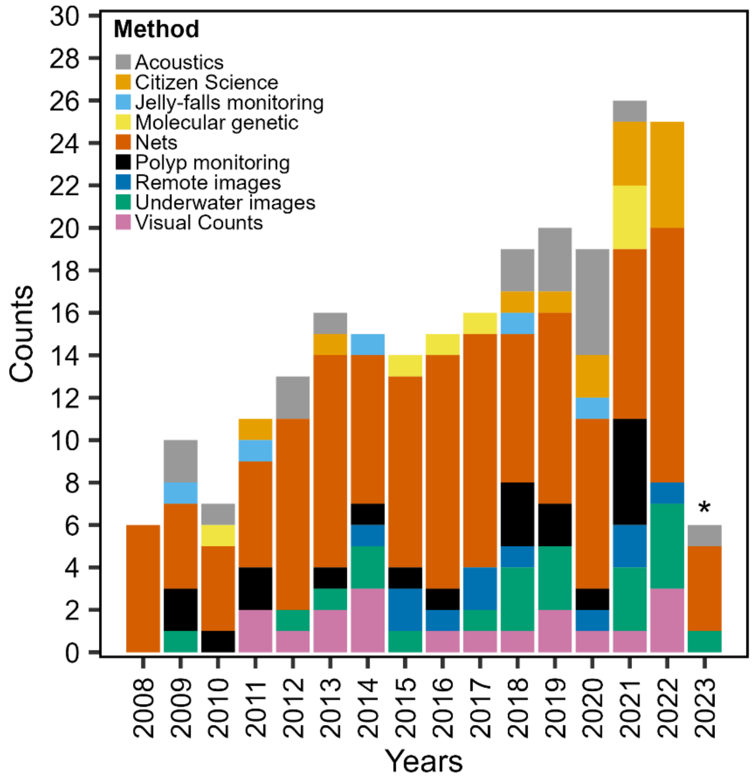


Figure 21: *Counts of reports of monitoring methods used on jellyfish outbreaks assessment and polyp monitoring by year, published between 2008-2023 (*articles published in 2023 are not representative as the literature research was performed until June of that year).*

Polyp stages have been most extensively monitored in the European and Japanese Seas, with only one study in the USA and one in Australia. Compared to the pelagic stage, articles focused on polyp monitoring are relatively scarce (n = 19). 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 (*Cyanea lamarkii*, *P. punctata*, *Nausithoe* cf. *rubra*, *Atorella sibogae* and *Atolla* sp.) and one Cubozoa (*Copula sivicksi*). Polyps were found in various substrates, including both natural (shells of clams *Spisula subtruncata* and *Mactra stultorum*, shells of dead clams, hollows of stones, under-surfaces 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 (undersides of floating piers, PVC, synthetic rubber, iron oxide, wood, granite, glass, floating docks, and plastic debris). The methods used are summarized in Table 10.

Table 10: Methods used for polyp monitoring, published from 2008 to 2023 (n=19) and the target species.

Methodology	Species	Reference
	Scyphozoa - Semaeostomeae	
SCUBA diving (pictures)	*Aurelia aurita**	Di Camillo et al. (2010)
SCUBA diving (pictures)	*Aurelia coerulea*	Marques et al. (2015)
SCUBA diving (pictures)	*Aurelia coerulea*	Marques et al. (2019)
SCUBA diving (direct observations)	*Aurelia aurita sensu lato*	Toyokawa et al. (2011)
SCUBA diving (pictures and videos)	*Aurelia aurita**	Makabe et al. (2014)
SCUBA diving (videos)	*Aurelia coerulea*	Dong et al. (2018)
SCUBA diving (pictures and polyp collection)	*Aurelia coerulea*	Yoon et al. (2018)
SCUBA diving (hard underwater substrates), artificial setting plates, floats in ports, marinas	*Aurelia aurita**	Van Walraven et al. (2016)
Pictures	*Aurelia labiata*	Purcell et al. (2009)
Artificial plates	*Aurelia aurita**	Janßen et al. (2013)
Automated detection and counting PoCo	*Aurelia* sp.	Vodopivec et al. (2018)
Snorkeling, wading and settling plate survey	*Aurelia* sp., *Aurelia aurita**	Rekstad et al. (2021)
NA	*Aurelia coerulea*	Seo et al. (2021)
Tows of a small Kamiyas dredge	*Chrysaora pacifica*	Toyokawa (2011)
Deep Digging Dredge and empty bivalve shells collected along the high-water line at the beach	*Chrysaora hysoscella*, *Cyanea lamarkii*	Van Walraven et al. (2020)
	Scyphozoa - Rhizostomeae	
Taqman PCR-based method	*Phyllorhiza punctata*	Bayha and Graham (2009)
	Scyphozoa- Coronatae	
ROV images	*Atolla* sp.	Zhulay et al. (2019)
9 manned submersible Shenhaiyongshi (deep sea)	*Atorella sibogae*, *Nausithoe* cf. *rubra*	Song et al. (2021)
	Cubozoa	
eDNA	*Copula sivickisi*	Bolte et al. (2021)

*ID must be confirmed after Scorrano et al. (2017)

Data from various monitoring techniques (e.g., counting methods and citizen science) have been combined with environmental information (e.g., currents direction, temperature, salinity) to create predictive models for forecasting the trajectories (Ferrer et al., 2015; Ferrer and González, 2021) or occurrences of gelatinous planktonic species at local scales. One of the primary challenges in ecological modelling is incorporating the entire biological complexity while maintaining computational reliability. In this context, trait-based models (which utilize functional traits such as body size, shape, or reproduction rates), mixed models (that integrate information on functional traits into correlative distribution models), and ecosystem-based approaches (where modelling focuses on the ecosystem functioning processes) have been developed to create more realistic and biologically informed predictions on jellyfish outbreaks and spatial occurrence patterns (Bosch-Belmar et al., 2021a; Lamb et al., 2019; Rahi et al., 2020; Ramondenc et al., 2020).

6.8 Discussion: recommendations to move forward

Considering changing ecosystems and the growing recognition of the importance of jellyfish, research into their monitoring, assessment, and management has become imperative. Climate change, eutrophication, overfishing, and other natural or anthropogenic stressors can alter the occurrence and frequency of jellyfish outbreaks, rendering them invaluable indicators of marine ecosystem health. While conventional management focuses on mitigating localized impacts, a shift towards predictive modelling is essential to counteract jellyfish crises more effectively and at a lower cost. MSFD stands as a milestone in EBM in Europe, with the goal of achieving GES. Despite its holistic approach, jellyfish received limited attention from Member States in their reporting cycles. Current efforts aim to rectify this by integrating jellyfish information into MSFD assessments, thereby recognizing their ecological importance across different levels.

To improve jellyfish monitoring, assessment, and management, we have compiled several key recommendations derived from our review:

Enhance monitoring efforts to support early warning and forecasting as well as efficient EBM.

Monitoring programs focused on gelatinous zooplankton are still scarce despite the important ecological roles of jellyfish in marine ecosystems, as well as their impacts and benefits for different socio-economic sectors and human health. Besides, conventional jellyfish monitoring methods, such as manual visual inspections and trawl nets, often do not provide adequate and unbiased datasets. Embracing innovative technologies and approaches such as underwater acoustics, automated counting, and identification through camera systems with artificial intelligence, citizen science involvement, eDNA sampling, remote sensing and modelling support, can offer cost-efficient ways to enhance monitoring and support research, assessments, and mitigation or preventive management strategies.

Standardized global monitoring through citizen science may offer invaluable datasets, boosting jellyfish monitoring and significantly advancing our knowledge of jellyfish ecology, distribution, and the mechanisms behind jellyfish outbreak. Such successful efforts have been undertaken for other taxa, e.g., reef fish and invertebrates through the Reef Life Survey (RLS) (Edgar and Stuart-Smith, 2014), which is an independent foundation originating in Australia. RLS coordinates standardized scuba surveys conducted by hundreds of trained citizen scientists across 55 countries on all continents. By September 2023, >16,000 surveys have been conducted, documenting over 5,300 species and >23 million individuals, resulting in a collection of half a million photographs and the publication of over 60 scientific papers.

Better understanding jellyfish outbreaks and their impacts

Overall, the complex interplay of many factors, such as overfishing, species translocations, eutrophication, climate change, and habitat modification suggests that human activities have played a significant role in promoting jellyfish outbreaks. Understanding these mechanisms is essential for effective management to restore and maintain balanced marine ecosystems. As various stressors continue to interact (with additive, synergistic, or antagonistic effects), the future of marine ecosystems and their potential shift to jellyfish-dominated states remain subjects of concern and study. However, in some cases the evidence supporting the notion that anthropogenic stressors contribution to jellyfish outbreaks is limited, and the underlying mechanisms remain poorly investigated (Pitt et al., 2018). Further research is needed to understand the specific causal mechanisms linking anthropogenic stressors to jellyfish outbreaks. This entails studying a diverse range of jellyfish species, conducting causation studies, considering ecosystem dynamics, analysing long-term data, and employing multidisciplinary approaches to provide more accurate insights into the factors driving jellyfish outbreaks. Moreover, research for refining the assessment of their impacts on biodiversity, food webs, human health, and socio-economic activities is needed. Collaborative research and analysis techniques are essential to gather comprehensive data on jellyfish impacts.

Consideration of polyp phase

The factors triggering outbreaks in natural environments are one of the biggest gaps in jellyfish research. The study of jellyfish's early phases, such as polyps and the first pelagic stages (i.e., ephyras), is crucial to understanding it. However, polyps are elusive. Among Scyphozoa and Cubozoa species (the most conspicuous jellyfish), 5% are holopelagic, 32% have a benthic stage, whilst the life cycle of the remaining 63% is unknown (estimated from Jarms and Morandini, 2019). In only 16% of species with benthic stage, polyps have been observed in the natural environment (i.e., 14 of 86 species), with the genus *Aurelia* and *Chrysaora* accounting for half of these observations (Kikinger, 1992; Cargo et al. 1996; Dawson et al. 2001, and references in Table 10). It is noteworthy that efforts to monitor these pivotal stages are scarce, with only 19 peer-reviewed articles found in the last sixteen years.

Addressing the polyp stage and ephyrae offers new avenues for assessing and managing jellyfish, particularly for interventions in the medusa recruitment phases. Many factors determine the timing and magnitude of scypho- and cubomedusae recruitment, such as the polyps abundance, the strobilation rates and the ephyrae survival rates (Pitt and Kingsford, 2003). A detailed comprehension of the spatio-temporal variability of recruitment of medusae will be invaluable to pelagic ecology and is essential for the development of sustainable jellyfish management strategies (Kingsford et al., 2000). It is particularly important when commercial harvest of species, such as large-sized Rhizostomeae (see section 3.1), is planned. Very limited information exists on jellyfish-fishing exploitation impacts on Rhizostomeae population dynamics (Brotz and Pauly, 2012; López-Martínez et al., 2020). Therefore, we recommend the establishment of specific sampling programs focused on identifying polyps' locations, determining the spatial extend of benthic populations, and estimating asexual reproduction rates with ephyrae production, their pelagic abundance, mortality and growth rates. In particular, recording (e.g., through video) polyps on artificial structures such as wind turbines as part of recurrent inspections of state of poles and wind park management may provide useful data in a cost-effective way. These *in situ* surveys, together with laboratory experiments on thermal tolerances, trophic ecology, and strobilation cues, would shed light on the environmental factors regulating jellyfish outbreak dynamics.

Integration with the MSFD framework

Integrating jellyfish monitoring, assessment, and management into the MSFD framework involves defining relevant criteria, indicators and thresholds as well as standardised methods for jellyfish status, pressures and impacts. These organisms can be considered in different descriptors, especially D2 (non-indigenous species), D4 (food-webs) and D5 (eutrophication). The indicators associated to those descriptors could encompass variables such as jellyfish biomass, species diversity, frequency of outbreaks, and their impact on other marine organisms. Defining clear thresholds helps identify when jellyfish populations exceed natural variability (GES) and become a concern for ecosystem health. By acknowledging the ecological significance of jellyfish and their intricate interactions with other species, policymakers can make informed decisions that promote sustainable marine management and mitigate the potential negative impact of jellyfish outbreaks.

Differentiating between anthropogenic and natural factors driving outbreaks is crucial for effective policy formulation. This ensures that interventions address the manageable causes of jellyfish outbreaks. Adaptive management, a key principle of the MSFD, involves a flexible and iterative approach to decision-making. This is particularly relevant for jellyfish management due to the dynamic and often unpredictable nature of jellyfish outbreaks. By continually monitoring and reassessing the effectiveness of management measures, adjustments can be made in response to changing conditions, ensuring that management remain relevant and efficient.

The coordination and complementation of data, methods and references or thresholds is key to reach consistency, efficiency and rationalize efforts and costs.

Ocean literacy to gain public awareness and education and minimize impacts to human health.

Ocean literacy, including education campaigns, is crucial in minimizing the impact of jellyfish outbreaks on public health and other activities like tourism, fisheries or marine facilities. Informing the public about jellyfish species, risks, and safety measures can encourage safer behaviour and proactive preparations and build a supportive and informed community. This not only provides valuable insights for scientists and researchers but also fosters a sense of stewardship among the public, making them active participants in observing, reporting and managing jellyfish populations.

Jellyfish and sustainable blue economy.

Economic analyses support the investment in monitoring programs and setting protective measures like anti-jellyfish nets and early warning systems when balancing their costs against the potential losses from jellyfish-related adverse impacts (Brodeur et al., 2016). Interestingly, the numerous potential ecosystem services of jellyfish (food provision, fertilizers, biotechnology, biomedicine, etc.) could serve to harvest new valuable marine resources while mitigating their adverse effects.

7. New tools and recommendations for a better management of harmful algal blooms under the European Marine Strategy Framework Directive

7.1 Introduction

The term 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; Kouakou and Poder, 2019; Brown et al., 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 well-being (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, 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 (Table S8).

Identifying the causative factors behind HAB events is a complex endeavour. Most HABs are natural phenomena that have historically occurred in various regions worldwide before human activities altered coastal and marine ecosystems. HABs involve a change of phytoplankton assemblages, which can arise in response to chemical or biological habitat alterations (Smayda, 2008). Various ecological mechanisms have been suggested to elucidate HAB outbreaks, including biological life strategies such as mixotrophic behaviour, swimming ability, allelopathy effects, multi-resource competition, and prey avoidance (Choi et al., 2023). However, it is widely accepted that the conditions favouring HAB outbreaks are also induced or facilitated by anthropogenic pressures, including 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., 2021b), habitat modifications (Garcés and Camp, 2012), and climate change (Anderson, 2014; Wells et al., 2015; Glibert and Burkholder 2018; Glibert, 2020).

One of the first legislations addressing HABs was enacted in the USA in 1998, known as the "Harmful Algal Bloom and Hypoxia Research and Control Act". In Europe, HABs are primarily managed as a public health concern (Food Hygiene Regulation (EC) No. 853/2004, Bathing Water Directive 2006/7/CE), but also within the Water Framework Directive (WFD, 2000/60/EC). Current 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. Nevertheless, the significant interconnections between HABs and various environmental and socio-economic issues highlight the need of a holistic, ecosystem-based approach to manage HABs through appropriate instruments and policies. Furthermore, neglecting HAB management in environmental policies may lead to future environmental challenges if affected socio-economic stakeholders resort to unregulated mitigation measures such as algicide application, ultrasound, clay disposal or biological treatment (Silliman, 2022).

In this context, the European MSFD (European Commission, 2008) represents a significant milestone by introducing an EBM approach 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 RSCs, a 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 criteria, thresholds, and targets 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, 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).

The aim of this study is to pave the way for the integration of HABs into EBM approaches, with a specific focus on the MSFD. The study aims to provide policy and decision makers with technical guidance and tools that can enhance the 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 EBM strategies.

7.2 Proposed conceptual decision support tools for guiding HAB management

Within the MSFD framework, we found the following principles as most relevant for contextualising 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 and their 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 (Elliot 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 (Fig. 22). MAMBO is nested within GES4HABs and assists in identifying HABs that are more amenable to management actions, thereby directing efforts and resources efficiently (Fig. 23). Hereafter the consecutive steps and criteria encompassed in GES4HABs and MAMBO are described.

7.2.1 GES4HABs entry point: The initial assessment

Although reactive local control measures will always be necessary to mitigate the impacts and risks of HABs (e.g., Food Hygiene Regulation (EC) No 853/2004, Bathing Water Directive 2006/7/EC) (Fig. 22), upstream management based on EBM approaches, 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, EBM aims 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 (Fig. 22). 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.

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).

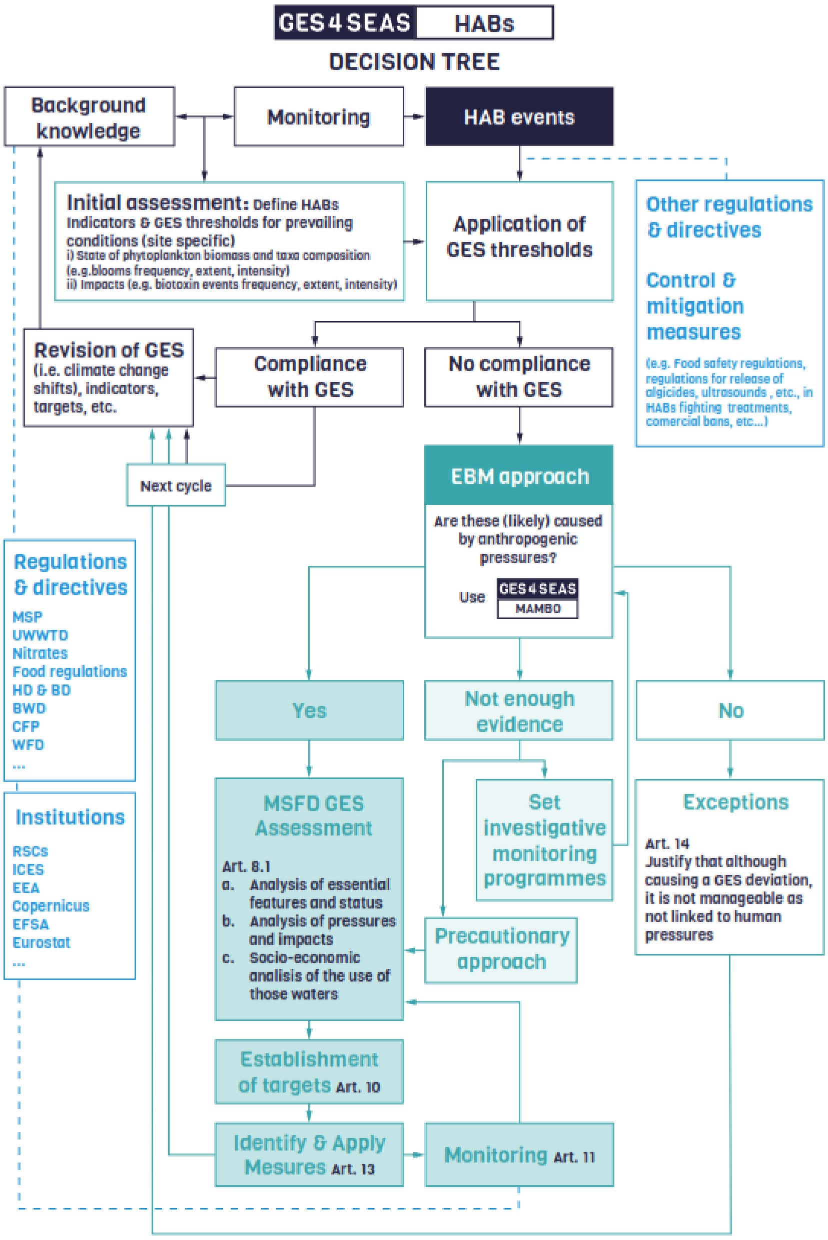


Figure 22: *GES4HABs Decision tree to guide policy makers and Marine Strategy Framework Directive (MSFD) stakeholders on the steps and decisions to support management and MSFD reporting actions related to different Harmful Algal Blooms (HABs) in their jurisdiction areas. GES: Good Environmental Status; 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 & BD: Habitats Directive and Birds Directive; BWD: Bathing Water Directive; CFP: Common Fisheries Policy; MAMBO: environMental mAtrix for the Management of BlOoms (see Fig. 23).*

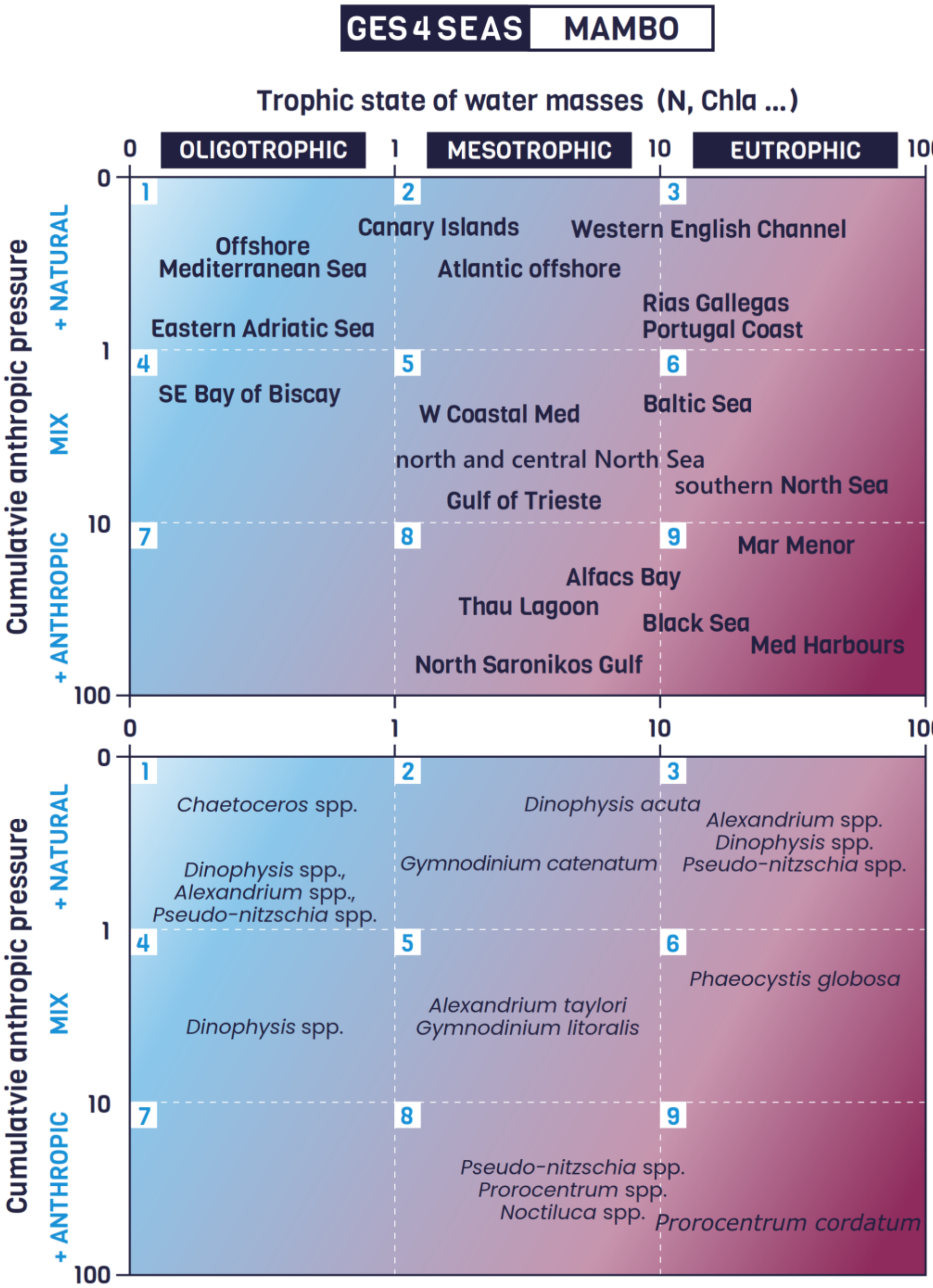


Figure 23: *Top: Representation of some marine geographical regions in the MAMBO (environMental mAtrix for the Management of BlOoms) matrix according to their associated trophic state (X axis) and anthropic influence level (Y axis). Bottom: Representation of some examples of Harmful Algal species occurrences 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 Table S9.*

The required criteria, specifications and methods 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) (Fig. 22). 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, (ii) determine whether HABs deviate from prevailing conditions, and (iii) anticipate potential new HABs or shifts in baselines due to global change.

