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

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

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

KEYWORDS

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

1 Introduction

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

Non-indigenous species (NIS) are defined as species that have spread beyond their natural biogeographical range to new regions with the aid of human actions (Essl et al., 2018). IAS are defined by the European Union (EU) IAS Regulation as "alien species whose introduction or spread has been found to threaten or adversely impact upon biodiversity and related ecosystem services" (European Union (EU), 2014), giving the term "invasive" a negative connotation. IAS have rapidly increased worldwide (Seebens et al., 2017), resulting in significant economic costs (Diagne et al., 2021). IAS have the capacity to profoundly alter the structure and functioning of native communities, often leading to the loss of native biodiversity, disruption of ecosystem services,

loss of socioeconomic values, and potential impacts on human health (Mazza et al., 2014; Tsirintanis et al., 2022). However, the impacts of IAS can have either (or both) "negative" (reducing the value of a specific property) or "positive" (increasing the value) consequences for specific ecological or socioeconomic attributes, and they can be highly context-dependent (Tsirintanis et al., 2022; Vimercati et al., 2022; Reise et al., 2023).

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

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

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

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

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

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

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

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

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

2 IAS information systems

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

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

The European Commission launched the European Alien Species Information Network (EASIN) in 2012 to support European NIS management policies (Katsanevakis et al., 2012; Katsanevakis et al., 2015). EASIN provides easy and open access to harmonized data and information on alien and cryptogenic species, sourced from global, regional, and national databases and

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

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

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

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

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

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

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

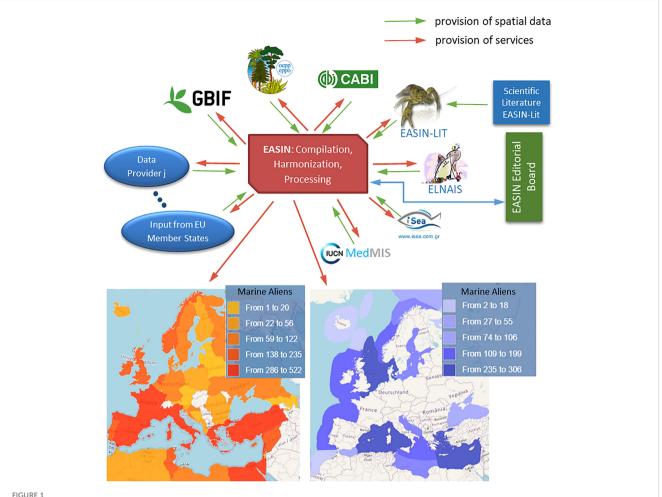
the long-term utility of a database depends not only on the employed technologies and project deliverables but also on sustained user demand and post-project maintenance (Olenin et al., 2014). Unfortunately, securing funding for database collaboration, adaptation, improvement, and maintenance is often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

One notable example is the DAISIE information system, a product of the project DAISIE (Delivering Alien Invasive Species Inventories for Europe). The project, with a European Commission contribution of €2.4 million, spanned 3 years starting in February 2005 (DAISIE, 2009). Its goal was to create a comprehensive resource on biological invasions in Europe, through an international team of leading experts in biological invasions, cutting-edge database design and display technologies, and an extensive network of European collaborators and stakeholders

(DAISIE, 2009). The system compiled and verified over 248 datasets from 98 European countries/regions, making it the world's largest invasive species database.

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

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



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).



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

3 Monitoring strategies

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

3.1 Monitoring the European seas

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

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

down and bottom-up approaches to influence and align monitoring efforts at regional and national levels.

3.2 National monitoring

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

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

3.3 Port monitoring

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

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

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

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

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

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

3.4 Molecular approaches

Recent years have witnessed an explosion in the application of molecular methods based on organismal or eDNA or RNA due to their rapid technological advancements (Fonseca et al., 2023). In the context of biodiversity monitoring, the most applied methods can be categorized into 1) methods targeted to specific species based on quantitative real-time PCR (qPCR) or digital PCR (dPCR; including

digital droplet PCR) and 2) untargeted methods based on metabarcoding of amplified taxonomic marker sequences using "universal" primers with broad coverage. Both types of methods