The next step commences with a new reporting phase, during which the HABs recorded during the reporting period should be compared to the reference values for prevailing conditions (GES thresholds) set in the initial assessment (Fig. 22). 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 initial 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? (Fig. 22).

7.2.2 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 HAB outbreaks, (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 (first axis), with their level of anthropic influence (second axis) (Fig. 23).

These axes were chosen because most connections between human activities and HABs related to nutrient supply, and MSFD contemplates HABs under descriptor D5, aiming to ensure that “the number, spatial extent and duration of harmful algal bloom events are not at levels that indicate adverse effects of nutrient enrichment”. Although the link with nutrient supply is more often associated with high-biomass HABs, the effect of nutrients in promoting HABs is neither uniform nor straightforward. It 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 favour 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 mobilization of trace metals in soils due to acidification (Granelli and Lipiatou, 2002), 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 harbours and dikes (Karlson et al., 2021). These pressures may even interact to produce larger effects, such as overfishing exacerbating eutrophication problems (Ferreira et al., 2011).

Recognising that the selected axes do not fully capture the complex interactions between different pressures and HABs but only the most relevant/likely 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 (Fig. 23), 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.

Fig. 23 shows a mock-up of a MAMBO matrix with two conceptual axes. For the quantitative application of MAMBO, these axes can be customised 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 based on user preferences, data availability, and regional characteristics (e.g., freshwater content, land use indices, or other anthropic indicators).

Several examples of HABs in European geographical areas, found in the reviewed literature, have been placed within the MAMBO matrix quadrants (Fig. 23) and briefly described in Table S9 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 towards the coast, resulting in a temperature increase that favours 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 (Pitcher and Fraga, 2015; Sordo et al., 2001). 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; Garcés and Camp, 2012; Basterretxea et al., 2005). 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, 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 Galicia Rias, it also thrives in eutrophic areas where excess nutrients from human activities create favourable 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 HAB species, 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 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 (Fig. 22): 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.

7.3 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 criteria that evaluate the state, or associated pressures and impacts of HABs. Although the MSFD currently addresses HABs solely within the eutrophication criterion D5C3, as described in Section 2.2, and their potential impacts on the “D1C6-pelagic broad habitat” state criterion (European Commission, 2017), it formally omits HABs un-related 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 Table S10.

In addition to the thematic context, indicators should be defined alongside quantifiable metrics 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 pressures-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. Threshold values, Ecological Quality Ratios (EQRs), trends, or supplementary information are crucial for properly interpreting the indicator results (Cusack et al., 2008).

7.3.1 Indicators for pressures causing HABs

The main abiotic factors 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 (Ryan et al., 2009; Kudela et al., 2010; McCabe et al., 2016; Pitcher et al., 2017; Heisler et al., 2008; Xiao et al., 2019). The conditions that trigger HAB outbreaks 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 HAB species seem to be stimulated by the availability of organic forms of nitrogen or phosphorus (Herndon and Cochlan, 2007; Kudela et al., 2008; Cochlan et al., 2008), 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 HAB 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 to 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 HABs (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 account for 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.

7.3.2 Indicators for HAB state

These indicators parallel those used for the assessment of phytoplankton but are specialized to address potentially harmful phytoplankton taxa. They also consider the frequencies or probabilities of their associated outbreaks (e.g., seasonal, occasional, potential). The commonly used indicators for phytoplankton and phytobenthos provide information on its composition, structure, or functions as detailed in Table S11.

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 HAB's anthropogenic origin is inconclusive, the indicator may not suffice to trigger management actions, according to GES4HABs (Fig. 22).

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 assessment from 2003, 2008 and 2017 (OSPAR 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, 2013; Funari et al., 2015), 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 (Havskum et al., 2004, Bustillos-Guzmán et al., 2004; Hayward et al., 2023), or according to their functional traits such as autotrophs-to - heterotrophs ratios) (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).

7.3.3 Indicators for HAB impacts

The indicators addressing the impact levels of different HABs should clearly address the corresponding types of impacts they produce (see Table S8).

7.3.3.1 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 on 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, behavioural 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): *Cyclotella choctawhatcheeana* (Jaanus et al., 2009), *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).

7.3.3.2 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). 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; Silva et al., 2013; Silva et al., 2018; Dean et al., 2020), as needed 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, as in the EU Regulation (EC) No 853/2004). These regulations also include the maximum PSP toxins 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-Villareal et al., 2022).

The impacts of HABs on human health can also be evaluated as societal costs that in precedent studies have focused on medical costs (medical cares and medical investigations) and individual expenses (lost wages, lost vacation time and transportation of patients to the hospital, etc.) (Sanseverino et al., 2016).

7.3.3.3 Impacts on socio-economic activities

Indeed, while substantial research is directed towards 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) (Martino et al., 2020; Hoagland and Scatasta, 2006; Sanseverino et al., 2016; Karlson et al., 2021). While reasonable estimates are often possible for harvest and 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 analysed the consequences of seafood trade bans at different scales (Basti et al., 2018). Dyson and Hupert (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, 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. In 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).

7.4 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 United States, European Union, and Asia and concluded that there is no one-size-fits-all approach.

Phytoplankton HABs occur in sunlit pelagic oceans, some at the surface other 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).

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 harbours 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). 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 (>5 µm). Additionally, there is a declining pool of expert taxonomists, further complicating the process (McQuatters-Gollop et al., 2017).

Thus, new approaches for more rapid, cost effective and precise microalgae cell counting and identification are being continuously developed and proposed to support HAB monitoring.

7.4.1 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 latest 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 (iv) nucleic acid-based detection methods (fluorescence in situ hybridization, sandwich hybridization assay, polymerase chain reaction techniques, metabarcoding, isothermal amplification technology, and gene chip). Liu et al. (2022) also provide 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 et al., 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 analysing 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, 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, 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 (Yarimizu et al., 2021; Murray et al., 2011; Pearson et al., 2021; Casabianca et al., 2014). 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 (Pearson et al., 2021; Drouet et al., 2022). 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; Gárate et al., 2022). 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).

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 analysed, and (iii) standardized protocols or guidelines. (e.g., Karlson et al., 2010; The U.S. Integrated Ocean Observing System (IOOS), 2017).

7.4.2 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 (EC) No 2074/2005), 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 characterisation 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 & 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 and have been responsible for some past poisoning incidents (Costa et al., 2017). Regulation (EC) No 853/2004 stipulates that testing requirements for live bivalve molluscs should apply equally to live echinoderms, live tunicates and live marine gastropods (EC, 2004b). 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).

7.4.3 Automated sampling methods and platforms

Significant progress has been made in the development of automatic sampling devices that can increase spatial coverage and frequency of sampling for a more comprehensive spatial and temporal observation of HAB dynamics (Boss et al., 2022; Nichols and Hogan, 2022) required for an indicator-based assessment of GES on the number, extent, and duration of HABs as required by MSFD legislation.

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 3m^3 of water that retain high densities of phytoplankton trapped in the mesh (Batten et al., 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 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 (Beckler 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-Villareal et al., 2022). These data can be eligible to support indicators related with some abiotic and biotic pressures on HABs.

However, although very promising 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., 2023b). 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 analysers that during the tested in-field profile 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-colour 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-colour 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. 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 polykrikoides* 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, 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 of human print like coastline changes (Murray et al., 2019) or location of aquaculture sites (Themistocleous, 2021) from high resolution true-colour images, or vessel densities and fishing effort from Automatic Identification Systems (AIS) (Robbins et al., 2022).

7.4.5 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 modelling 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, (ii) delineate areas with higher risks for HABs based on historical data, iv) predict, in real- or near real-time, the risk of HAB outbreaks, 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-IOC-IAEA, 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 that combines remote sensing, modelled hydrographic data, local algae and biotoxin modelled data to forecast water quality for Scottish shellfisheries that can benefit science-based development of harmful algae indicators.

Very recently, FAO-IOC-IAEA (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.

7.4.6 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 organisations (EU 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)** (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**, 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 et al., 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 harmonise 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 harmonising 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.
- 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 characterisation. Phytoplankton, Zooplankton, ocean hydrography and nutrients for Northern European countries are compiled and available at ICES, including historic data. Minelli et al. (2021) demonstrate a practical case study of the Open Science principles applied to a long-term marine dataset collected in the Northern Adriatic Sea between (1965–2015). Such efforts open up useful collaborations but has issues in reporting and trust in scientific recognition.
- The **Coastal and Oceanic Plankton Ecology, Production and Observation Database (COPEPOD)**, developed by the US National Marine Fisheries Service to 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 visualisations of phytoplankton and concurrent environmental conditions. Access to raw data often needs to be requested to contributors.
- **EMODnet Biology** provides open and free access to interoperable data and products on marine species (angiosperms, benthos, birds, fish, macroalgae, mammals, 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. At other times, toxins are not measured by agencies if a second toxin or health concern is noted.

- **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 FAIR (Findable, Accessible, Interoperable, Reusable) principles meant to optimise 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.

After their study, Minelli et al. (2021) concluded that despite the initial and still existing mistrust, opening up research projects and data is more than just a best practice because it improves transparency of research (thus increasing the credibility of researchers, the reproducibility of science, and the reuse of products), supports many international initiatives and regulations, and encourages cooperation between scientists across different fields and laboratories.

7.5 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 towards EBM approaches is essential to prevent to some extent and counteract HAB crises more effectively and cost-efficiently.

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. 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, recognising 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:

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 harmonised or standardised best practices to support joint large-scale assessments and synergistic and optimised 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.

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).

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 different ecosystem components and socio-economic 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.

International and cross-sectoral cooperation to increase synergies and optimise 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 organisations currently dedicated to HAB management (food safety and public health authorities, environmental managers, scientific organisations, food producers, marine spatial planners, etc.) should be closely examined to build bridges of cooperation, avoid duplication, optimise efforts, and focus new resources to fill the identified gaps.

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 towards 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.

8. Discussion and Recommendations

The four comprehensive reviews on IAS, HABs, jellyfish outbreaks, and the decline of top predators assessed the scientific background on drivers-pressure-state-impacts links of these components, their linkages to ecosystem services and societal benefits including human health and welfare, the existing knowledge gaps, and the state-of-the-art and best practices in monitoring, predicting, and managing these events and their consequences. The reviews also evaluated the potential of novel methods such as, among others, eDNA, metabarcoding, biologgers, and remote sensing. This work provided essential recommendations for improving monitoring, assessments, and management, summarized herein. **With this Deliverable, we contribute to achieve the OUTCOME 4 of the call - i.e., EBM approaches and policy measures for activities to reduce pressures and lead to the achievement of GES.**

8.1 Recommendations for improving IAS management

- **Expand Marine Coverage in the IAS Regulation:** Currently, the IAS Regulation in Europe inadequately covers marine biological invasions, despite the significant impact of these invasions on biodiversity and ecosystems. **The regulation should be updated to include more marine species based on scientific advice and risk assessments, which should be consider within the MSFD and other legislation.**
- **Learn from Biosecurity Practices of Other Countries**: Europe should learn from countries like New Zealand, Australia, and the USA, which have established effective biosecurity systems for managing IAS. Collaboration and knowledge **sharing with these nations can improve Europe's IAS management strategies.** Facilitating workshops that bring together top-tier policymakers, marine researchers, managers, and representatives from diverse countries can foster collaborative information exchange and shared learning, ultimately strengthening the global management efforts against marine IAS.
- **Enhance Monitoring and Early Warning Systems**: Efforts to monitor marine IAS should be increased **in terms of spatial and temporal coverage**. **Innovative techniques** like eDNA and citizen science **should be employed** to streamline data collection and early warning systems.
- **Improve Predictive Models**: Accurate prediction of invasive species' current and future distribution is vital for conservation efforts. Models should consider biological traits, biotic interactions, environmental conditions, and available data from both native and invaded

ranges to enhance prediction accuracy. **In this way, Open Science can be a powerful way to use open data in such models.**

- **Conduct Cumulative Impact Assessments**: Evaluating the cumulative impacts of multiple IAS on marine ecosystems is essential for effective management. **These assessments help prioritize actions and resource allocation to mitigate IAS effects.**
- **Assess Positive Impacts and potentially Exploit NIS**: Instead of viewing all NIS as harmful, scientists and policy makers should consider both negative and positive consequences on recipient ecosystems. NIS can have potential benefits for ecosystem services, human well-being, and biodiversity, e.g. by creating novel habitats or as new commodities contributing to food provision**. However, exploration of commercial exploitation and bioprospecting of certain IAS should be approached cautiously, considering potential risks and unintended outcomes**.
- **Increase Funding for IAS Management:** To address the growing costs and impacts of IAS, there needs to be a substantial increase in economic resources allocated to prevention, control, research, long-term management, and eradication measures. **Allocation of funds should prioritize prevention as the primary line of defense against IAS introductions. However, it is equally crucial to invest in the development of eradication and control strategies. International cooperation and strategic planning are essential** to secure adequate funding for these efforts.
- **Establish EU Funding Mechanisms for Information Systems**: Adequate funding is crucial to sustain information systems like EASIN, which gather and provide data on NIS in Europe. **Financial support for national institutions and scientific networks is necessary** to ensure a continuous flow of information and knowledge to EASIN.

8.2 Recommendations for improving the conservation of marine top predators

- **Embrace Holistic and Adaptive Approaches**: To effectively conserve marine top predators and biodiversity, there is a need to move away from a strictly sectoral approach and adopt more holistic and adaptive decision-making strategies. **This includes a multidisciplinary understanding of socio-ecological and economic elements and integrating them into conservation efforts**. To recognize that top predators rely on the entire ecosystem at large scales, thus comprehensive EBM approaches are needed to support their conservation and resilience, **including mandatory measures to reduce bycatch.**

- **Utilize the DAPSI(W)R(M) Framework**: The DAPSI(W)R(M) framework is proposed as an extended version of the DPSIR model, considering the benefits offered by nature. This comprehensive **framework links natural and social sciences with governance and management and includes conservation** as a key management measure, making it great for communication.
- **Recognize Cumulative Impacts**: Biodiversity loss in marine ecosystems can have far-reaching consequences, including disruptions in ecosystem functioning and cross-system connectivity. Recognizing cumulative impacts under a risk-management approach **and implementing measures to mitigate them is crucial**.
- **Implement Effective Conservation Measures**: The recovery of marine animal populations, especially top predators, can be slow and complex. **It requires sustained conservation measures, robust EBM, and an understanding of historical population baselines**.
- **Incorporate Essential Ingredients for EBM**: Effective EBM efforts **should include ecological connections, scientific knowledge, adaptive and integrated management, stakeholder involvement, recognition of ecosystem dynamics, consideration of socio-ecological links, and acknowledgment of ecosystem variability.** In particular, ecosystem-based fisheries management (EBFM) should rely on basic principles of fisheries biology (i.e. fishing all stocks below the FMSY threshold) and ecology (i.e. fishing less over low trophic-level species such as forage fish as they are bottlenecks to transfer energy from the planktonic food web to upper trophic levels).
- **Learn from Success and Failure Stories:** Lessons from both successful and unsuccessful conservation stories of marine top predators emphasize the importance of **robust knowledge, education (ocean literacy), adaptive management measures, stakeholder involvement, and mitigation of bycatch as crucial drivers for success.**
- **Invest in Management Measures**: There is a need for political will to implement necessary management measures. **Mitigation measures are imperative to reverse the adverse impacts on marine top predators.** Mitigation options include the establishment of marine protected areas, the enforcement of fisheries regulations, and the promotion of sustainable fishing practices. **Bycatch mitigation, including technological, operational, and socioeconomic measures, has been successful in reversing the decline of top predators.**
- **Integrate Research into Management**: The integration of research findings into large-scale management is crucial (e.g., in the MSFD Programmes of Measures). **Collaboration with**

stakeholders, effective communication of benefits, and the use of tools like the 'Conservation Evidence' initiative can help bridge the gap between research and management.

- **Build Long-term Monitoring and develop Novel Tools**: Effective monitoring of marine top predators requires long-term data collection. Traditional methods, combined with novel technologies like biologging devices and genetic techniques (eDNA analysis), **can enhance our understanding of these species and their interactions.**
- **Implement Systematic Conservation Planning**: Implement systematic conservation planning for marine spatial prioritization to guide conservation efforts**, including the location and management of MPAs** (combining spatial and temporal protected areas, and ecological corridors) while minimizing socio-economic costs and evaluating potential economic benefits.

8.3 Recommendations for managing jellyfish and their outbreaks

- **Enhance Monitoring Efforts**: Increase efforts in monitoring jellyfish populations, **adopting innovative technologies** like underwater acoustics, automated counting, camera systems with artificial intelligence, citizen science involvement, eDNA sampling, remote sensing, and modelling to gather more comprehensive data.
- **Standardize Global Monitoring**: Encourage standardized monitoring of jellyfish populations through citizen science initiatives, similar to the Reef Life Survey for other taxa, to advance knowledge of jellyfish ecology and distribution.
- **Better Understand Jellyfish Outbreaks**: Investigate the various factors, including overfishing, species translocations, eutrophication, climate change, and habitat modification, that contribute to jellyfish outbreaks. **Further research should focus on understanding the specific causal mechanisms linking anthropogenic stressors to these outbreaks**.
- **Consider Polyp Phase**: Investigate the early phases of jellyfish, such as polyps and ephyrae, **to gain insights into their recruitment dynamics**. Implement specific sampling programs to locate polyps, estimate reproduction rates, and understand environmental factors influencing outbreak dynamics.
- **Integrate within the MSFD**: Integrate jellyfish monitoring, assessment, and management into the MSFD framework, for adequate EBM. **Define relevant criteria, indicators, and thresholds for jellyfish status, pressures, and impacts within descriptors such as non-indigenous**

species, food webs, and eutrophication, and also consider them in the MSFD Programmes of Measures.

- **Differentiate Anthropogenic and Natural Factors**: Clearly differentiate between anthropogenic and natural factors driving jellyfish outbreaks to formulate effective policies that address manageable causes, within the MSFD and other legislation. **Implement adaptive management principles to respond to changing conditions, under an EBM approach.**
- **Promote Ocean Literacy**: Raise public awareness and education about jellyfish species, risks, and safety measures to minimize their impact on public health, tourism, fisheries, and marine facilities. **Encourage the public to report jellyfish populations and be proactive in managing them.**
- **Explore Sustainable Blue Economy**: **Investigate the potential economic benefits of jellyfish,** such as food provision, biotechnology, and biomedicine, to leverage their ecosystem services for sustainable marine resource utilization while mitigating adverse effects.

8.4 Recommendations for managing HABs

- **Recognize Ecosystem Alteration**: Acknowledge that **HAB outbreaks** are often a reflection of ecosystem alterations, and while they cannot be completely eliminated, they **can be prevented at some extent or their impacts mitigated.**
- **Integrate HABs into MSFD**: Promote the integration of HABs into the MSFD assessments **to recognize their relevance in marine ecosystems and socio-economic issues**.
- **Adopt proposed decision supporting tools** to assist MSFD reporters in deciding when and how include HABs in the MSFD, two decision supporting tools are proposed: the **GES4HABs decision tree and the MAMBO matrix**: The first one establishes the different steps to guide the decisions on management strategies. 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.
- **Design Tailored Solutions**: Recognize that **there is no one-size-fits-all solution for managing HABs**, and specific tailored solutions are needed for different affected areas and different HAB species.

- **Build Harmonized Best Practices**: **Encourage international and cross-sectoral coordination** to define harmonized or standardized best practices for monitoring, analysis, assessment, data management, and more to support joint large-scale assessments and optimized strategies.
- **Establish Sustained Monitoring**: Implement sustained long-term monitoring programs with appropriate strategies to better understand HAB outbreaks, their causes, impacts, and other related factors. **Ensure data quality and adherence to international standards, as well as Open Science to make those data available**.
- **Incorporate New Technologies**: Explore the use of new technologies such as genomic methods, automated samplers, remote sensing, early warning systems, and artificial intelligence models **for more cost-effective and efficient HAB monitoring**.
- **Identify Links and Indicators**: Identify, demonstrate, and quantify the links between HABs, their causes, and their impacts on ecosystems and socio-economic activities. **Select appropriate indicators and thresholds to guide management measures within the MSFD.**
- **Encourage Cooperation and Resource Optimization**: Define roles and cooperation mechanisms between various organizations involved in HAB management **to avoid duplication of efforts** and optimize resources.

8.5 Concluding remarks

The comprehensive reviews on IAS, HABs, jellyfish outbreaks, and the decline of top predators have provided valuable insights into the complex dynamics of these critical issues affecting marine ecosystems. These reviews have not only assessed the scientific underpinnings of these challenges but have also explored their interconnectedness, their impacts on ecosystem services, and the gaps in our knowledge. The state-of-the-art monitoring, prediction, and management practices, including the potential of novel technologies, have been thoroughly examined. As we conclude this study, **we extract overarching recommendations that apply to the management of all four issues, underlining the need for a holistic and adaptive approach to safeguard marine ecosystems and the benefits they provide to society.**

Holistic Ecosystem-Based Management

A common thread running through these challenges is the call for a shift from conventional, localized management approaches towards holistic, ecosystem-based strategies. EBM recognizes the intricate interplay of species, habitats, and environmental factors within marine ecosystems as well as the economic and social interactions between the ecosystem and humans. By embracing this approach, we can address the root causes and cumulative impacts of these issues more effectively. For instance, GES4SEAS plans to consider the cumulative impacts of multiple IAS, HABs, and jellyfish outbreaks by expanding CIMPAL (currently restricted to IAS only).

Integrated Decision-Making Frameworks

Adopting integrated decision-making frameworks, such as the DAPSI(W)R(M) model, helps bridge the gap between scientific knowledge and effective governance and management. These frameworks facilitate a comprehensive approach that considers both the ecological and socio-economic elements of marine ecosystem management. Implementing such frameworks enhances our ability to assess the impacts of these challenges, prioritize actions, and optimize resource allocation. Through the implementation of such integrated decision-making frameworks in GES4SEAS' Learning Sites, we anticipate learning in practice how such frameworks can improve marine governance and management and how sensitive they are to numerous interactions and cumulative effects as well as cascades of interconnected aspects.

Collaboration and Knowledge Sharing

International cooperation and knowledge sharing, under the Open Science basis, are paramount in addressing these challenges. Learning from successful biosecurity practices in countries like New Zealand, Australia, and the USA can significantly enhance our ability to manage IAS. Similarly, adopting standardized monitoring practices in citizen science initiatives, as was done for the Reef Life Survey, can advance the quality and quantity of available data and our understanding of IAS, HABs, jellyfish outbreaks, and the dynamics of top predators. Collaborative efforts across borders allow us to pool resources, share expertise, and collectively develop effective strategies.

Adaptive Management, Long-Term Monitoring, and Novel Technologies

The dynamic nature of these challenges calls for adaptive management and long-term monitoring. This approach recognizes that solutions may need to evolve over time as our understanding deepens and conditions change. To effectively conserve top predators, and mitigate the impacts from IAS, HABs, and jellyfish outbreaks, sustained, well-funded, and long-term monitoring programs are essential. Incorporating traditional methods with novel technologies, like biologging devices and eDNA analysis, among others, can provide the necessary insights into these issues. Increased funding is essential to enhance monitoring, enabling more comprehensive and effective management of these marine ecosystem challenges.

Public Engagement and Education

Engaging the public and fostering ocean literacy play a critical role in managing these challenges. By raising awareness about the impacts of IAS, HABs, jellyfish outbreaks, and top predator declines, we can encourage responsible behaviours and proactive reporting. Informed communities become active participants in monitoring and managing these events, contributing valuable data and insights.

Preparedness and Anticipation

Actively intensify efforts towards EBM strategies to address the challenges posed by changing environmental conditions, climate change, and expanding human activities in marine waters. Emphasize resilience and sustainability in ecosystem management. Develop and implement adaptive monitoring frameworks capable to early identify critical changes in marine ecosystems.

In conclusion, the management of IAS, HABs, jellyfish outbreaks, and the decline of top predators in marine ecosystems demands an integrated, adaptive, and collaborative approach. By implementing these overarching recommendations, we can better protect marine ecosystems and their services, benefiting both nature and society.

9. References

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10. Annex

10.1 Supplementary text

Supplementary Text 1. Review of proposed or applied management options for marine IAS of EU interest

A global review was conducted to seek information on proposed or globally applied management options for marine species included in the list of IAS of EU interest, i.e., *Plotosus lineatus* and *Rugulopteryx okamurae*, and species recently proposed but not included in the last update of the Union list (Commission Implementing Regulation 2022/1203), or congeneric species with similar characteristics (Table A). Species recently proposed but not included in the EU list are *Pterois miles*, *Lagocephalus sceleratus*, *Boccardia proboscidea*, *Schizoporella japonica*, *Hemigrapsus sanguineous*, *Rapana venosa*, and *Perna viridis*.

There are no examples of successful eradication or control of *Plotosus lineatus.* The direct removal of the species with intensive targeted fishery, especially during the spawning period, has been proposed by Galanidi et al. (2017) as an approach that could be effective in controlling its populations. Additionally, Galanidi et al. (2017) stated that the species is considered edible in its native range, and recommended promoting human consumption and its exploitation by small-scale fisheries to control its population and mitigate its impacts.

Rugulopteryx okamurae cannot be eradicated if established; eradication in new regions could be feasible only if it is detected very early, and response is very fast based on an effective method, good coordination and communication, and sufficient funding (see Section 4.7 for examples of early detection – fast eradication of other macroalgae). Eradication would be difficult, but there are examples of species with similarly high propagation capacity, such as *Caulerpa taxifolia*, that were successfully eradicated after early detection (Anderson 2005). Nevertheless, there are no known effective eradication or control methods for *R. okamurae* that have been implemented or assessed as potentially effective in its invaded range.

For *Pterois miles/volitans*, physical removal methods have been extensively applied in the western Atlantic and the Mediterranean. These include lionfish culling by divers, often with public participation (e.g., by organizing lionfish tournaments), physical removals involving fishers, promoting the targeted fisheries of the species and human consumption (or other uses), developing specific fishing gear such as the 'Gittings' traps (Harris et al., 2020), and recently developing UW robots, which may harvest lionfish (Sutherland et al., 2017) (Table A). The latter two methods ('Gittings traps' and UW robots) can operate in deep waters, inaccessible by divers. Rebuilding top predator populations (i.e., rehabilitating the environment) may have positive effects in controlling lionfish, but it should be considered as a long-term strategy with limited effectiveness in the short-term; proactive, targeted removals by humans appear to be the only management option that can effectively control lionfish populations (Ulman et al., 2021). Ulman et al. (2022), synthesizing successes and failures from two decades of management in the western Atlantic, advise against the practice of feeding lionfish to native fish to promote predation and suggest implementing bounty programs to incentivize lionfish harvest. The first practice created safety issues for divers as some large predators associated divers with food, and attacks on humans increased. It is acknowledged that eradicating the lionfish is impossible, but continuous removals may effectively (at a lower cost) control its populations at sufficiently low levels to mitigate their impacts (e.g., Green et al., 2014; Usseglio et al., 2017).

Eradication of *Lagocephalus sceleratus* in its invaded range in the Mediterranean Sea is impossible as the species is already widespread and abundant and also due to its high fecundity, mobility, and long duration of the early life stages. To control its population, targeted, intense fishing pressure on the species' breeding population by the coastal professional fleet, promoted by a bounty (3 €/kg), has been implemented in Cyprus since 2012, with anecdotal information by fishers of effective reduction of its population and mitigation of its socio-economic impacts (A. Petrou, pers. comm). Furthermore, a food-web modelling study using Ecopath with Ecosim investigating scenarios on the fishing mortality of *L. sceleratus* concluded that the species (1) was significantly affected by targeted increased fishing mortalities, (2) can return to its initial biomass in only a few years if fishing mortality ceases, and (3) with zero fishing mortality, its biomass would increase by around 50% before reaching equilibrium (Michailidis et al., 2023). Other proposed management options (Table A), which would need additional research, are the mass trapping using pheromones to collect mature reproductive individuals and the creation of demand for commercial harvesting of the species, to be used for human consumption (highly unlikely) or fishmeal after detoxification or pharmaceutical purposes. Several ongoing research projects investigate potential commercial uses of the species, which could promote its targeted fishery (e.g., https://lagomeal.gr/, https://lionhare.hcmr.gr/, https://imbbc.hcmr.gr/project/explias/).

Eradication of *Boccardia proboscidea* in the wild is considered unlikely unless for a localized, early detected, small population (Galanidi and Zenetos 2019). Due to its tube-dwelling or boring lifestyle, mechanical removal cannot be conducted without removing the associated substrate, which complicates any physical removal effort. Chemical treatment for eradicating localized, early detected populations has never been attempted for the species (Galanidi and Zenetos 2019) but might be an option. As the species is favoured by increased organic matter, achieving good environmental status and solving eutrophication issues may contribute to avoiding outbreaks of the species (Galanidi and Zenetos 2019). Several effective methods have been developed to control *B. proboscidea* or congeneric species in infected bivalves in aquaculture farms. Handley and Bergquist (1997) found that spionid infestations (including the congeneric *Boccardia acus* and *Boccardia chilensis*) are avoidable by growing oysters above extreme low water neap and 0.5 m above the mud substratum. Handlinger et al*.* (2004) reported that the best treatment for mud worms (including the congeneric *Boccardia knoxi*) in abalone grow-out facilities was air-drying of stock. The diatom-derived polyunsaturated aldehyde 2,4-decadienal was experimentally found effective as a potential chemotherapeutic agent against the larvae of *B. proboscidea*, and its use was proposed to control the species in cultured abalone facilities (Simon et al*.*, 2010). A variety of management options for controlling mud worms in shellfish farms (with varying effectiveness by species) has been reviewed by Spencer et al. (2021), including keeping shellfish free of mud, air exposures, long tidal exposures, frequent cleaning, freshwater treatments, salt brine soaks, extended cool air storage, heat treatments, treatment with calcium hydroxide, treatment with mebendazole and various combinations, as e.g., the SSSP (Super Salty Slush Puppy) treatment initially developed by Cox et al. (2012).

Eradication of *Perna viridis* would be possible only for a localized, early detected, small population. The species is problematic for cooling pipes, and several methods to control it have been implemented, including chlorination and heat treatment (Rajagopal et al*.*, 1996, 2006). Its survival was significantly inhibited during aerial exposure, and mortality synergistically increased with increasing temperatures and exposure time and by acute change of salinity to 15 or below (McFarland et al., 2015). Manual removal has been effective after early detection to inhibit the establishment of the species in Australia (Sewell et al., 2018 and references therein). Successful eradication of the congeneric species *Perna perna* has been achieved by its physical removal by dredges (Hopkins *et al.* 2011).

Rapana venosa is strongly associated with natural and cultured bivalve beds, and thus the most effective system for early detection would involve bivalve producers and local fishers (Galanidi 2019a). Targeted removal has not been attempted for *R. venosa.* In the Black Sea, it supports an important fishery with high revenues (~ € 12 million annually), and its management has been controversial (Janssen et al., 2014; Demirel et al., 2021). The Scientific, Technical and Economic Committee for Fisheries (STECF 2015) has suggested that this fishery should not be managed to achieve Maximum Sustainable Yield (MSY), and fishing activities should not be constrained so that the *R. venosa* stock is reduced at levels below MSY. On the other hand, *R. venosa* has been highlighted by the General Fisheries Commission for the Mediterranean (GFCM) as one of the eight priority species in the Black

Sea for which fisheries advice is needed, and based on that, the Black Sea countries initiated surveys to provide recommendations for the sustainable exploitation of the species (Demirel et al., 2021). Offering a bounty, promoting local consumption, and encouraging local restaurants to develop recipes for the species was a strategy applied in the Chesapeake Bay to control the species' population (Mann and Harding, 2003).

The probability of early detection is minimal. Hence the eradication of *Hemigrapsus sanguineus* is considered unlikely, and it has not been attempted anywhere in its invaded area (Galanidi, 2019b). Nevertheless, "crab condos" (i.e., artificial habitat collectors for small crabs) have been proposed as a monitoring tool for early detection in high-risk areas of introduction (Hewitt and McDonald, 2013). The bivalve *Crassostrea gigas*, listed in Annex IV of Council Regulation 708/2007, constitutes an exception to the restrictions of translocation and can be moved without risk assessment or quarantine. As *H. sanguineus* can be introduced as contaminants of oysters, a ban on oyster transfers from areas invaded by *H. sanguineus* may prevent further introductions in new areas (Galanidi, 2019b). Biological control using castrating rhizocephalan barnacle species from the native range of *H. sanguineus* (i.e., alien to Europe) has been proposed as a potential control measure; however, extensive research is needed to ensure the safety of native fauna (Galanidi, 2019b). *Hemigrapsus sanguineus* is preyed preferential by certain native crustacean-eating fishes in Long Island Sound (USA), and thus enhancing predator populations via proper management has been proposed in that region as a way to control its populations (Heinonen and Auster, 2012).

There are no examples of successful eradication or control of *Schizoporella japonica*. Due to the small size of propagules and early colonies, taxonomic uncertainty, and the high expertise needed to identify the species, early detection and rapid response are unlikely (Sewell, 2019). If, however, the species is detected early in a new location, eradication techniques using chemicals such as bleach may be applied. General removal methods of fouling populations from vessels, e.g., dry-docking or new technology in-water removal systems, could be applied (Sewell, 2019). Using environmental DNA (eDNA) in high-risk areas may assist early detection of its introduction.

References are provided after Table S4

Supplementary Text 2. Materials and Methods of section 5.6 "Success stories: factors for success"

The main search was performed through the Web of Science and SCOPUS databases in January 2023. The search string used was: (TITLE-ABS-KEY (management OR conservation OR measure OR protection) AND TITLE ("population increase" OR recovery OR effective* OR success* OR rebound* OR improv*) AND TITLE-ABS-KEY ("top predator*" OR "apex predator*" OR "marine mammal*" OR dolphin OR whale OR seal OR "sea lion" OR otter OR porpoise OR "polar bear" OR cetacean OR "elasmobranch*" OR shark OR ray OR skate OR sawfish OR tuna OR swordfish OR billfish OR grouper OR "marine bird" OR seabird) AND TITLE-ABS-KEY (marine OR sea OR ocean OR benthos OR benthic OR gulf OR bay OR archipelago OR reef)). Only papers in English were considered; no restriction on the year of publication was set. The literature search resulted in 786 articles after the removal of duplicates. Additionally, 639 papers not identified in the initial search were added for screening; these were identified from the reference lists of selected articles, the NOAA Fisheries website (https://www.fisheries.noaa.gov/), the Conservation Evidence website (https://www.conservationevidence.com/), and experts' suggestions (Figure S1). The search path used in the NOAA fisheries website was 'Resources & Services > Publications > (i) Published Research, (ii) Key reports, (iii) Outreach Materials' tabs. The categories searched were for the 'Topic', (i) Endangered species conservation and (ii) Marine Mammal Protection', and for the 'Species Category', (i) Fish & Sharks, (ii) Whales, (iii) Dolphins & Porpoises, and (iv) Seals & Sea Lions. In the Conservation Evidence website, the categories searched were (i) Marine Fish Conservation, (ii) Marine and Freshwater Mammal Conservation, and (iii) Bird Conservation' restricted to marine habitats.

Initially, only titles and abstracts were screened against these criteria. This first phase produced 181 articles using the same criteria to analyze the full text.

The eligible papers were classified into five groups:

1. bibliographic information;
2. species-specific and study-specific information: i.e., species scientific name as in WoRMS (2023); taxonomic group; relevant marine realm and province according to Spalding et al. (2007); the country where the research was conducted; the geographical scale of the study (local, national, regional, global);
3. information about conservation actions: i.e., type of conservation action; start year; duration; cost; conservation target; indicators of success; factors contributing to success; factors contributing to failure (elsewhere, if discussed in the paper);

4. stakeholder groups involved;
5. threat(s) mitigated through the conservation action(s).

In addition, the IUCN status and population trend of the assessed species were extracted from the IUCN Red List (IUCN, 2023).

10.2 Supplementary Tables

Table S1. *Number of recorded impact cases per circle compartment for Figures 5, S1, and 6. Information retrieved from Tsirintanis et al. 2022.*

Figure 5 values					
Negative impacts			**Positive impacts**		
Mechanism of impact	**Number of impacts**	**Impact on:**	**Mechanism of impact**	**Number of impacts**	**Impact on:**
Competition for resources	246	Biodiversity	New Commodities	186	Provisioning services
Creation of novel habitat	105	Biodiversity	New biotic materials	2	Provisioning services
Predation	52	Biodiversity	New food source for fish	1	Provisioning services
Modification of sedimentation	13	Biodiversity	Creation of novel habitat	1	Provisioning services
Release of toxins	12	Biodiversity	Creation of novel habitat	84	Biodiversity
Disease transmission	11	Biodiversity	Food provision	21	Biodiversity
Reduction of light penetration	11	Biodiversity	Bioturbation	7	Biodiversity
Bioturbation	6	Biodiversity	Filter-feeding	7	Biodiversity
Filter-feeding	4	Biodiversity	Modification of trophic flows	5	Biodiversity
Modification of trophic flows	4	Biodiversity	Modification of sedimentation	3	Biodiversity
Anoxia	3	Biodiversity	Control of invasive species	2	Biodiversity
Introduction of parasites	1	Biodiversity	Creation of novel habitat	19	Regulating services
Biofouling	45	Provisioning services	C sequestration	18	Regulating services
Entanglement in nets	32	Provisioning services	Biofiltration	15	Regulating services
Habitat degradation	18	Provisioning services	Bioturbation	5	Regulating services
Competition for resources	16	Provisioning services	Control of pathogens	3	Regulating services
Direct predation	15	Provisioning services	Macroalgae function as biofilters	2	Regulating services
Clogging intake pipes	5	Provisioning services	DMSP production	1	Regulating services

Habitat degradation	75	Regulating services	Materials for research	70	Cultural services
Filter-feeding	13	Regulating services	Biomonitoring	44	Cultural services
Rapid nutrient uptake	7	Regulating services	Reduction of decomposing algae	3	Cultural services
Emission of greenhouse gasses	2	Regulating services	Novel habitat	2	Cultural services
DMSP production	1	Regulating services	Aesthetic improvement of seascape	1	Cultural services
Massive mortality	1	Regulating services			
Habitat degradation	38	Cultural services			
Algae washed ashore	32	Cultural services			
Jellyfish invasions	6	Cultural services			
Navigation impediment	4	Cultural services			
Biofouling	2	Cultural services			
Stinging	36	Human health			
Poisoning/Intoxication	24	Human health			
Biting	1	Human health			

Figure S1 values					
Negative impacts			**Positive impacts**		
Mechanism of impact	**Number of impacts**	**Impact on:**	**Mechanism of impact**	**Number of impacts**	**Impact on:**
Competition for resources	141	Biodiversity	New commodities	186	Provisioning services
Creation of novel habitat	86	Biodiversity	New biotic materials	2	Provisioning services
Predation	39	Biodiversity	New food source for fish	1	Provisioning services
Release of toxins	11	Biodiversity	Creation of novel habitat	77	Biodiversity
Modification of sedimentation	9	Biodiversity	Food provision	18	Biodiversity
Disease transmission	7	Biodiversity	Filter-feeding	3	Biodiversity
Reduction of light penetration	4	Biodiversity	Bioturbation	2	Biodiversity

Bioturbation	3	Biodiversity	Control of invasive species	2	Biodiversity
Anoxia	2	Biodiversity	Modification of sedimentation	2	Biodiversity
Filter-feeding	2	Biodiversity	Materials for research	60	Cultural services
Introduction of parasites	1	Biodiversity	Biomonitoring	33	Cultural services
Biofouling	41	Provisioning services	Reduction of decomposing algae	3	Cultural services
Entanglement in nets	32	Provisioning services	Biofiltration	7	Regulating services
Direct predation	11	Provisioning services	C sequestration	3	Regulating services
Competition	7	Provisioning services	Control of pathogens	3	Regulating services
Clogging intake pipes	4	Provisioning services	Creation of novel habitat	3	Regulating services
Habitat degradation	1	Provisioning services			
Algae washed ashore	30	Cultural services			
Habitat degradation	6	Cultural services			
Navigation impediment	4	Cultural services			
Jellyfish invasions	3	Cultural services			
Biofouling	2	Cultural services			
Habitat degradation	27	Regulating services			
Emission of greenhouse gasses	2	Regulating services			
Filter-feeding	1	Regulating services			
Massive mortality	1	Regulating services			
Stinging	18	Human health			
Poisoning/Intoxication	9	Human health			
Biting	1	Human health			

Figure 6 values	
Negative impacts	**Positive impacts**

Strength of evidence	**Number of impacts**			**Strength of evidence**	**Number of impacts**
Robust	119			Robust	97
Medium	386			Medium	308
Limited	336			Limited	97

Table S2. Eradication efforts for marine IAS globally - reasons for success/failure. Information retrieved from Katsanevakis (2022) and updated.

Species [Tax. group] – objective	**Outcome [Approach]**	**Reasons for Success/Failure of management efforts**	**Reference**
Caulerpa taxifolia [Macroalga] - eradication	Successful [chemical: coverage by PVC sheeting and injection of sodium hypochlorite]	Fast response after detection; suitable method; secured funding; adequate expertise and knowledge on the biology of the species; knowledge on the uses, ownership and characteristics of the infested site; experience in aquatic plant eradication; locally driven efforts; public buy-in; spatially localized introduction; sufficient awareness.	Anderson 2005
Kappaphycus spp. [Macroalgae] - control	Failure [physical: manual removal]	The ability of the species to re-grow from minute attachment points that could not be effectively removed manually.	Conklin & Smith 2005
Kappaphycus spp. [Macroalgae] - control	Successful experimentally [biological: control by native sea urchins]		Conklin & Smith 2005
Sargassum muticum [Macroalga] - control	Failure [physical: handpicking]	Overall efficiency of the operation was low.	Critchley et al. 1986
Sargassum muticum [Macroalga] - control	Failure [chemical: use of herbicides]	None of the herbicides tested were satisfactory for use (lack of selectivity, large doses required, large period of time the herbicides need to be in contact with the alga, and the problem of chemical application in the marine environment	Critchley et al. 1986
Sargassum muticum [Macroalga] - control	Failure [biological: control by native grazers]	Scarcity of grazers; preferences for a diet comprising other algae.	Critchley et al. 1986
Sargassum muticum [Macroalga] - control	Successful [physical: mechanical removal by trawling]	High efficiency of the method; limited ecological damage.	Critchley et al. 1986

Sargassum muticum [Macroalga] - control	Successful [physical: mechanical removal by cutting]	Efficient engineering (conversion of an agricultural corn-cutting implement)	Critchley et al. 1986
Sargassum muticum [Macroalga] - control	Conditionally successful [physical: mechanical removal by suction]	Efficient engineering	Critchley et al. 1986
Caulerpa taxifolia [Macroalga] - control	Failure [physical: manual removal]	Labour intensive; the alga often became fragmented during the removal process and any fragments could spread and re-establish	Glasby et al. 2005
Caulerpa taxifolia [Macroalga] - control	Failure [physical: jute matting]	*Caulerpa taxifolia* was found growing between the joints of the jute and through any tears that had occurred during deployment.	Glasby et al. 2005
Caulerpa taxifolia [Macroalga] - control	Successful [chemical: deployment of salt]		Glasby et al. 2005
Undaria pinnatifida [Macroalga] - control	Successful [physical: manual removal]	Long-term commitment coupled with vector management and education initiatives to reduce the chances of re-inoculation and spread.	Hewitt et al. 2005
Ascophyllum nodosum - [Macroalga] - eradication	Successful [physical: manual removal]	Relatively quick initiation of the eradication efforts after initial detection (10 weeks); continuous monitoring of the site after eradication.	Miller et al. 2004
Caulerpa taxifolia - [Macroalga] - eradication (experimental)	Potentially successful [chemical: use of Cu^{2+}]		Uchimura et al. 2000
Caulerpa taxifolia - [Macroalga] - eradication (experimental)	Successful [chemical: using chlorine bleach]		Williams & Schroeder 2004
Undaria pinnatifida - [Macroalga] - eradication	Successful [physical: a combination of physical removal of sporophytes by divers and heat treatment]	Fast response after initial detection; a suitable new method was developed and employed; sufficient funding; adequate knowledge about the biology of the target pest existed; adaptive and integrated management targeting multiple life history stages; effective communication with the local community and other stakeholders that enabled managing public	Wotton et al. 2004

		expectations and gain support for the programme.	
Caulerpa taxifolia - [Macroalga] - control	Failure [biological: use of a sea slug as a control agent]	Instead of destroying the algal frond, the sea slug cut fronds into tiny living fragments capable of regenerating. Thus, the species may facilitate *C. taxifolia* dispersal instead of controlling it.	Žuljevic et al. 2001
Terebrasabella heterouncinata - [Polychaete] - eradication	Successful [physical: host removal]	Good knowledge of the biology and ecology of the pest species and epidemiological theory allowed the implementation of a successful eradication program that did not targeted directly the introduced species (which would have been impractical due to its microscopic size) but its main native host.	Culver & Kuris 2000
Sabella spallanzanii - [Polychaete] - eradication	Failure [physical: Systematic culling by divers]	Late initiation of eradication efforts; confinement was not possible.	Read et al. 2011
Mytilopsis sallei - [Mollusk] - eradication	Successful [chemical: Chemical treatment. 187 tonnes of liquid sodium hypochlorite and 7.5 tonnes of copper sulphate]	Very fast response, after initial detection; very good local and national coordination; flexibility in amending existing legislation; strong community support; full-time public relations team assigned to the problem, which ensured that relevant stakeholders and the media were provided updated and accurate information.	Bax et al. 2002
Magallana (Crassostrea) gigas - [Mollusk] - control	Successful [physical: culling with a hammer]		Guy and Roberts 2010
Perna perna - [Mollusk] - eradication	Successful [physical: dredging]	Fast response after initial detection; a suitable method was employed; sufficiently funding was quickly secured; experts knowledgeable about the biology of the target pest were consulted so that success criteria could be developed.	Hopkins et al. 2011
Carcinus maenas - [Crustacean] - control	Unknown [Biological: control by a parasitic barnacle]		Lafferty & Kuris 1996
Callinectes sapidus - [Crustacean] - control	Unknown [Physical: promoting targeted fishery]		Mancinelli et al. 2017

Didemnum vexillum [Ascidian] - control biofouling on shellfish (experimental)	Failure [Biological: use of a snail as control agent]	The snail did not notably consume or scour *D. vexillum* from shellfish under the conditions provided.	Carman et al. 2009
Ciona intestinalis [Ascidian] - control biofouling on shellfish	Successful [Chemical: exposure to 5% acetic acid for 30 sec]		Carver et al. 2003
Didemnum vexillum [Ascidian] - eradication	Failure [combination of Physical & Chemical: smothering soft-sediment habitats with uncontaminated dredge spoil, wrapping wharf piles with plastic, smothering rip–rap habitats using a geotextile fabric, and various other approaches based on water blasting, air drying or chlorine dosing.	Ineffectiveness of some of the applied methods that allowed the species to reproduce and spread further; substantial delays in initiating the eradication program - one of the first major set-backs from an eradication perspective was the (erroneous) classification of *D. vexillum* as an indigenous organism, which initially postponed any action; slow decision-making and lack of long-term commitment at regional level; the roles of both central and local government in marine biosecurity were unclear with no clear lines of authority.	Coutts and Forrest 2007
Styela clava, Botryllus schlosseri, Botrylloides violaceus, Didemnum vexillum - [Ascidian] - control (experimental)	Partially Successful [Biological: using native predators as control agents]		Epelbaum et al. 2009
Didemnum vexillum - [Ascidian] - control (experimental)	Successful experimentally [Physical & Chemical: dilute acetic acid, dilute bleach, freshwater, brine and hypoxia		McCann et al. 2013
Didemnum vexillum - [Ascidian] - control (experimental)	Successful experimentally [Chemical: spraying with 5% acetic acid]		Piola et al. 2009
Didemnum vexillum - [Ascidian] - eradication	Failure [Physical & Chemical: encapsulation in reinforced PVC restricting water flow, food and oxygen; occasional application of a chemical accelerant]	Substantial delays after initial detection; slow decision-making process; inadequate knowledge of the biology of the species; lack of funding causing delays in follow-up attempts.	Sambrook et al. 2014

Pterois volitans/miles - [Fish] - control	Conditionally successful [Physical: removal programs of lionfish involving recreational or commercial divers, and fishers.		Barbour et al. 2011
Pterois volitans/miles - [Fish] - control	Successful [Physical: removal by divers using hand-nets]	Combination of good knowledge of the biology of the species, modelling, and large-scale manipulative field experiment.	Green et al. 2014
Pterois volitans/miles - [Fish] - control	Successful [Physical: engagement of volunteers in annual derbies - collection using hand nets and/or pole spears]	Adequately promoting derbies to attract large numbers of volunteers; training volunteers to the use of appropriate tools and means to safely remove lionfish.	Green et al. 2017
Pterois volitans/miles - [Fish] - control	Successful [Physical: lionfish traps (Gittings traps)]	This method covers deep habitats that are inaccessible to spearfishing by divers, i.e., it was designed to complement an already tested method. Controlling lionfish may be combined with the development of a targeted commercial fishery and thus bring benefits to fishers and support the fish supply chain, hence having multiple socio-ecological benefits.	Harris et al. 2020
Pterois miles - [Fish] - control	Successful [Physical: removals by volunteers by SCUBA diving using a removal toolkit (pole spears, containers, and puncture-resistant gloves)	Adequately training volunteers to the use of appropriate tools and means to safely remove lionfish; involvement of national authorities to issue permissions for fishing using SCUBA (which is otherwise prohibited) and approval of the removal method.	Kleitou et al. 2021
Pterois volitans/miles - [Fish] - control	Unknown [Physical: culling through public participation – organizing derbies]		Malpica-Cruz et al. 2016
Pterois volitans/miles - [Fish] - control	Unknown [Physical: harvesting by divers]		Morris & Whitefield 2009

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Table S3. *Control of Lagocephalus sceleratus in Cyprus*

IAS scientific name	*Lagocephalus sceleratus*
Common name	Silver-cheeked toad-fish
Main impact(s) of the IAS (environmental, economic etc.)	Within two decades from its introduction in 2003, *L. sceleratus* formed abundant populations in the eastern Mediterranean. It is a high predator that feeds on invertebrates and fish, including many commercial species (Kalogirou, 2013; Giakoumi et al., 2019; Hussain et al., 2020). The invasion of *L. sceleratus* constitutes a major threat to Mediterranean fisheries with significant economic losses (Coro *et al.* 2018). Furthermore, *L. sceleratus* contains the paralytic neurotoxin tetrodotoxin (TTX) in its skin, tissues and internal organs, which can be lethal for humans or cause various severe symptoms (Tsirintanis et al., 2022 and references therein). Hence, its marketing and consumption are banned in the EU (Regulation 854/2004/EC), and most Mediterranean countries and the species has no commercial value and thus is not targeted by fisheries. There have also been incidents of *L. sceleratus* attacks on swimmers with seriously inflicted wounds and amputations caused by their sharp bite (Sümen and Bilecenoğlu, 2019). In Cyprus, *L. sceleratus* has a significant negative impact on fisheries, damaging fishing gear and catch, incurring substantial economic losses, and forcing fishers to adjust their fishing practices (gear, depths, time of the day) to avoid the species (Katsanevakis et al., 2009; Tsirintanis et al., 2022).
Location of management (also provide area in km^2 if known)	The territorial waters of Cyprus (nationwide)
Objective of management (e.g., rapid eradication, containment, population control)	Population control
Time frame of management measure(s) (if ongoing when did it start, planned end date)	The Management Plan was submitted in 2011 and entered into force in 2012. It is ongoing, and it not expected to end in the near future.
Implementing body (e.g., Ministries, regional government, MPA managers)	The measure has been implemented by the Department of Fisheries and Marine Research, Ministry of Agriculture of the Republic of Cyprus, in the framework of the Operational Programs for Fisheries 2007-2013 and 2014-2020.
Who/which bodies were involved in defining/establishing the measure(s)? (e.g., scientific organisations, public administration, EC, private companies, stakeholders)	There was strong demand and lobbying by coastal fishers' associations for implementing the measure, as the abundance increase of *L. sceleratus* strongly impacted them. The Management Plan was prepared by the Department of Fisheries and Marine Research based on fishers' demands and public pressure on taking mitigation measures and taking into account the results of the Research Program on "*Lagocephalus sceleratus* in the coastal waters

	of Cyprus". Two private environmental consultancy companies (AP Marine and MER) participated in the Research Program.
Relevant legislation (what is the legislation applied for establishing the measure? e.g., CFP, IAS Regulation)	This is a measure contained in legislation adopted by a Member State (Cyprus). The measure is associated with the Regulation of Common Fisheries Policy (CFP), and its rationale is to mitigate the species' breeding population. It was included in the Operational Programme Thalassa 2014-2020 and precisely in measure 1.18, "Plan for combatting *Lagocephalus sceleratus* in the coastal waters of Cyprus".
Management measures used (detailed description of the management measures applied)	To mitigate its impacts, the Cypriot Department of Fisheries and Marine Research has implemented a Management Plan to control *L. sceleratus'* populations in the coastal zone of Cyprus. The Management Plan concerns the targeted, intense fishing pressure on the species' breeding population by the coastal professional fleet of Cyprus. This measure financed collective groups of fishers that own a professional fishing license and are members of one of the local fishers' associations, recognised by the Pancypriot Association of Professional Coastal Fishermen. The collective groups that applied to this measure and were selected were compensated based on the total mass of *L. sceleratus* individuals landed (and destroyed) for a fixed price of 3 €/kg. In the Operational Program for Fisheries 2007-2013, four calls were issued for proposals by fishers' groups, and there was a 50% national – 50% EU co-funding. In the Operational Program for Fisheries 2014-2020, two calls were issued (specifically under measure 1.18, "Plan for combatting *Lagocephalus sceleratus* in the coastal waters of Cyprus"; the second call until the end of 2023), and funding was 25% national – 75% EU. Fishers must deliver the caught fish to the coordinator of their group, who massively delivers fish for incineration to a private company, in the presence of a Department of Fisheries and Marine Research representative who verifies the delivered quantities. The group coordinator is later paid based on the confirmed quantities and distributes the payment to the participating fishers based on their contributions.
Science used to underpin the measure (evidence used for supporting the adoption and implementation of the measure)	A research program on "*Lagocephalus sceleratus* in the coastal waters of Cyprus" was conducted by the Department of Fisheries and Marine Research of Cyprus during 2009-2010 (Michailidis 2011). The research aimed to assess the distribution, growth, reproduction and diet of the species, the environmental and meteorological conditions that favour it, possible reasons for its successful adaptation to the new environment, and possible solutions to mitigate its impacts. According to the project's stated objective, "the results and conclusions of this study are necessary for the creation of a correct scientific background, and subsequently for the design of management plans or taking other measures". In summary, sampling of *L. sceleratus* individuals from fishers was conducted between 18/10/2009 and 27/4/2010. Laboratory examination for collecting the necessary biological data was assigned through tender procedures to private companies (AP Marine and

	MER). The coastline of Cyprus was divided into nine sub-regions, and at least 50 individuals per week and sub-region were examined. In the lab, size, gender, maturity, and stomachic contents were recorded. Environmental data were also collected (sea surface temperature and lunar phase). Furthermore, to study the species' behaviour', the scientific team members participated in commercial fishing cruises, and *L. sceleratus* individuals were kept alive in the Research Facilities of the Department of Fisheries and Marine Research. Overall, >60,000 individuals were collected, with a biomass c.a. 30 tonnes. There was high spatial variation in catches, with the highest catches in the south-eastern part of Cyprus. These areas were identified as the reproduction fields and nursery areas of the species. Reproduction in Cyprus waters occurs mainly in June. Stomachic contents included mostly cephalopods (octopus, cuttlefish, and squid) and fish, mainly of the genus *Siganus*, *Mullus*, *Scorpaena*, and *Diplodus*, and some crustaceans. A large percentage of stomachic contents included nets, indicating that the species regularly feeds by attacking fish caught in nets, causing substantial damage to the gear. In their stomachs, hooks and baits were also found, documenting that the species also attacks longlines causing damage and loss of catches. The species was fished over all main habitat types (rocky, sandy, muddy, seagrass), indicating a lack of habitat specificity. Fishing gear damage occurs mainly during daylight (indicating that the species highly depends on visual cues for predation) and can be limited if fishers leave their gear overnight and collect it very early in the morning. In the framework of the Research Program, some possible solutions to mitigate *L. sceleratus'* impacts were investigated. One possible solution that was investigated was exporting the species to Far East countries (Japan, China, Korea), where it could have a commercial value. In these countries, many chefs are trained to extract parts of the flesh of puffer fish that are non-toxic and serve them as a highly-valued dish (called fugu in Japan). Nevertheless, the specific species of pufferfish is not used for fugu, there was no demand for it, and several legislative restrictions prevent the possible export of the species. Population control of *L. sceleratus* through targeted fishing was proposed as a possible solution, in particular in sites of high abundance during the reproduction period of the species, such as the southeastern coast of Cyprus (Deryneia - Cavo Greco – Cavo Pyla – Cavo Kiti), especially during May and June. Adapting small-scale fishing activities (e.g. avoiding certain areas of high concentrations; collecting the fishing gear early in the morning) is also a way to mitigate the negative impacts of *L. sceleratus* on coastal fisheries.
Effectiveness of management (how effective was the measure at meeting the	There was no scientific evidence of the measure's effectiveness before its adoption and implementation, as there was no precedent in applying such a measure for the species in the Mediterranean or elsewhere. It is a management measure of low total economic cost but high economic and social benefits for coastal fishers. Its

objective, provide results of management actions)	socioeconomic benefits contributed most to its adoption rather than any scientific evidence for its effectiveness. As claimed by Antonios Petrou, scientific advisor of the Pancypriot Association of Professional Coastal Fishers, coastal fishers have noted the effectiveness of this measure in reducing the population of *L. sceleratus* and mitigating its impacts on coastal fisheries. Damages in fishing gear have been reduced in the last years, and fishers may now use their gear even during daylight with low chances of severe damage by *L. sceleratus*. According to Mr Petrou, this empirical knowledge of fishers who have observed that in specific locations, the catch of *L. sceleratus* per unit of effort has been substantially reduced is good evidence for the measure's success, which needs to be continued. However, it has to be noted that unstandardized catches may be misleading, and fishers' opinions may be subjective due to the essential economic benefits they receive through this measure. An existing Ecopath model of the insular shelf of Cyprus was recently created by Michailidis et al. (2019). This model was recently updated with recreational fisheries data (Michailidis et al., 2020), which formed the basis for using Ecopath with Ecosim to describe the structure and functioning of the shelf ecosystem of the island of Cyprus (eastern Mediterranean) and simulate a series of scenarios related to fisheries and ecosystem management strategies (Michailidis et al., under review). In the latter study, a total of 32 scenarios were tested related to either change in the fishing effort by the fishing fleet or changes in fishing mortality of selected predatory and invasive groups, along with the business as usual scenario. Among the scenarios included in the analysis were scenarios of increased or reduced fishing mortality of pufferfish and lionfish to assess the effect that such removals could have on their abundances. Invasive lionfish and pufferfishes were significantly affected by targeted increased fishing mortalities but seemed to be able to return to initial biomasses in only a few years when mortalities went back to normal. Specifically, simulations suggested that if targeted removals stopped for any reason and fishing levels went back to normal, these species would be able to rebound pretty quickly, in about the same time it took to remove them, slightly faster for the pufferfishes than the lionfish. In zero fishing mortality scenario simulations, the pufferfishes and the lionfish biomasses increased by around 50% before reaching equilibrium. These modelling results indicate that *L. sceleratus* populations could have been at a higher level without any measures and the specific management measure needs to be continuous to avoid the population's rebound at high levels.
Stakeholder engagement (who was involved in the management, which stakeholder groups were communicated with etc.)	There was substantial stakeholder involvement as the Research Program and the resulting Management Plan were primarily initiated by the strong demand of fishers. The Management Plan was based

	on regional-scale information retrieved through the related Research Program and the scientific opinion of regional experts. There was a co-management scheme with fishers. Groups of fishers had to agree to form a partnership and submit a proposal in the related call for implementing the Management Measure. Each such partnership has a head who takes over the collection of all caught fish and, when adequate quantities have been accumulated, delivers them for incineration in the presence of a Department of Fisheries and Marine Research representative who validates the amounts. Subsequently, the Ministry pays the head of the partnership, who distributes the reimbursement to participating fishers and manages all related expenses (cost for incineration, transportation, etc.) as agreed in the partnership.
Public acceptance (Did the project receive positive support from the public)	The measure was bottom-up driven with strong public acceptance. There was a political decision to implement the specific management measure, following strong pressure from fishers' associations and the public.
Challenges faced (what were the key challenges in meeting the management objective and how they were overcome if relevant, incl. biology of species)	The main issue with *L. sceleratus* is that it has no commercial value due to its toxicity and thus has not been targeted by fisheries. This measure gave value to the species, increased its fishing mortality, and controlled its population. There is ongoing research in Greece and Turkey on finding potential uses for the species, which, if achieved, may render the specific Management Measure unnecessary as it is implemented now. A challenge faced in implementing the specific measure is the often long delay in the payments of the fishers after the delivery of their catches for bureaucratic reasons. This may discourage them from fully engaging in *L. sceleratus* targeted fishing and reduce their total effort.
Information on resources needed (e.g., equipment and personnel)	Commercial fishers implement the measure; no equipment is needed other than their fishing gear. From the Department of Fisheries and Marine Research, limited personnel time is devoted to verifying the delivered quantities for incineration and arranging the fishers' payments.
Costs of the management action, who was the donor?	Between 2012 and 2021 (10 years), 1,035,150 € were spent for 345,050 kg of *L. sceleratus*. The measure was funded by the Operational Programs for Fisheries 2007-2013 and 2014-2020.
Side effects of management measures (both positive and negative, e.g. impacts to non-target species, or economic activities)	There were no negative side effects of the management measure. The targeted *L. sceleratus* fishery using hand lines is very selective with almost no bycatch. Due to the spread and substantial increase in abundance of *L. sceleratus* in the coastal waters of Cyprus after 2006, fishers suffered significant impacts and severe economic losses. There were formal requests by the Pancypriot Association of Professional Coastal Fishermen to the Department of Fisheries and Marine Research for such a measure to protect their profession. Hence, socio-economic considerations, i.e. supporting the coastal fisheries of Cyprus that

	were severely impacted by the introduction of *L. sceleratus*, were the main driver for the approval and implementation of this measure, which in any case also has a substantial ecological effect. Fishers and the public support the continuation of this measure, as they see important socio-economic benefits. Coastal fishers are the main group benefiting from the measure; there is no evident group that loses from its implementation.
Restoration efforts (were any measures undertaken during or after the study, and if so were they effective?)	Not relevant.
Acknowledgements	This case study is adapted from work and interviews conducted in the framework of the 'Study on ecosystem-based approaches applied to fisheries management under the Common Fisheries Policy for Mediterranean and the Black Seas', EASME/2020/OP/0012. Interviews were conducted with Dr Nikolas Michailidis (Fisheries and Marine Research Officer, Department of Fisheries and Marine Research of Cyprus) and Mr Antonis Petrou (scientific advisor of the Pancypriot Association of Professional Coastal Fishers).
Link to online website/resources	https://circabc.europa.eu/sd/a/78ca567f-de91-4ec1-83c9-f69e26218bc3/Lagocephalus%20sceleratus%20RA.doc
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Table S4. Relevant papers on management options for marine IAS of EU interest

Species	Management option (implemented/proposed)	Reference
Pterois miles/volitans	Lionfish culling through public participation (implemented)	Malpica-Cruz et al., 2016
	Lionfish harvest by divers (proposed)	Morris and Whitefield, 2009
	Mobilizing volunteers to participate in lionfish culling through derbies (implemented)	Green et al., 2017
	Training volunteers and organizing lionfish removal events by SCUBA diving using a removal toolkit (pole spears, containers, and puncture-resistant gloves) (implemented)	Kleitou et al., 2021
	Physical removal programs of lionfish involving recreational or commercial divers, and fishers (implemented)	Barbour et al., 2011
	Lionfish physically removed by divers from selected reefs	Green et al., 2014
	Using ‘Gittings’ traps for controlling lionfish populations in deep waters and promoting a commercial lionfish fishery	Harris et al., 2020
	Encouraging local removals (culling by citizens or during organized tournaments), development of a lionfish fishery, protecting species that control lionfish abundance (proposed)	Côté and Smith, 2018
	Targeted removals (harvesting by fishers or culling by volunteers) (implemented)	Frazer et al., 2012
	Culling is proposed as the best method available to control lionfish populations (proposed)	Côté et al., 2014
	Lionfish control using fishing mortality (exploitation for human consumption) and targeted removal (proposed based on modelling)	Morris et al., 2011
	Targeted removals by spearfishing (implemented)	Harms-Tuohy et al., 2018
	Trapping holds great promise as a low-cost method to allow lionfish removal from depths below diver limits; new computer-vision technology and underwater robotics are being tested to aid in lionfish removal and may play a major role in lionfish population management on mesophotic environments in the future (proposed)	Andradi-Brown, 2019

	Using UW robotics to stun lionfish with an electric shock and retrieve them for human consumption; applicability at greater depths than divers (implemented experimentally) https://www.robotsise.org/	Sutherland et al., 2017
	Using an autonomous UW robot that uses a computer vision system to distinguish lionfish and a revolving carousal holding eight detachable spear tips (implemented experimentally) https://www.therobotreport.com/underwater-robot-autonomously-hunts-lionfish/	na
	Developing a lionfish market for local consumption (proposed)	Yandle et al., 2022
	Optimized culling of lionfish by considering seascape structure and movement behaviour through metapopulation modelling (proposed)	Tamburello et al., 2019
	Involving citizens in organized culling/removal, tournaments/derbies, and promoting the consumption of the lionfish (review of the role of citizen science; implemented)	Clements et al., 2021
	Conducting routine removals; encouraging the development of recreational and commercial lionfish fisheries; engaging local communities and resource users (e.g., with lionfish removal tournaments). Adaptation of current conservation policies might be needed to enable lionfish removals in areas where spearfishing with scuba was otherwise prohibited for conservation purposes. (proposed)	Ulman et al., 2022
	Rebuilding native top predator populations (nevertheless, even if such conservation plans are successful, this is a long-term strategy) (proposed)	Ulman et al., 2021
Plotosus lineatus	Physical removal to control populations with intensive targeted fishery, especially during the spawning period (similar to the program implemented in Cyprus for Lagocephalus sceleratus, see Table S3). (proposed)	Galanidi et al., 2017
	Promoting human consumption to support its exploitation by small-scale fisheries (proposed)	Galanidi et al., 2017
Lagocephalus sceleratus	Targeted, intense fishing pressure on the species' breeding population by the coastal professional fleet, promoted by a bounty (3 €/kg) (implemented)	Michailidis et al., 2023
	Sustainable management of *Coryphaena hippurus*, a predator of juvenile *Lagocephalus sceleratus* (proposed)	Kleitou et al., 2018

	Rebuilding native top predator populations (nevertheless, even if such conservation plans are successful, this is a long-term strategy) (proposed)	Ulman et al., 2021
	Mass trapping using pheromones to collect mature reproductive individuals (proposed)	Galanidi and Zenetos, 2018
	Harvesting for commercial purposes, other than human consumption (for pharmaceutical purposes or detoxification of its flesh to be used for human consumption)	Galanidi and Zenetos, 2018
	Direct removal with intensive targeted fishery using fyke nets, handline, longline (baited and without bait), and purse seine (when schooling) (proposed)	Hakan Kaykaç et al., 2017
	Harvesting for exploiting its flesh to produce fishmeal utilized in Mediterranean aquaculture, after deactivating tetradotoxin (ongoing research, see: https://lagomeal.gr/)	na
Rugulopteryx okamurae	Manual removal utilizing trained volunteers (but with unknown and uncertain results) (proposed)	Tsirika, 2020
Boccardia proboscidea	Chemical treatment for eradicating localized, early detected populations; as the species is favoured by increased organic matter, achieving good environmental status and solving eutrophication issues may contribute in avoiding outbreaks of the species (proposed)	Galanidi and Zenetos, 2019
	Infestations can be avoided by growing oysters above extreme low water neap and 0.5 m above the mud substratum (based on a study of infestations by four spionid species, including the congeneric *Boccardia acus* and *Boccardia chilensis*) (proposed)	Handley and Bergquist, 1997
	The best treatment for mud worms (including the congeneric *Boccardia knoxi*) in abalone grow out facilities was found to be simple air-drying of stock (implemented)	Handlinger et al., 2004 & Lleonart et al., 2003
	Using the diatom-derived aldehyde 2,4-Decadienal as a chemotherapeutic agent against larvae of *B. proboscidea* and other shell-infesting polychaetes in the abalone culture industry (experimentally tested)	Simon et al., 2010
	Freshwater treatment was effective to control *Boccardia acus* in farmed *Tiostrea chilensis* in New Zealand (implemented)	Dunphy et al., 2005
	Drying and using a freshwater dip plus drying for two days were both highly effective (>95%) at killing mud worms without negatively impacting Pacific oyster survival (experimentally tested)	Martinelli et al., 2022

	(Review of management options for controlling shell-boring polychaetes in shellfish aquaculture): management approaches to keep oysters free of mud; air exposures; long tidal exposures; frequent cleaning; freshwater treatments; salt brine soaks; extended cool air storage; heat treatments; SSSP (Super Salty Slush Puppy) treatment initially developed by Cox *et al.* (2012); treatment with calcium hydroxide; treatment with mebendazone; various combinations (implemented; effectiveness varies with species)	Spencer et al., 2021
Perna viridis	Physical removal of the congeneric *Perna perna* from a deep (c. 44 m) soft-sediment habitat through dredging (implemented; successful eradication)	Hopkins et al., 2011
	Aerial exposure at low or high temperatures; acute change of salinity to 15 or below (experimentally tested)	McFarland et al., 2015
	Continuous or intermittent chlorination of cooling pipes to control fouling by *Perna viridis* or heat treatment (implemented)	Rajagopal et al., 1996, 2006
	Physical removal by hand (implemented)	Sewell et al., 2018
Rapana venosa	Collaboration with bivalve producers and local fishers for early detection (implemented)	Galanidi, 2019a
	Banning shellfish introductions from areas where *R. venosa* is present to prevent new introductions (proposed)	Fey et al., 2010; Galanidi 2019ª
	Physical removal by divers and fishers (potentially including volunteers) for eradication or control; strategic development of baited traps (proposed but assessed as probably ineffective)	Galanidi, 2019a
	Commercial fishery (implemented in the Black Sea)	Janssen et al., 2014; STECF, 2015; Demirel et al., 2021
	Offering a bounty for collected whelks and encouraging local restaurants to develop recipes for the species (implemented)	Mann and Harding, 2003 [cited in Fey et al., 2010]
	Promotion of local consumption (proposed)	Galanidi, 2019a

	Opening of a fishery directed to exploit *R. venosa* (proposed, Uruguay)	Carranza et al., 2010
Hemigrapsus sanguineous	Ban of oyster transfers from areas invaded by *H. sanguineus* may prevent further secondary introductions in new areas (proposed)	Galanidi, 2019b
	Combination of physical removal techniques to control *H. sanguineus* populations (manual removal on shore and by SCUBA divers, artificial habitat collectors, and baited traps) (proposed)	Galanidi, 2019b
	Biological control using the castrating rhizocephalan barnacle species *Polyascus* (=*Sacculina*) *polygenea*, *Sacculina nigra*, *Sacculina senta*, and *Sacculina yatsui* (alien in Europe) (proposed)	Galanidi, 2019b
	Using crab condos for the early detection of the species in areas of high risk of introduction (implemented)	Hewitt and McDonald, 2013
	Enhancing populations of native predatory fishes that prey upon *H. sanguineus* through proper management to control the species (proposed)	Heinonen and Auster, 2012
Schizoporella japonica	If detected early in a new location, eradication techniques using chemicals such as bleach may be applied; also general removal methods of fouling populations from vessels (e.g., dry-docking or using new technology in-water removal) (proposed)	Sewell, 2019

References of Supplementary Text 1 and Table S4

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***Table S5**: Definitions of type of evidence categories considered sensu Katsanevakis et al. (2014).*

Type of evidence	Definition
Manipulative Experiment	Field or laboratory experiments with treatment and control units that are accompanied with randomized selection of the experimental units
Natural experiment	Experimental units are selected by nature and non-randomly
Direct observation	Observations or direct measurements of the impact where there is no doubt
Modelling	Studies that draw conclusions on impacts based on ecosystem models
Non-experimental based correlations	Conclusions on impacts are made solely based on correlations between contemporary observations of the species' status and the impact
Expert judgment	Conclusions about the impact are based solely on experts' opinion

***Table S6**: Magnitude of impacts categories sensu Blackburn et al., 2014.*

Magnitude of impact category	Definition
Minimal	A species is classified as having 'Minimal impacts' when it exerts a negligible effect on the native biodiversity.
Minor	A species is classified as having 'Minor impacts' when it leads to the reduction of the fitness of individuals, without causing declines in population densities, and when it does not exhibit any impact that would warrant classification in a higher impact category.
Moderate	A species is classified as having 'Moderate impacts' when it leads to declines in the population densities of native species, without altering the structure of the community or the biotic and abiotic composition of ecosystems, and when it does not exhibit any impact that would warrant classification in a higher impact category.
Major	A species is classified as having 'Major impacts' when it results in the local or population extinction of at least one species, but the changes in the community structure and biotic or abiotic composition of ecosystems are reversible after the pressure is halted, and without qualifying for classification in the 'Massive impact' category.
Massive	A species is classified as having 'Massive impacts' when it results in the replacement and local extinction of native species, and triggers irreversible changes in the structure of communities and the abiotic or biotic composition of ecosystems

Table S7: Adverse impacts, and the jellyfish species causing them, identified in this study.

	Provisional services					Regulating and maintenance services	Cultural services	Human health	
	Food provision (Fisheries and Aquaculture)				Water storage and provision	Ocean nourishment	Recreation and tourism		
Species	Obstruction of fishing	Reduction of stocks	Problems to aquaculture	Potential vectors of pathogens	Shutdowns of nuclear power plants, desalination plants and pumping systems	Alterations in nutrient cycling and biogeochemical processes	Jellyfish outbreaks, mass strandings and beach closures	Stings	Potential vectors of pathogens
Ctenophora									
Mnemiopsis leidyi	✓	✓		✓					
Pleurobrachia pileus		✓							
Bolinopsis infundibulum			✓						
Scyphozoa									
Aurelia aurita	✓	✓	✓	✓	✓		✓	✓	
Aurelia labiata	✓								
Aurelia coerulea									✓
Pelagia noctiluca	✓	✓	✓	✓			✓	✓	
Rhizostoma pulmo	✓			✓				✓	✓
Rhopilema nomadica						✓	✓	✓	
Rhopilema esculentum	✓		✓		✓			✓	
Rhopilema hispidum	✓		✓		✓		✓	✓	
Chrysaora hysoscella	✓						✓	✓	
Chrysaora lactea	✓							✓	
Chrysaora plocamia	✓	✓	✓		✓		✓	✓	
Chrysaora fuscescens	✓	✓							
Chrysaora melanaster					✓			✓	
Chrysaora chinensis	✓		✓				✓	✓	
Cotylorhiza tuberculata	✓								
Periphylla periphylla	✓					✓			
Lychnorhiza malayensis	✓		✓		✓		✓		
Lychnorhiza lucerna	✓								
Phyllorhiza punctata	✓	✓					✓		
Acromitus flagellatus	✓	✓	✓				✓		

Acromitus hardenbergi	√		√						
Nemopilema nomurai		√						√	
Crambionella orsini					√				
					√				
Lobonemoides robustus		√					√		
Phacellophora camtschatica	√								
Cyanea spp.	√		√	√	√		√	√	
Catostylus mosaicus						√		√	
Cassiopea andromeda							√		
Linuche unguiculata								√	
Stomolophus meleagris								√	
Hydrozoa									
Velella velella	√		√				√		
Blackfordia virginica		√							
Olindias muelleri							√	√	
Olindias sambaquiensis	√							√	
Olindias formosus								√	
Muggiaea atlantica			√						
Muggiaea kochii			√						
Dipleurosoma typicum			√						
Solmaris corona			√						
Phialella quadrata			√	√					
Aequorea sp.	√								
Apolemia uvaria			√						
Physalia physalis			√				√	√	
Neoturris pileata				√					
Moerisia sp.						√			
Gonionemus oshoro								√	
Geryonia proboscidalis								√	
Agalma okeni								√	
Corymorpha bigelowi								√	
Porpita porpita								√	
Cubozoa									
Chiropsalmus quadrumanus	√							√	
Tamoya haplonema	√							√	

Tamoya ohboya								√	
Carybdea marsupialis							√	√	
Chironex fleckeri								√	
Keesingia gigas								√	
Carukia barnesi								√	
Carukia shinju								√	
Chiropsoides buitendijki					√			√	
Malo maxima								√	
Malo kingi								√	
Alatina alata								√	
Alatina rainensis								√	
Gerongia rifkinae								√	
Morbakka fenneri								√	
Tunicata									
Salpa maxima	√						√		
Ihlea magalhanica			√						
Dolioletta gegenbauri						√	√		

Table S8: Examples of reported impacts by Harmful Algal Blooms (HABs). Marine ecosystem services are based on the typology by Liquete et al. (2013)

Impact	Mechanisms of harm	References
Human health	Seafood consumption is the primary vector of HAB-related human intoxications and deaths. Marine biotoxins may be accumulated in farmed and/or wild seafood (shellfish, crustaceans and fish). In Europe, five different chemical groups are regulated for now: Paralytic Shellfish Poisoning (PSP) toxins, domoic acid (Amnesic Shellfish Poisoning, ASP), okadaic acid group toxins (Diarrheic Shellfish Poisoning, DSP), yessotoxins and azaspiracids. Other marine toxins (e.g., ciguatoxin, brevetoxins and cyclic imines) can be monitored on the basis of national control programmes.	Regulation (EC) No 853/2004; Regulation (EU) 2019/627; Regulation (EU) 2021/1709; James et al. (2010); Visciano et al. (2016); Lamas et al. (2019); Zingone et al. (2021); Otero and Silva (2022); FAO, IOC and IAEA (2023).
	Inhalation or contact with aerosolized or water dissolved toxins (e.g., toxins produced by *Ostreopsis* spp., *Karenia brevis* and cyanobacteria) may also provoke health issues like eye and ear irritation, skin reactions, liver damage, and respiratory, gastrointestinal, and neurologic symptoms. These conditions often lead to a temporary closure of the bathing waters.	Grattan et al. (2016;) Parsons et al. (2018); Brand (2018); Zingone et al. (2021); Berdalet et al., (2022); Manganelli et al. (2012); Backer et al. (2015); Figgatt et al. (2017); Hu et al. (2020).
Impacts on marine populations	Toxins produced by HABs can cause mass mortalities events of wild and farmed marine species.	Landsberg et al. (2009); Hsia et al. (2006); Katsanevakis et al. (2014); Mardones (2020); Yan et al. (2022).
	Bioaccumulation of toxins in certain species through the food web may affect their physiological condition, fecundity, recruitment success, growth, behaviour, and survival.	Landsberg (2002); Estrada et al. (2010); de Boer et al. (2012); Smayda (2019).
	Mechanical alterations such as the increase in water viscosity or production of mucilage/foam can affect swimming ability of pelagic species, and/or reduce water column oxygenation causing mass mortalities to many benthic species such as gorgonians, corals, and sponges.	Balkis-Ozdelice et al. (2021); Raine et al. (2001); Edvardsen et al. (2007); Samdal and Edvardsen (2020); Zingone et al. (2021); Topçu and Öztürk (2021); Özalp (2021).
	The siliceous cell walls and spines of some diatoms can harm and kill fish.	Bell (1961).
	During the decay stage of high biomass HABs, decreased dissolved oxygen concentration and increased levels of NH4-N or sulphides, may cause mass mortalities of local marine populations.	Yan et al. (2022); Pitcher and Jacinto (2019).
Ecosystem processes / functioning	Reduction of nutrients and carbon transfer in food-webs. This affects inter-specific competition. In addition, the remineralisation process can substantially vary depending on the local conditions	Landsberg et al. (2009); Katsanevakis et al. (2014); Burkholder et al. (2018); Smayda (2019).
	Change of the physical and chemical properties of seawater, e.g., reduced light penetration can affect benthic macrophytes.	Katsanevakis et al. (2014).
	Alteration of foraging behaviour favouring predators' preferences for toxin free preys, leading to modifications in ecosystem structure and function (e.g., dramatic	Kvitek and Bretz (2004, 2005); Burkholder et al. (2018;) Briland et al. (2020).

	changes in zooplankton abundance and community structure can disrupt pelagic food webs).	
	Mucilage formation (i.e., secretion of vast quantities of extracellular organic substances) caused by HABs under certain environmental conditions, may affect other organisms (light and oxygen availability, viscosity changes, etc.).	Brush et al. (2020); Totti et al. (2005); Savun-Hekimoğlu and Gazioğlu (2021); Karadurmuş and Sari (2022).
	Life cycle maintenance: HABs may adversely affect populations when occurring in key habitats like spawning and nurseries areas, or migratory routes.	Hansen et al. (2004); de Boer et al. (2012).
Food provision and food safety	Reduction of growth rates in farmed fish	Boalch and Harbour (1977); Boalch (1984); Nehring (1998); Raine et al. (2001); Davidson et al. (2009); Ribeiro et al. (2012); Samdal and Edvardsen (2020); Zingone et al. (2021); Eilertsen and Raa (1995).
	Pathologies in juveniles and adults of wild fish species	Esenkulova et al. (2022).
	Sub-lethal and lethal toxicity for farmed fish and shellfish larvae with potential implications to recruitment	Aanesen et al. (1998); May et al. (2010); de Boer et al. (2012); Rolton et al. (2015); Castrec et al. (2020); Bruslé (1995).
	Closures in fish and shellfish trade and aquaculture facilities due to the presence of toxins in harvested seafood.	Ribeiro et al. (2012); Sanseverino et al. (2016); Zingone et al. (2021); Yan et al. (2022).
	Clogging of fishing gears by mucilage produced by HABs disrupting fishing activities	Boalch and Harbour (1977).
Water provision	Smell of decomposing biomass caused by mass mortalities provoked by HABs.	Schoemann et al. (2005); Katsanevakis et al. (2014).
	Closure of desalinisation plants due to clogging of pump filters or water contamination.	Anderson et al. (2017).
Air quality	Some species can produce substances whose transformation and release into the air might impact the chemical quality of the atmosphere (e.g., dimethylsulphoniopropionate, enzymatically converted into dimethylsulphide (DMS) and oxidized)	Fletcher (1989); Davison and Hewitt (1992); Schoemann et al. (2005).
Recreation and tourism	Reduction of the attractiveness of coastal areas due to discolouration of water, the production of foam, mucilage formation, the accumulation of dead fish and invertebrates and the smell of decomposing matter	Sanseverino et al. (2016); Kalkavan (2021).
Maritime operations	Clogging of sea chest filters and causing overheating and damages to the main engine, generators, compressors, or the cooling systems, damaging ballast pumps and ballast water treatment systems, blocking emergency fie pumps, and increasing operational costs	Uflaz et al. (2021).

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Table S9: Examples of Harmful Algal Blooms (HABs) and involved species reported in different areas in Europe along with their likely anthropogenic or natural causes. This table in 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 (environMental mAtrix for the Management of BlOoms) matrix. Q: Quadrant number in the MAMBO matrix.

Q	Geographical region	Harmful algal species event [occurrence]	Likely reported causes (anthropogenic/natural)	References
1	Mediterranean Sea offshore	*Chaetoceros* spp.	High biomass diatom and *Chaetoceros spp*. blooms commonly associated to *the* well-developed deep chlorophyll maximum in the nutricline. Persists during a large part of the year.	Estrada et al. (1993); Siokou-Frangou et al. (2010).
1	Eastern Adriatic Sea	*Dinophysis* spp., *Alexandrium* spp., *Pseudo-nitzschia* spp.	Regular DSP toxic events along the Croatian coasts, sporadic elevated concentrations of PSP and ASP toxins. The occurrence of toxic species is associated with hydrological and physical factors, such as precipitations, temperature, freshwater inflow. Also the nonlinear connection with positive phase of NAO index was found. Offshore (low biomass) blooms of toxic species possibly caused by the transport with less saline waters from the Italian coasts.	Ninčević Gladan et al. (2008, 2020): Arapov et al. (2020); Ujević et al. (2010, 2012).
2,3	Galician Rias	*Gymnodinium catenatum*	Biogeographical expansion, towards higher latitudes due to increasing sea surface temperatures combined with important cyst assemblages near upwelling influenced areas.	Pitcher and Fraga (2015).
2	Canary Islands	*Trichodesmium erythraeum* (cyanobacteria)	In August 2004 an extensive bloom was observed in the Gran Canaria and Tenerife during the warmest summer since 1912, following a storm with Sahara dust deposition providing Fe known to boost the growth of diazotrophic cyanobacteria.	Ramos et al. (2005).
2	Azores-Santo Cristo Lagoon	*Alexandrium minutum*	First bloom in the Azores producing high PSP exceedances, water discolouration, death of small pelagic fish, toxification of shellfish resources, and human poisonings after consumption of shellfish. Attributed to the species geographic expansion, installation of cysts and blooming conditions such as haline stratification.	Costa et al. (2017) and refs therein.
2,3	Western English Channel	*Karenia mikimotoi*	Blooms attributed to persistent summertime rainfall and input of low-salinity, high-nutrient river water.	Barnes et al. (2015).
2,3	Western English Channel	*Dinophysis* spp., *Dinophysis acuta*, *Karenia mikimotoi*, *Noctiluca scintillans*, *Protoceratium reticulatum*, *Prorocentrum cordatum*, *Pseudo-nitzschia* spp.	Observed variations in the extent and duration of HAB events were linked to the differences either side of the “start point” frontal system in water circulation patterns and plankton assemblages, including zooplankton grazers.	Brown et al. (2022).
2,3	Western English Channel	*Karenia mikimotoi*, *Noctiluca scintillans*,	Record exceeded levels during an exceptional marine warming period of 2018 with highest NAO index.	Brown et al. (2022).

		Protoceratium reticulatum, *Prorocentrum cordatum*		
2,3	English Channel	*Pseudo-nitzschia* spp.	Six different *Pseudo-nitzschia* species (toxic and non-toxic), generally elevated in spring and autumn, this may vary in coastal versus open water locations with species showing different physico-chemical triggers.	Klein et al. (2010); Downes-Tettmar et al. (2013); Stern et al. (2023).
2,3	Northern Bay of Biscay (Penzé Bay)	*Alexandrium minutum*	The maximum abundance occurs 5 days after temperature, river flow and tide values were optimal, and irradiance was high or very high. Bloom decline was accompanied by decreased river and by increasing tides.	Guallar et al. (2017).
2-3	Eastern English Channel-Southern North Sea	*Phaeocystis globosa.*	1994-2018 regularly foam-forming blooms showed positive linear relationship with Dissolved Inorganic Nitrogen (DIN), before 2000. After 2000, decreasing trends in DIP and DIN are not clearly reflected in the trends of *P. globosa* and diatoms, which suggest that other factors, such as competition for resources are also important.	Lefebvre and Dezécache (2020).
3	Barents Sea	*Trichormus variabilis*	Mass blooms leading to fish mortality in the estuarine of the Pechora River	Vershinin and Orlova (2008) and refs therein
3	Norwegian Sea Lyngen fjord	*D. acuminata*	Peaks every year during the summer when the surface temperature is above 7.8 C, producing Diarrhetic Shellfish Toxic events.	Silva et al. (2023).
3	Norwegian Sea Lofoten & Tromsø	*Chrysochromulina leadbeateri*	1991 and 2019 Fish mortalities	Karlson et al. (2021) and refs therein.
3	Arctic Ocean	*Alexandrium catenella*	Biotoxins accumulate in the marine trophic chain. A recent study on stranded and captured mammals in Alaska detected saxitoxins in 10 out of 13 species analysed (whales, seals, porpoises, etc.), including those consumed by local populations. In some specimens, the saxitoxin reached risk levels for both the fauna and people.	Anderson (2021); Lefebvre et al. (2016).
3	Faroe Islands	*Alexandrium catenella*	PSP-producing *A. tamarense* were recorded for the first time in the Faroe Islands in 1984, and a serious fish kill took place. *A. tamarense* was found in the Limfjord area, Denmark, in 1983, 1985, 1986 and 1987, and PSP was recorded for the first time in 1987.	Moestrup and Hansen (1988).
2,3	Galician Rías	*Dinophysis acuminata, D. acuta, D. ovum, D. sacculus, D. tripos, Pseudo-nitzschia australis, Azadinium* spp., etc.	Toxic HAB events (mainly diarrhetic (DSP) and paralytic shellfish poisoning (PSP)) caused by dinoflagellate species are commonly observed during the upwelling season (spring and summer) and during the autumn transition from dominance of upwelling-favourable to downwelling-favourable winds.	Fraga et al. (1988); Reguera et al. (2012).

2	Portugal coast	*Gymnodinium catenatum*	Blooms associated with coastal upwelling plumes in Portugal, and with the upwelling relaxation in las Rias, thus independent from anthropogenic nutrients.	Moita et al., (2006, 2016); Reguera et al. (2012); Ruiz-Villareal et al. (2016).
3,4	Southern Brittany (French Atlantic coast)	*Lingulodinium polyedra*	An unprecedented bloom of *Lingulodinium polyedra* developed along the French Atlantic coast in July 2021 and lasted six weeks. The bloom caused hypoxia events, and concentrations of yessotoxins in mussels, below the safety threshold. Attributed to the unusual environmental summertime conditions, as well as the establishment of considerable seed banks.	Mertens et al. (2023).
4	SE Bay of Biscay	*Dinophysis* spp.	Transport processes have revealed important to explain the yearly OA toxic events produced by *Dinophysis spp*. in the Bay of Biscay. Other ecological factors that can play a role in the growth of these mixotrophic flagellates are the availability of prey, light or ammonium.	Batifoulier et al. (2013); Muñiz et al. (2018); Bilbao et al. (2020), Hariri et al. (2022); Hattenrath-Lehmann et al. (2021); Moita et al. (2016); Silva et al. (2023).
4	SE Bay of Biscay	*Centrodinium punctatum Alexandrium ostenfeldii, A. minutum*	The recently discovered toxicity of *C. punctatum* and its presence during the autumn and winter PSP events off the Basque coast makes it a probable causative species candidate even if *Alexandrium* spp. have been primarily proposed as responsible species, *Gymnodinium catenatum* has never been detected in these waters.	Ferrer et al. (2019); Li et al. (2019); Shin et al. (2020); Rodríguez-Cabo et al. (2021).
5	Celtic Sea	*Alexandrium minutum,* (incl. non-toxic strains), *Alexandrium catenella, Dinophysis acuminata, D. acuta, D. ovum, Pseudo-nitzschia australis, P. seriata, Karenia mikimotoi*	Within the UK there are two populations of *A. minutum* grouping with strains from Northern France and Southern Ireland. There is a degree of interconnectivity due to oceanic circulation and a high level of shipping and recreational boating. *A. minutum* typically occurs in sheltered locations, with cell growth during periods of stable water conditions. Fine sediments provide cyst deposits for ongoing inoculation to the water column.	Lewis et al. (2018).
5	Western Mediterranean Coast	*Alexandrium taylori Gymnodinium litoralis*	These proliferations are frequent in the beaches of the Costa Brava primarily influenced by nutrient inputs from local from groundwater, rivers, or temporary Mediterranean rivers. During the summer months, local winds contribute to maintaining high cell abundances at the beach.	Garcés et al. (1999); Garcés and Camp (2012); Basterretxea et al. (2005); Reñé et al. (2011).
5	Western Mediterranean Coast (Campania and	*Alexandrium* spp., *Dinophysis* spp., *Prorocentrum* spp.,	40 potentially toxic species and 5 taxa responsible for water discolorations have been observed between 1984-2004. However no harmful events have been recorded: Only in a few cases has a pre-alarm status been reached because of DSP toxins. An apparent relationship between noxious	Zingone et al. (2006); Satta et al. (2014).

	Sardinian coasts)	*Pseudo-nitzschia* spp., *Karlodinium*	species and grain size suggests that vegetative cells may be recruited from cyst beds in beach sediments in Sardinian coasts.	
5	Adriatic Sea-Gulf of Trieste	*Dinophysis* spp., *Alexandrium* spp., *Pseudo-nitzschia* spp., *Ostreopsis* cf. ovata, mucilage events	Quite regular yearly DSP events, caused by *Dinophysis* species (*D. sacculus*, *D. caudata*, *D. fortii*, *D. tripos*), mainly attributed to natural causes. Potentially toxic *Alexandrium* and *Pseudo-nitzschia* species are common members of the phytoplankton community, but no toxicity has been observed so far. High biomass blooms were characteristic for this area in the past triggered by eutrophication and often succeeded by hypoxia in the bottom layer. After the 2000', an oligotrophication trend was detected in the northern Adriatic, due to hydroclimatic changes and reduced anthropogenic phosphorus loading. In the Gulf of Trieste this resulted in the reduction of seasonal diatom blooms and the predominance of the smaller sized phytoplankton. Periods of (mostly summer) mucilage events unique to northern Adriatic triggered by complex processes in part related to phytoplankton production.	France and Mozetič (2006); Lipizer et al. (2017); Mozetič, et al., (2010, 2012); Zingone et al., (2021); Brush et al., (2020)
5,6	Northern and central North Sea	*Prymnesium, Chrysocromulina, Alexandrium catenella, Alexandrium ostenfeldi, Alexandrium pseudogonyaulax, Dinophysis acuminata, D. acuta, D. norvegica, P. australis, P. seriata, Azadinium, Karenia mikimotoi, Phaeocystis*	Explaining the detailed mechanisms behind the exceptional dinoflagellate blooms recorded in the late 1980s in the northern and central North Sea areas is difficult, but they coincided with anomalous oceanic incursion of Atlantic into the North Sea. During this period, unprecedented blooms of the oceanic indicator diatom *Thalassiothrix longissima* and substantial increase in the catch of horse mackerel (*Trachurus trachurus*) were recorded.	Edwards et al. (2006)
6	North Sea/ Skagerrak	*Chrysocromulina polypis*	Occasionally observed in the North Sea. Their first occurrence in 1988 was considered food web disruptive. it was hypothesised that it was linked to turbulence and high nutrient loading.	Maestrini and Graneli (1991)
6	Belgian coast	*Phaeocystis globosa*	The trophic efficiency of the *Phaeocystis* ecosystem could be related to N:P imbalance created by changing DIN and DIP loads to the Belgian coastal zone.	Lancelot et al. (2009)
5,6	Kattegat and Skagerak	*Pseudochattonella* spp.	The southern Norway coast, Skagerrak and into the Kattegat *Pseudochattonella* spp. has reportedly killed fish since 1998 on a regular basis. *Pseudochattonella*-blooms were not observed in the Skagerrak and the Kattegat before 1998. The blooms are now common in this area. It is possible that *Pseudochattonella* was introduced to the area, e.g., by ballast water.	Andersen et al. (2015); Karlson et al. (2021); Eckford-Soper and Daugbjerg (2016).

6	Western Baltic	*Pseudo-nitzschia* spp.	*Pseudo-nitzschia* blooms are regularly recorded in the western part of the Baltic at intermediate salinities at concentrations that close the shellfish fishery. In the west Baltic, *Pseudo-nitzschia* spp. blooms are associated with eutrophication, and the anthropogenic association was evidenced in the Little Belt by an accidental urea spill in 2016 that prompted prolonged blooms of *Pseudo-nitzschia* spp. Only one closure for ASP to date in Sweden.	Olesen et al. (2020); Hasle et al. (1996).
6	Central part of the Baltic	Surface cyanobacteria blooms, Nitrogen fixing cyanobacteria	Before the nineteen-sixties, surface blooms were rarely observed, but parallel to the increasing eutrophication the water body experienced an increased development of summer surface blooms were observed. The HELCOM regularly reports the microscopic counts of cyanobacteria from the various sub-basins of the Baltic. Also *Karlodinium* caused fish kills on west coast of Baltic and Finnish coast of Gulf of Finland. The nitrogen fixing (diazotrophic) filamentous cyanobacteria in the Baltic Sea have a competitive advantage compared to other phytoplankton when concentrations of dissolved inorganic nitrogen is low and there is phosphate available. This has resulted in an increase in cyanobacterial blooms in the Baltic Sea. It also means that N2 gas in the air is introduced into the Baltic Sea system, a form of natural eutrophication that is an effect of nutrients introduced anthropogenically. Nitrogen fixation is more metabolically costly at higher salinities and although the diazotrophic cyanobacteria from the Baltic Sea may grow in the Kattegat and the Skagerrak their competitive advantage is lost.	Finni et al. (2001); Karlson et al. (2021); Kownacka et al. (2020).
8	North Saronikos Gulf Gulf of Kalloni	*Pseudo-nitzschia* spp., *Alexandrium* spp.	21 potentially harmful microalgae (bloom-forming and/or toxic) were identified including 3 diatoms and 18 dinoflagellates. The densities of each species were analyzed in time and space and in relation to environmental parameters. Some species such as *Alexandrium insuetum*, *Heterocapsa circularisquama*, *Karlodinium veneficum*, *Scrippsiella trochoidea*, and *Ceratium* spp. developed high cell concentrations, particularly during a *Pseudo-nitzschia calliantha* winter bloom.	Spatharis et al. (2009).
8-9	Black Sea	*Pseudo-nitzschia* spp., *Prorocentrum* spp., *Noctiluca* spp.	Potential toxic species (*Dinophysis, Prorocentrum, Gonyaulax, Lingulodinium, Protoceratium, Alexandrium)* are often found in the taxonomic composition of phytoplankton from the summer-autumn season in the NW Black Sea. The presence of potentially toxic species in the water does not occur in toxic events. Blooms of *Pseudo-nitzschia* and *Prorocentrum* are common in early summer and autumn in the NW Black Sea coastal area. However, after 2000, there were particular non-diatoms phenomena developed in low salinity values and high nutrients of shallow water conditions favorable to the emergence of high-intensity phytoplankton blooms. The occurence of *Noctiluca scintillans* showed that the blooms are not limited to specific season but occur mainly during summer-autumn in the last years.	Boicenco et al. (2019); Lazăr et al. (2019): Bişinicu et al. (2021).

9	Northwestern and eastern Blck Sea	Non-toxic harmful phytoplakton blooms	The shallow brackish waters eutrophied by the drainage of the Danube, Dnieper, Dniester, and Bug rivers is a classic example of permanent non-toxic HABs accompanied by mass mortality of marine biota because of hypoxia. In addition, the shadowing of the bottom macrophytes by a layer of blooming phytoplankton may contribute to the dying of macroalgae at the places of constant blooms.	Vershinin and Orlova (2008) and refs therein.
9	Cabrera Island, NW Mediterranean Sea	*Prorocentrum* spp.	Members of this genus have been observed in areas with anthropogenic influence, such as Mediterranean coastal areas that have experienced significant changes due to human activities. These species are known to respond to fluctuations in nutrient levels, particularly nitrogen, which are often introduced as a result of groundwater discharge.	Garcés et al. (2011).
9	Mediterranean estuaries	*Pseudo-nitschia* spp.	*Pseudo-nitzschia* blooms are consistently observed throughout the year in Alfacs Bay. The occurrence and patterns of *Pseudo-nitzschia* blooms showed that these blooms are not limited to specific seasons but occur regularly throughout the year.	Andree et al. (2011).
9	Thau lagoon	*Alexandrium pacificum*	Thau Lagoon, located in the Mediterranean coastal region, has been affected by the presence of *Alexandrium pacificum*, the dynamics of this species in the lagoon seems to be associated to environmental conditions (nutrients) and the life cycle of the species (resting cysts).	Laabir et al. (2013); Collos et al. (2009).
9	Papas Lagoon-Ionian Sea	microalgal community mainly composed by dinoflagellates (eight to species and raphidophyceae	Papas lagoon seems to function as a reservoir of toxic microalgae commonly found in the Mediterranean ecoregion whose perennial coexistence, succession and proliferation is attributed to their mixotrophic abilities and complex life cycles. HABs occur under contrasting environmental conditions (e.g., summer multi-species HAB in a high salinity mixed water column and winter single-species HAB in low salinity stratified waters).	Papantoniou et al. (2020) and refs therein.
9	Mediterranean Harbour	*Alexandrium minutum*	*A. minutum* consistently produces blooms with very high abundances in most harbours on the Catalan coast (NW Mediterranean Sea). However, it is detected sporadically and in very low concentrations on the beaches of this same coast. These blooms serve as a clear example of the consequences of constructing harbours for some toxic species. The establishment of a large bed of cysts in these harbours, the input of nutrients, and the anti-cyclonic conditions also favour these proliferations within the harbours.	Estrada et al. (2010); Van Lenning et al. (2007); Sampedro (2018); Anglés et al., (2012); Garcés and Camp, (2012).
9	Celtic Sea.Cork harbour	*Alexandrium minutum, A. ostenfeldii*	These HAB species are localized in the North Channel due to its retentive nature. Their dynamics are closely linked to tidal dilution.	GEOHAB (2010).
9	Black Sea-Azov Sea	*Heterosigma akashiwo*	Ichtiotoxic blooms in desalinated eutrophic waters.	Vershinin and Orlova (2008).

References of Table S9

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Table S10: Potential relevance of different Harmful Algal Bloom (HAB) cases and the European Marine Strategy Framework Directive (MSFD) Descriptors (D) and criteria (C).

MSFD Descriptors	Relevance of HABs
D1 - Biological diversity is maintained. The quality and occurrence of habitats and the distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions.	HABs can have significant impacts on the diversity, distribution, and abundance of marine species, populations and communities in pelagic and benthic habitats. This can be caused by the alteration of the water column chemistry (e.g., oxygen depletion caused by eutrophication), but also by releasing toxic substances into water and air, by reducing light penetration or by altering viscosity (Chai et al., 2020; Varkitzi et al., 2018; Magliozzi et al., 2023). All these alterations can negatively impact pelagic habitats (D1C6) but also species groups of birds, mammals, reptiles, fish and cephalopods, thus potentially involving D1C2 (“Species abundances”), D1C3 (“populations structures”, D1C4 (“Species distribution patterns”) and D1C5 (“Habitats extent and condition”).
D2 - Non-indigenous species introduced by human activities are at levels that do not adversely alter the ecosystems.	There is a rather unanimous agreement for reporting phytoplankton NIS in D2 criteria (Tsiamis et al., 2021). However due to the large gaps in knowledge, more work is needed on marine NIS of phytoplankton in Europe to consider assessing them against a GES threshold for the time being (Tsiamis et al., 2021). When doable, D1C1 (“number of new established species since last reporting”) and D2C2 (“Abundance and spatial distribution of established non-indigenous species”) could be applied.
D3 - Populations of all commercially exploited fish and shellfish are within safe biological limits, exhibiting a population age and size distribution that is indicative of a healthy stock.	HABs may affect the recruitment, growth, and natural mortality rates (sometimes causing mass mortalities) of several commercially exploited (wild and farmed) species, due to oxygen depletion or toxicity. Although this descriptor focuses on fishing pressure on wild stocks, impacts of HABs on these stocks occurring specially in spawning and/or nursery areas/seasons might be relevant to consider via D3C2 (“Spawning stock biomass”) or D3C3 (“Age and size distributions”) for affected commercially exploited stocks and regions.
D4 - All elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity and levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity.	HABs do alter the structure and function of food webs during their outbreaks. However, there are few studies about their long-term effects on the food webs in affected ecosystems. Based upon the affection types of HABs on food webs any of the D4 criteria could be applied: D4C1 (“Diversity of the trophic guild”), D4C2 (“The balance of abundance between trophic guilds”), D4C3 (“Size distribution between individuals and the trophic guild”), and D4C4 (“Productivity of trophic guild”).
D5 - Human-induced eutrophication is minimised, especially adverse effects thereof, such as losses in biodiversity, ecosystem degradation, harmful algal blooms and oxygen deficiency in bottom waters.	MSFD includes D5C3 as a secondary criterion to assess the number, extent, and duration of HABs. D5C3 is meant to be applied only for HABs related to eutrophication pressures (European Commission, 2022). Nevertheless, this criterion would be also very useful to assess all HABs including toxic and nuisance HABs not linked to eutrophication processes. Under this descriptor, accompanying criteria for eutrophication causes are relevant as several cases of HABs caused by eutrophication have been reported (Glibert et al., 2005, 2010). In Europe, Karlson et al. (2021) showed that HABs may be indirectly favoured by eutrophication, which can cause a change in the distribution and frequency of HABs. In this context, the

	following criteria should also be assessed: D5C1 (“Input of nutrients”), D5C2 (“Chlorophyll-a), D5C4 (“Depth of photic limit”), and D5C5 (“Concentration of dissolved oxygen”). Moreover, D5C6 (“Abundance of opportunistic macroalgae”), D5C7 (“The species composition and abundance of benthic macrophytes”), and D5C8 (“The species composition and abundance of benthic macrofauna”) could be applied in certain cases.
D6 - Sea-floor integrity is at a level that ensures that the structure and functions of the ecosystems are safeguarded and benthic ecosystems, in particular, are not adversely affected.	If a linkage of HABs with sea floor alteration (via habitat change) is identified in the assessment units, the relevant D6 criteria (European Commission, 2010) may also be used.
D7 - Permanent alteration of hydrographical conditions does not adversely affect marine ecosystems.	Different human activities (e.g., land claim, barrages, sea defences, ports, wind farms, oil rigs, pipelines, heat and brine outfalls, etc.) causing permanent alterations of hydrographic conditions in an area, for example, residence time, stratification, and distribution of turbidity and heat plumes may affect the risk of HAB outbreaks. For instance, Garcés and Camp (2012) found that substantial modifications of the Mediterranean Catalan coastline created more confined waters and led to an increase of HAB events over the last 50 years. In these cases, D7C1 (“Spatial extent and distribution of permanent alteration of hydrographical conditions”) or D7C2 (“Spatial extent of each benthic habitat type adversely affected due to permanent alteration of hydrographical conditions”) might be added in the assessment.
D8 - Concentrations of contaminants are at levels not giving rise to pollution effects.	The list of chemical compounds in water, sediments, fish and shellfish matrices relevant for this descriptor, concern those issued from human activities (industry, urban water waste, agriculture, etc.). The list does not include marine biotoxins that, although “polluting” the environment, are natural substances released by microalgae.
D9 - Contaminants in fish and other seafood for human consumption do not exceed levels established by Community legislation or other relevant standards.	Although the term "contaminants" in D9 is interpreted as "hazardous substances present in fish as a result of environmental contamination for which regulatory levels have been set for human consumption or for which the presence in fish is relevant", according to Swartenbroux et al. (2010), marine biotoxins should not be includes as contaminants in D9 as considered not directly linked to human activities, and because managed under other regulatory instruments prompting controls on harvesting. Anyhow, some Member States are including marine biotoxins in the reporting of MSFD Descriptor 9 (Tornero et al., 2021), although this information is likely to be obtained from the national food control systems.
D10 -Properties and quantities of marine litter do not cause harm to the coastal and marine environment.	n/a
D11 - Introduction of energy, including underwater noise, is at levels that do not adversely affect the marine environment.	n/a

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Table S11. Indicators that have been used or potentially relevant/useful for Harmful Algal Blooms (HABs) state assessments. This is not a comprehensive list, nor a list of recommended or eligible indicators to assess HABs status but aims to give an overview of different attempted approaches.

Indicators for HABs	Metrics and thresholds	References	Notes
Presence, abundance, biomass of phytoplankton and phytobenthos species	Cell abundance of toxin-producing taxa, site-specific thresholds for particular taxa (e.g., *Alexandrium* spp., *Dinophysis* spp., and *Pseudo-nitzschia* spp.), and population trends.	Food Regulation (EU) 2019/627; ICES (2015).	
	In bathing water bodies with HAB risk, abundances of some species/groups are monitored (e.g., *cyanobacteria, Ostreopsis* cf. *ovata, Coolia monotis, Prorocentrum lima*). Thresholds are set at national level (e.g., Italy: Funari et al., 2015).	Bathing Waters Directive (2006/7/EC).	
	Chrysochromulina polylepis, *Karenia mikimotoi*, *Alexandrium* spp., *Dinophysis* spp., *Prorocentrum* spp., *Phaeocystis* spp. (colony form), *Noctiluca scintillans.*	OSPAR (2003).	Different thresholds for same taxa in different countries. In some cases, thresholds vary between assessments.
	+Karenia mikimotoi;+Pseudo-nitzschia spp.*;+Chattonnella* spp.*;+Odontella sinensis;+Verrucophora* spp.	OSPAR (2008, 2017).	
	Phaeocystis spp.	Germany_MSFD - Araújo et al. (2019); Magliozzi et al. (2023).	
	Noctiluca scintillans.	Romania, Bulgaria- MSFD; BSIMAP, 2017.	
	Phytoplankton biomass.	MSFD: Latvia - Araújo et al., (2019); Magliozzi et al., (2023). BSIMAP (2017).	
Phytoplankton multi-metric indices	Taxon list: 40% above the percentage of samples with at least one bloom defined by category and taxon size: small – 250.000 cells/L (unicellulars < 20 µm without chain); large: 100.000 cells/L (colonial species < 20 µm + sp. > 20 µm.	France-OSPAR (2008).	
	Phytoplankton index IE: sum of the occurrence of any species (> 106), plus Phaeocystis (>106), plus total cell counts (>107) and counts of chlorophyll >10 µg/l over a five-year period. Assessment level: >25%.	UK-OSPAR (2008).	
	Percentage of samples with at least one bloom defined by category and taxon size: small: 250 000 cells l^{-1} (unicellulars < 20µm without chain), large: 100 000 cells l^{-1} (colonial species < 20µm + sp. > 20µm). Elevated levels > 40% of samples above reference abundances.	France-OSPAR (2017).	

	Phytoplankton tool combining indices for chl-a, elevated counts and seasonal succession. Combines: • 90th percentile chl-a – across growing season (Mar - Oct) • Elevated cell counts – Average combined % exceedance of three metrics: (i) count (%) of Chl-a exceeding 10 µg l^{-1}, (ii) count (%) of individual taxa exceeding 250,000 or 500,000 cells l^{-1}, (iii) count (%) of total taxa exceeding 10^6 or 10^7 cells l^- • Seasonal succession of functional groups – average % exceedance from the reference envelope for diatoms and dinoflagellates grouping	UK -OSPAR (2017) - WFD (Devlin et al., 2009).	
	Cyanobacterial Bloom index (CyaBI) surface accumulation (using earth observation) and biomass (in situ measurement) of Cyanobacteria above a threshold.	HELCOM (2017, 2018, 2023a); MSFD: Sweeden, Germany, Poland, Portugal; Araújo et al. (2019); Magliozzi et al. (2023).	
	Cyanobacteria surface accumulation combining information on volume, length of bloom period and severity of surface accumulations estimated from remote sensing observations.	MSFD: Finland - Araújo et al. (2019); Magliozzi et al. (2023).	
	Phytoplankton tool combining 90th percentile, elevated counts and seasonal successions.	MSFD: Portugal - Araújo et al. (2019); Magliozzi et al. (2023).	
	Maximum concentration of blooming species.	MSFD: Sweeden - Araújo et al. (2019); Magliozzi et al. (2023).	
	Molecular taxonomy of potentially toxic species.	MSFD: Bulgaria- Araújo et al. (2019); Magliozzi et al. (2023).	
	Average taxonomic distinctness (e.g., degree to which individuals in an assemblage are related).	Clarke and Warwick (2001).	
	Diatom/Dinoflagellate index.	HELCOM (2018b, 2023b).	
	PH1 Plankton Lifeform indicator		
	Biological quality element phytoplankton communities, referring to Shannon index, number of species, Sheldon index, %MEC, DE% and Chl-a.	Petrova and Gerdzhikov (2015).	
	Seasonal succession of Dominating Phytoplankton groups.	HELCOM (2018c)	
	PH1/FW5: Changes in phytoplankton and zooplankton communities.	Holland et al.,(2023)- for OSPAR QSR 2023	
	PH2: Changes in Phytoplankton Biomass and zooplankton abundance.	Louchart et al., (2023a)- for OSPAR QSR 2023	
	PH3: Changes in Plankton Diversity.	Louchart et al., (2023b)- for OSPAR QSR 2023	

	Habitat distributional range and extent of (EO1-1). Phytoplankton and zooplankton of coastal, shelf and oceanic waters- No references.	UNEP/MAP (2016).	
	Condition of Habitat's typical species and communities (EO1-2) of Phytoplankton and zooplankton of coastal, shelf and oceanic waters. No references.	UNEP/MAP (2016).	
Presence/abundance of cyst forms	>50% of *Lingulodinium machaerophorum* in cyst assemblages linked to cultural eutrophication in Norwegian fjord.	Dale et al. (1999).	
	Cyst banks.	Garmendia et al. (2013).	
Metabolic or nutrient status	Protein profiles of *Prorocentrum triestinum.*	Chan et al. (2004).	
Size structure indicators	Normalized Biomass Size-Spectra parameters (NBSS-Intercept, NBSS-Slope and NBSS-R2.	Garmendia et al. (2013).	
Pigment concentrations and pigment ratios	90th percentile value of chlorophyll-a calculated over the defined growing season in a six-year period (different thresholds for different areas and countries).	European Commission (2018) - Northeast Atlantic.	
	90th percentile of Chl-a calculated over the year in at least a five-year period.	European Commission, (2018) - Mediterranean Sea.	
	Chlorophyll-a average.	European Commission, (2018) - Baltic Sea.	
	Chlorophyll-a.	HELCOM (2018a, 2023); UNEP-MAP Commission Decision 2018/229.	
	Chl-a trends.	Prins and Enserink (2022) for OSPAR QSR 2023.	Based on *in situ* data or on satellite data.
	Average of surface chlorophyll-a during summer months.	EEA (2022).	
	Monthly and seasonal mean chlorophyll-a in estuarine systems.	Sutula et al. (2017).	San Francisco Bay (USA).
Functional indicators	Carbon and chlorophyll-a ratio and primary production.	Jakobsen and Markager (2016).	
	Margalef's Mandala define phytoplankton functional groups by mapping the distribution of different phytoplankton species in an ecological space defined by turbulence and nutrient levels.	Margalef (1978, 1979).	
	Four phytoplankton functional groups can be distinguished from a multivariate analysis analysis: (1) bloom-forming dinoflagellates, (2) winter diatoms, (3) summer-autumn diatoms, and (4) large dinoflagellates and elongated diatoms. Potentially harmful species are distributed through all the clusters.	Vila and Masó (2005).	

	Balance between heterotrophy and autotrophy.	Pereira et al. (2010); Seoane et al. (2011). Havskum et al. (2004).	
	Functional traits (e.g., N-fixing, motility, buoyancy, mixotrophy, cell size, harmfulness) are related to physical and chemical features in the environment.	Weithoff and Beisner, (2019).	
	Proposal of indicators based on different phytoplankton functional traits in the Baltic Sea.	Lehtinen et al. (2021).	
Blooms (frequency, amplitude, peak, spatial extent)	Blooms per year in the seasonal cycle.	Ferreira et al. (2011); Carstensen et al. (2015); Hansson (2006); Kahru et al. (2020).	
	Risk maps of *Phaeocystis globosa* in the southern North Sea and *Karenia mikimotoi* blooms in the Western English Channel.	Kurekin et al. (2014).	From satellite.
	Pseudo-nitzschia in the Galician upwelling area.	Torres Palenzuela et al. (2019).	From satellite.
	Karenia brevis in the Gulf of Mexico.	Stumpf et al. (2003); Cannizzaro et al. (2008); Carvalho et al. (2011).	From satellite.
	Cochlodinium polykrikoids in the Persian Gulf.	Ghanea et al. (2016).	From satellite.
	cyanobacterial-dominance blooms in the Benguela upwelling area.	Matthews et al. (2012).	From satellite.
Phenology indicators	Mean Chl a concentration of the seasonal cycle. Maximum Chl a concentration of the seasonal cycle. Bloom amplitude:Difference between Chl a maximum and mean. Bloom peak:Day of year (DOY) of Chl a Maximum. DOY of initiation of the main bloom in the seasonal cycle. DOY of termination of the main bloom in the seasonal cycle. Duration of the main bloom in the seasonal cycle. Bloom area:Biomass of the main bloom in the seasonal cycle. Total biomass accumulated during the seasonal cycle.	Ferreira et al. (2011).	Linked to phytoplankton. Not specifically related with HABs.

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10.3 Supplementary Figures

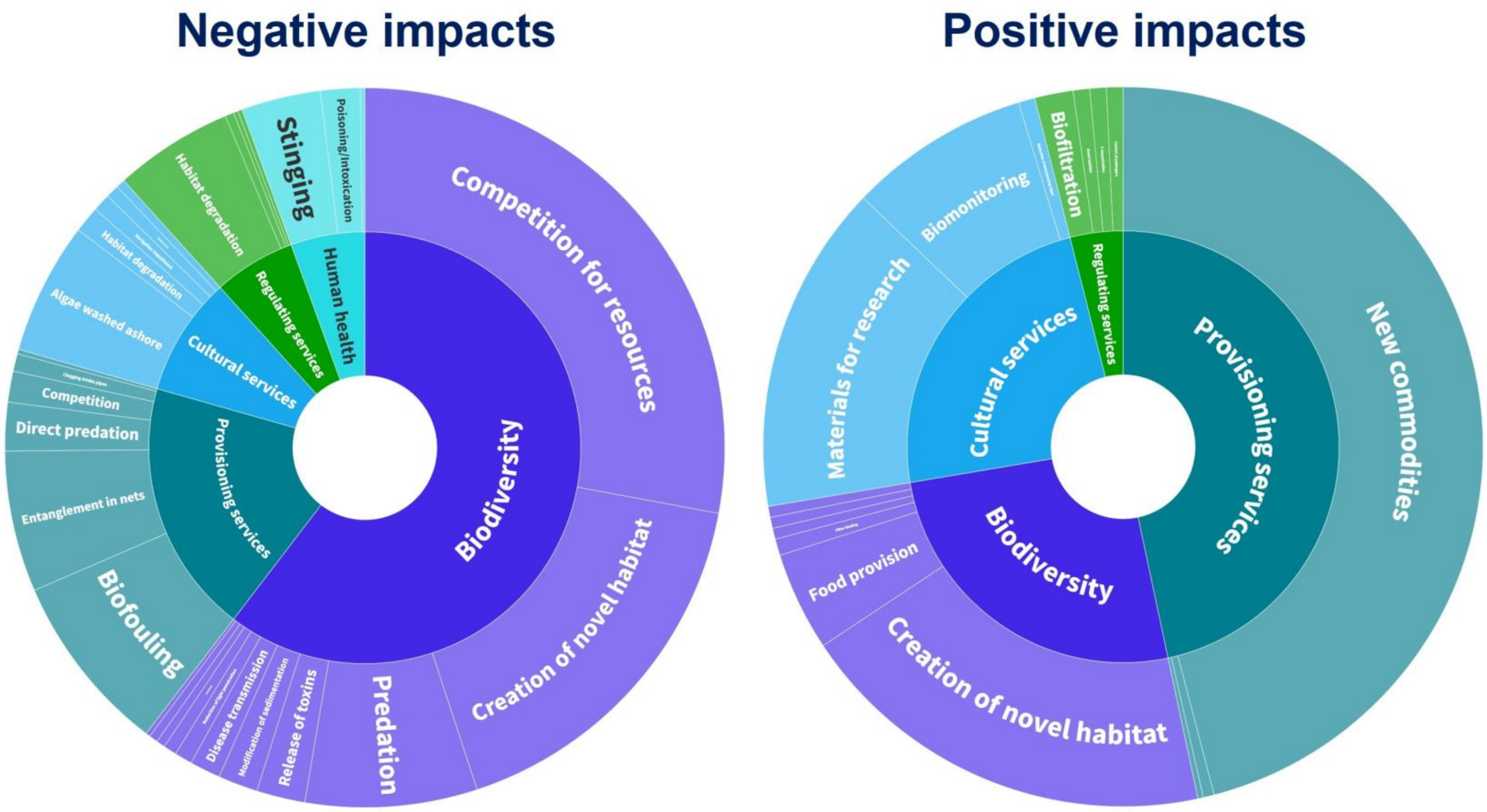

Figure S1. Mechanisms (outer circle) of IAS impacts on biodiversity, ecosystem services and human health (inner circle) in the Mediterranean sea (circle compartment size corresponds to sample size), for negative (left) and positive (right) impacts, excluding limited strength of evidence derived by expert judgement.

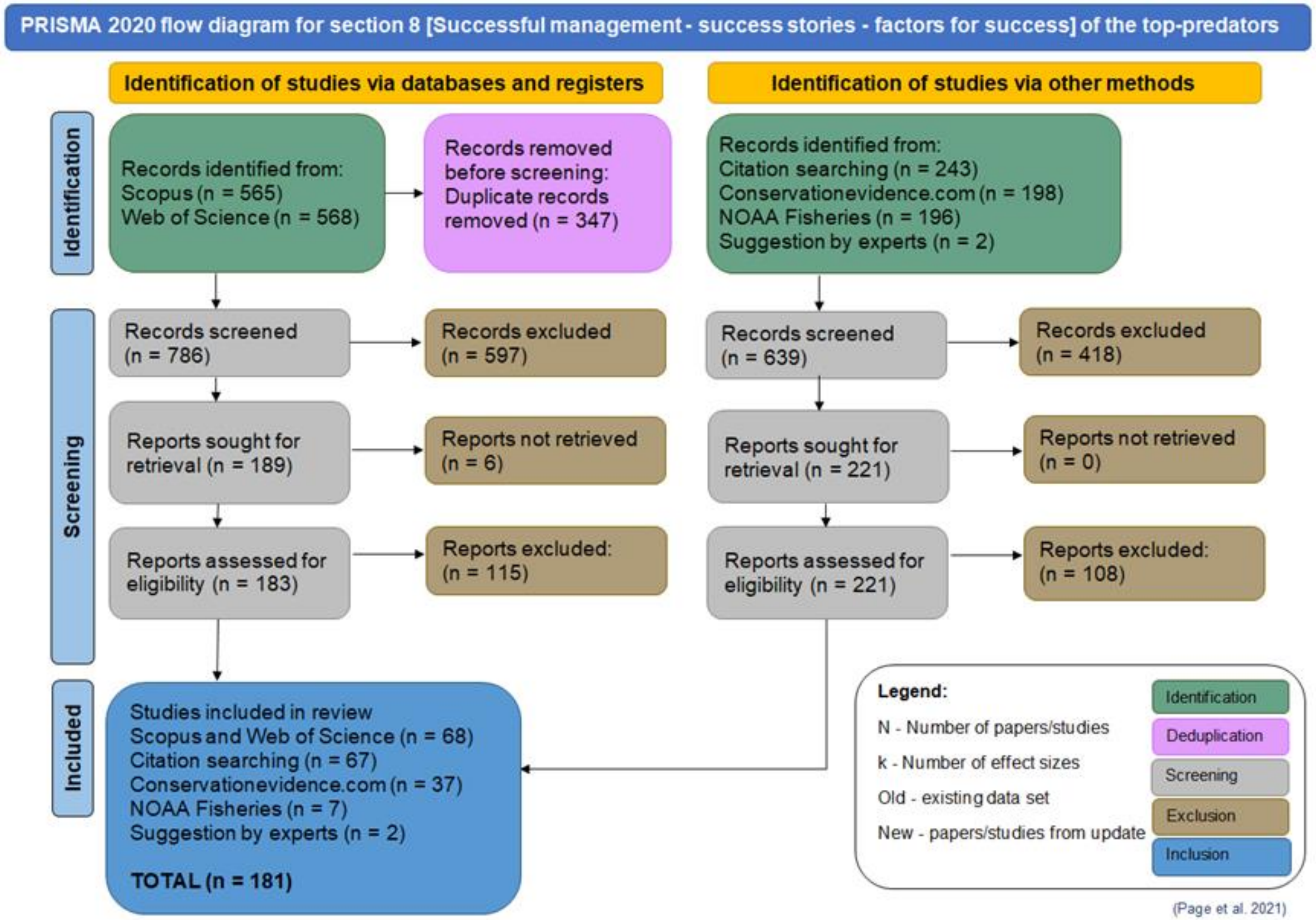

Figure S2: PRISMA flow diagram for the systematic review conducted to investigate successful management cases of top predators

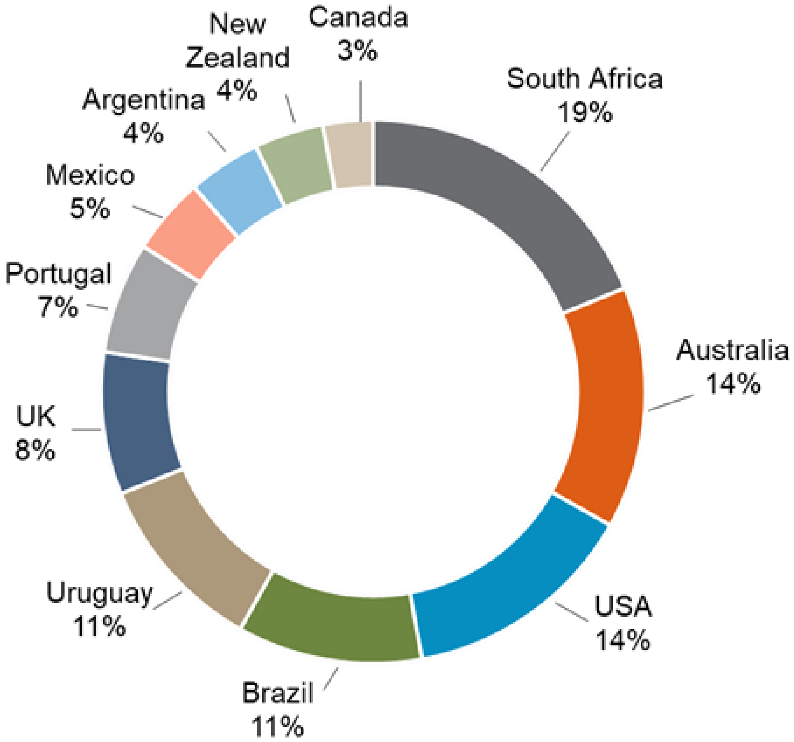

Figure S3: Success stories by country.

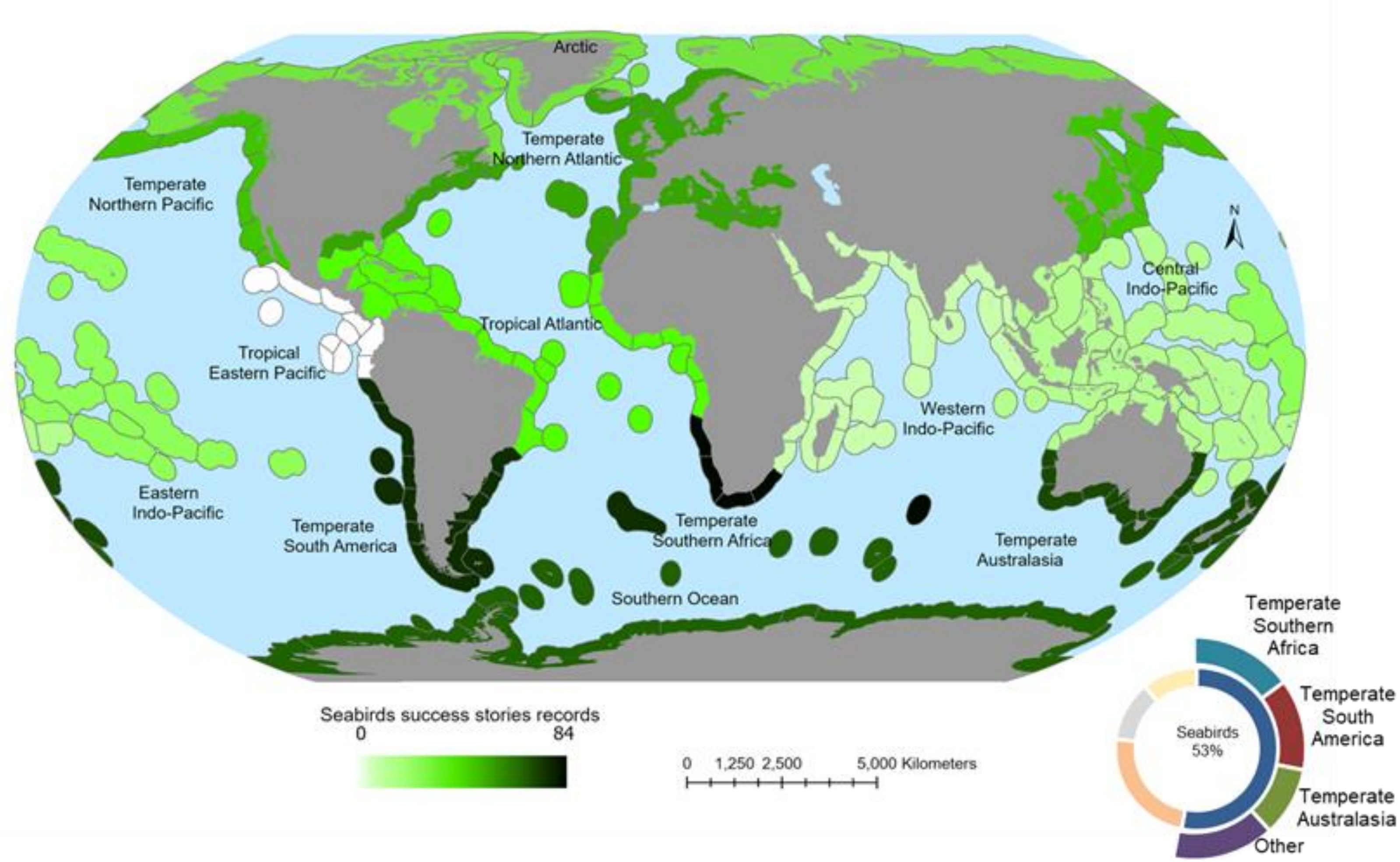

Figure S4: Spatial distribution for the taxonomic group of seabirds success stories in the twelve marine realms, sensu Spalding et al. (2007)

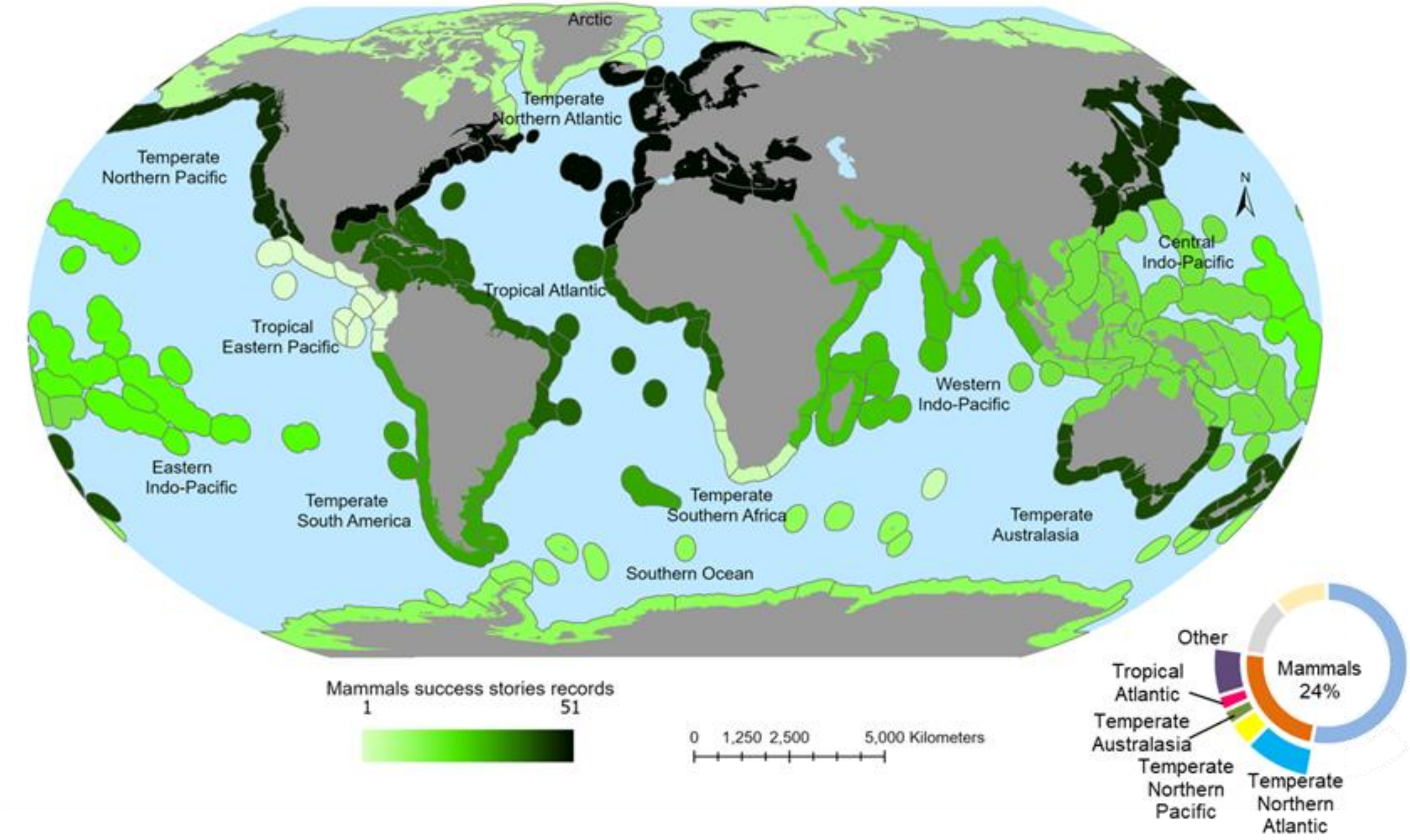

Figure S5: Spatial distribution for the taxonomic group of mammals success stories in the twelve marine realms, sensu Spalding et al. (2007)

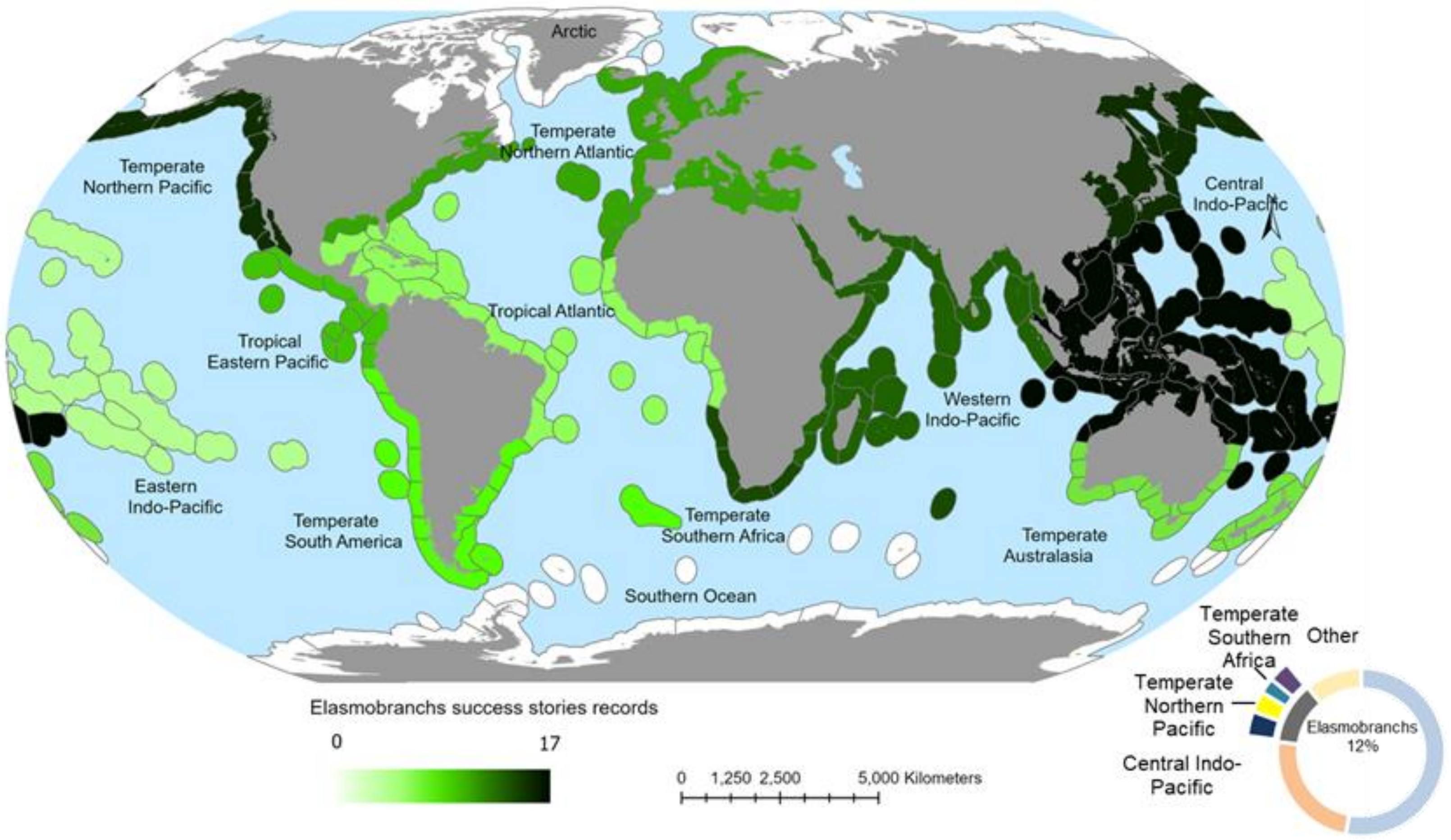

Figure S6: Spatial distribution for the taxonomic group of elasmobranchs success stories in the twelve marine realms, sensu Spalding et al. (2007)

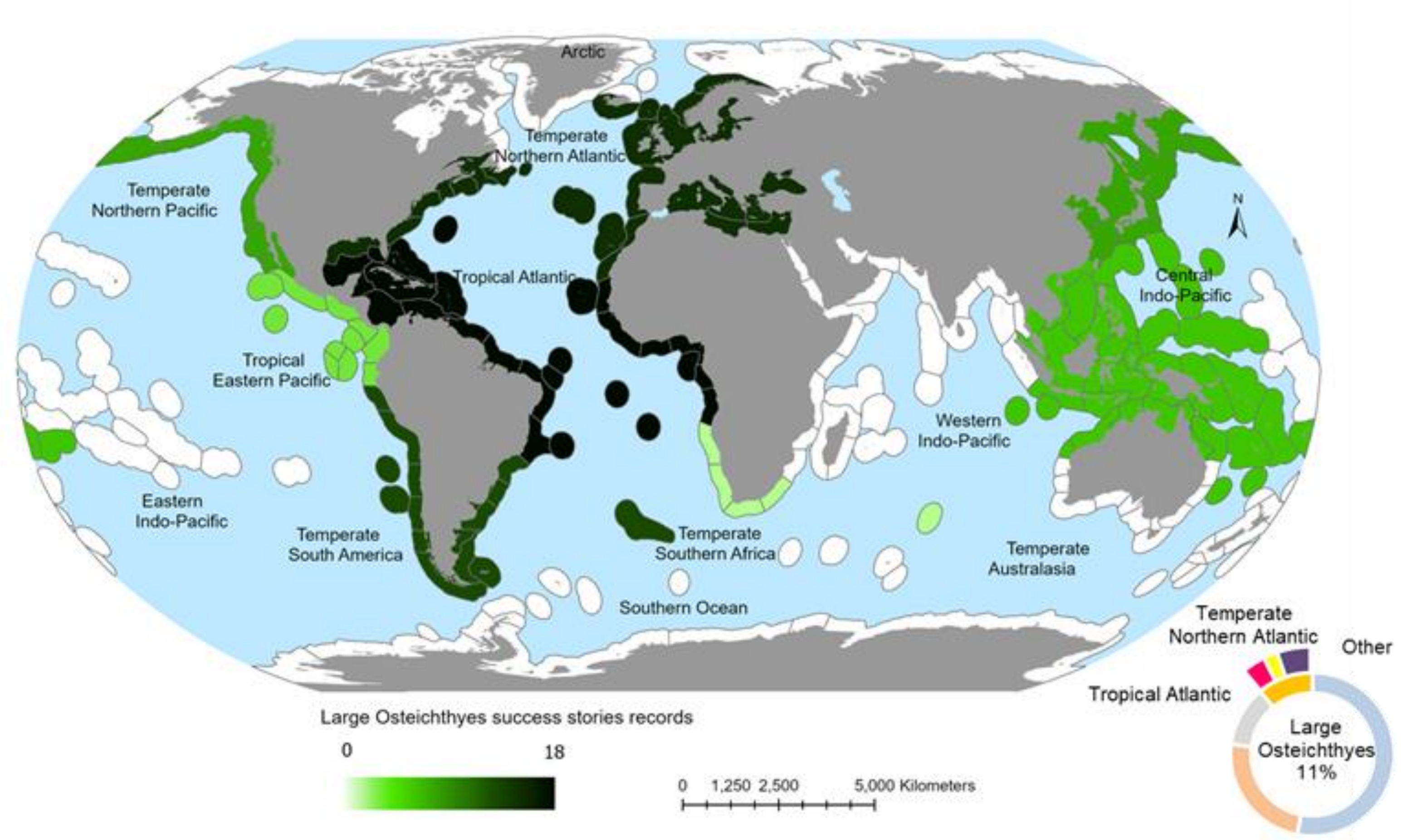

Figure S7: Spatial distribution for the taxonomic group of large Osteichthyes success stories in the twelve marine realms, sensu Spalding et al. (2007)

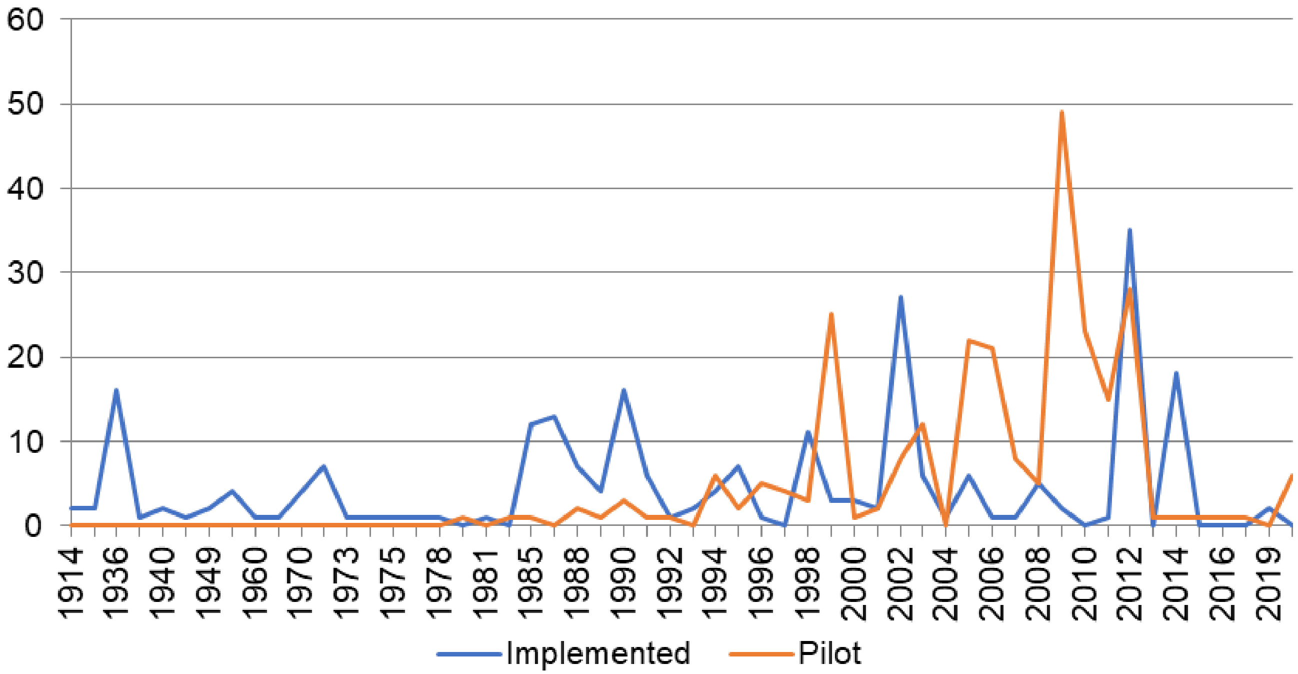

Figure S8: Number of success stories by starting year; pilot and implemented actions are indicated separately.

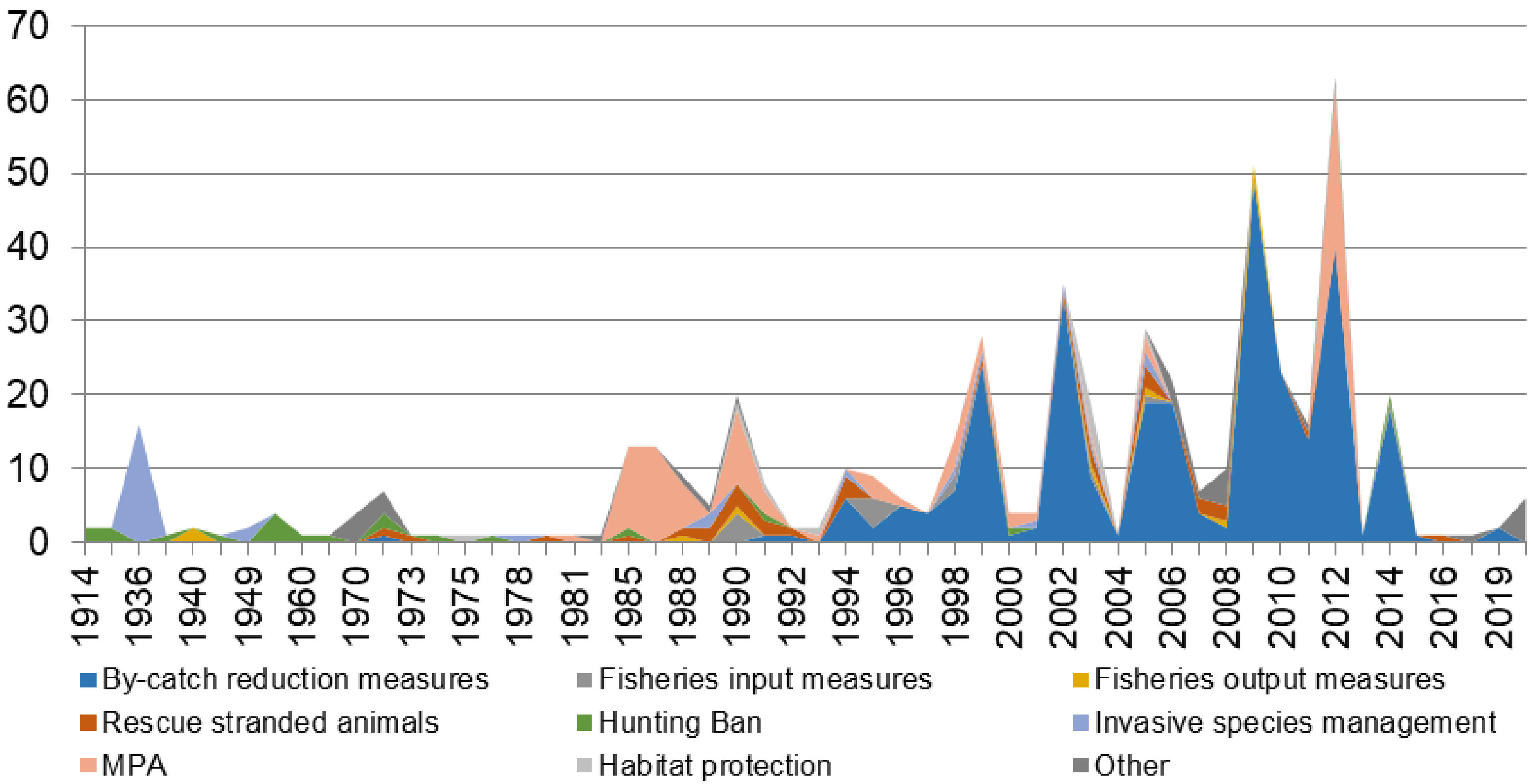

Figure S9: Cumulative plot of the number of success stories by starting year; the various types of actions are indicated with different colors.

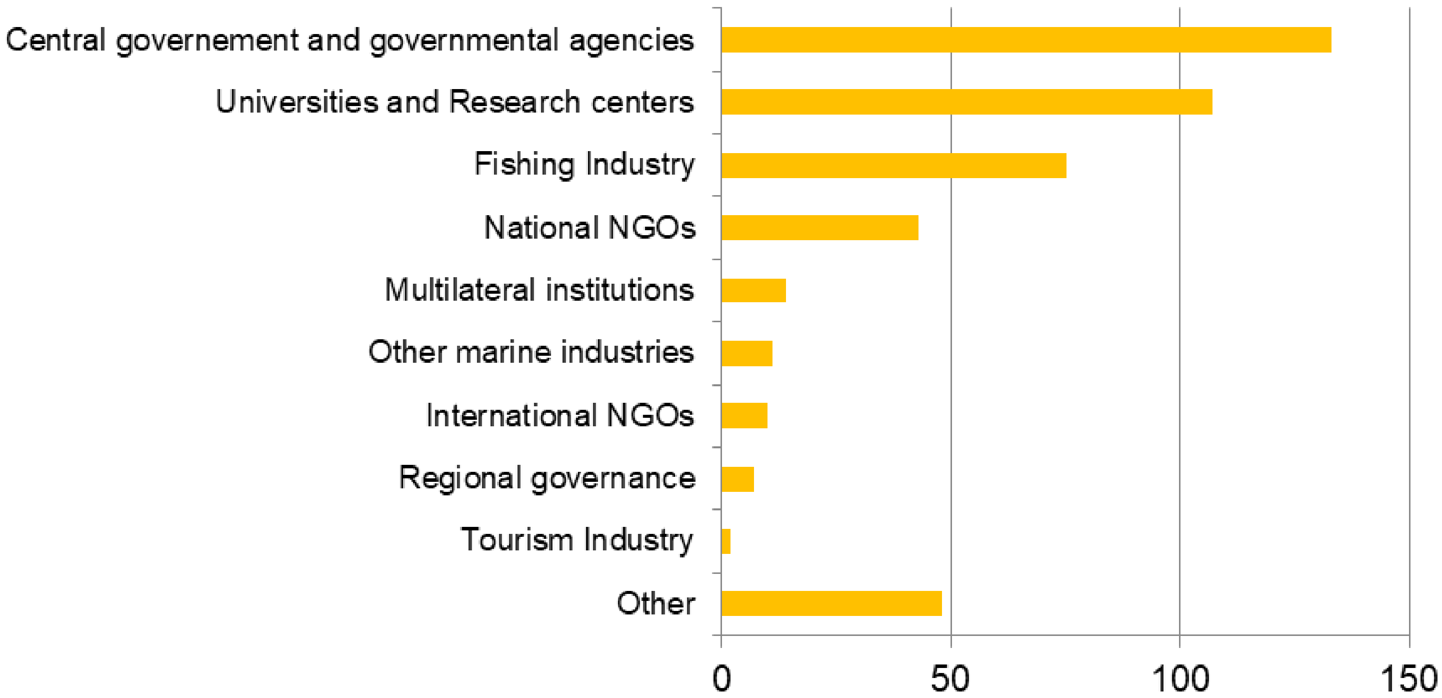

Figure S10: Stakeholder groups involved in the conservation actions of the reviewed studies (number of times each group was involved in the 181 reviewed studies).

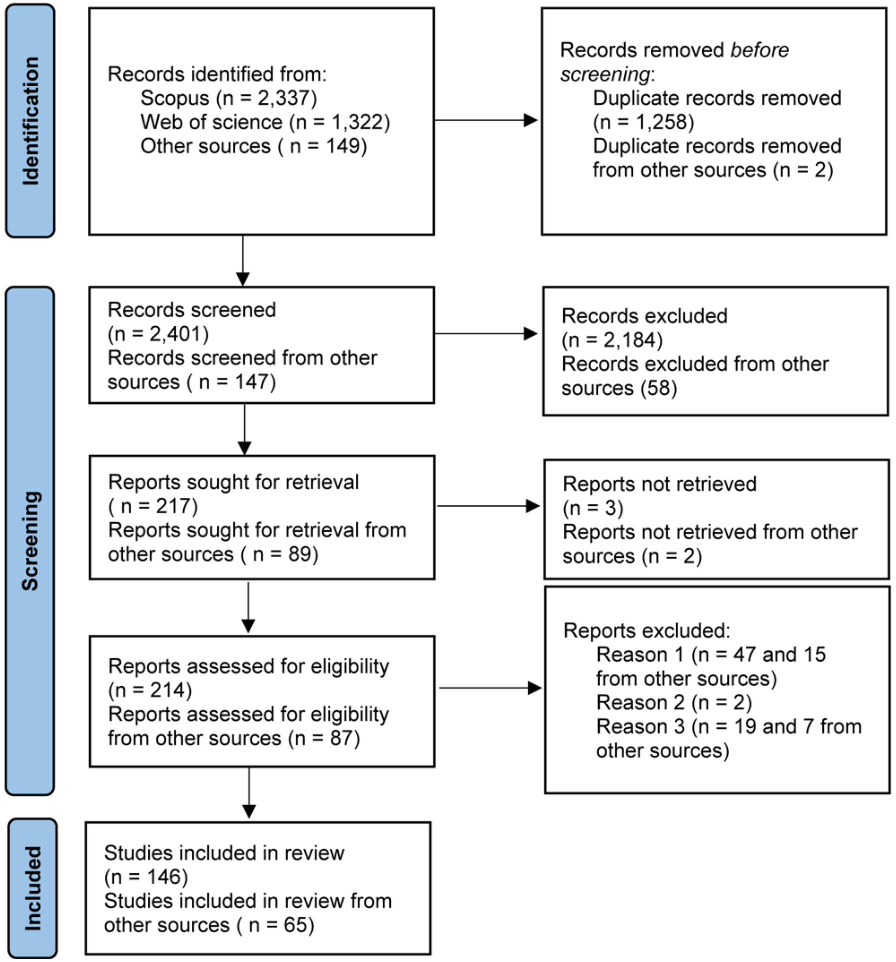

Figure S11: Schematic diagram of article selection on jellyfish impacts through the screening steps. Reason 1= out of scope (e.g., no negative impacts reported or not about jellyfish species), Reason 2= language and Reason 3= publication type (e.g., review; note that all retrieved review articles were screened for citation identification and relevant articles were added for screening as "Other sources").

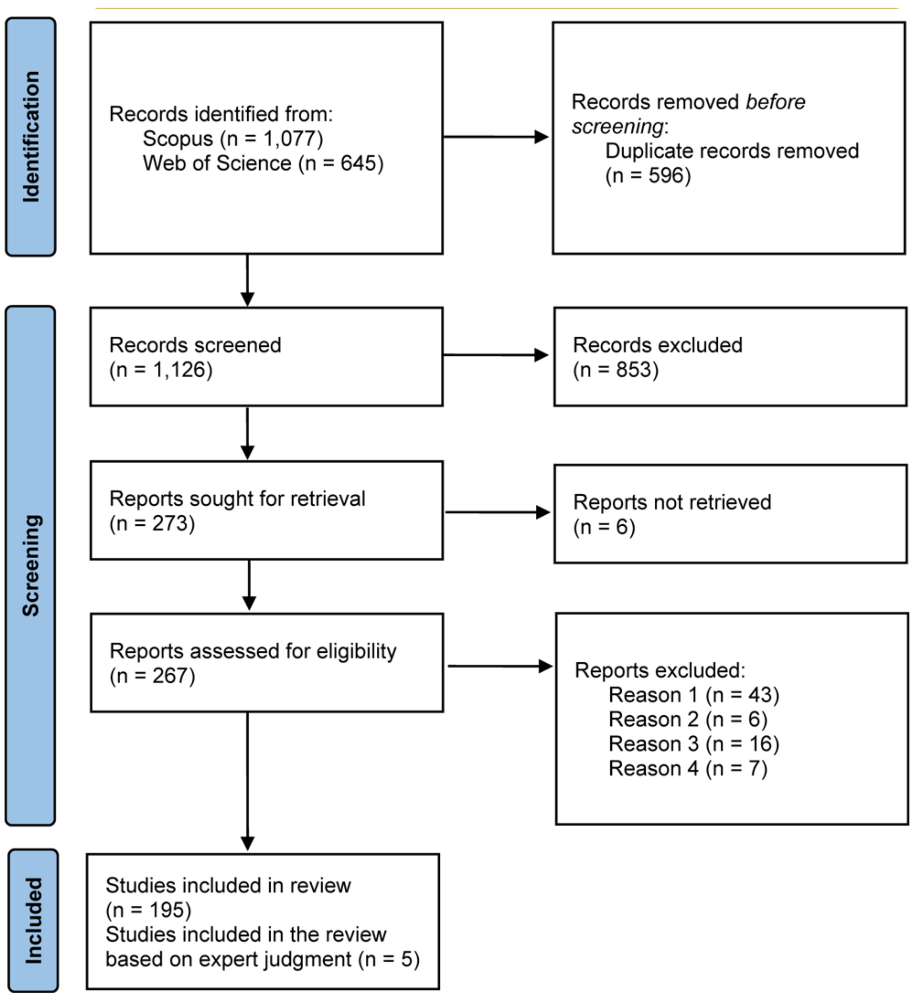

Figure S12: Schematic diagram of article selection through the screening steps undergone for global jellyfish monitoring. Reason 1= not jellyfish monitoring, Reason 2= language, Reason 3= publication type, Reason 4= modeling

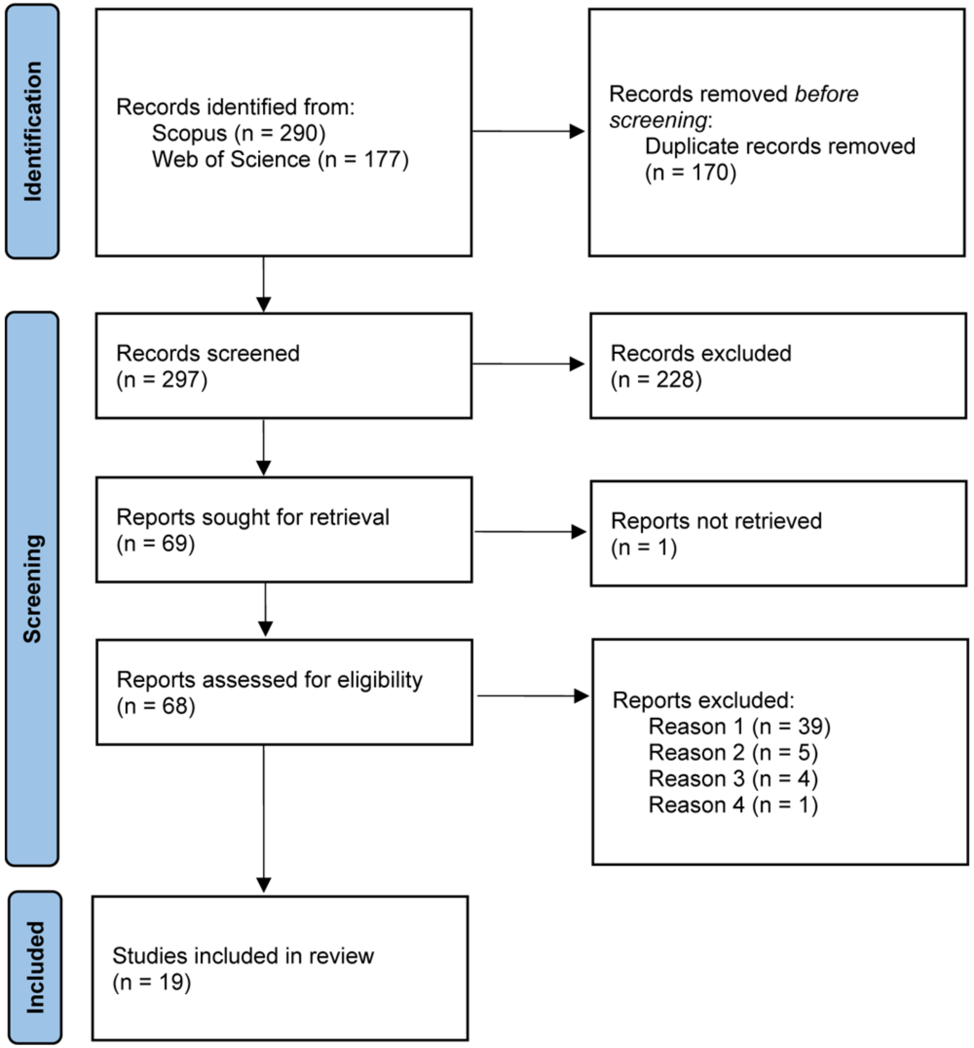

Figure S13: Schematic diagram of article selection on polyp monitoring through the screening steps. Reason 1= not polyp monitoring, Reason 2= Hydrozoans, Reason 3= freshwater species, Reason 4= publication type.


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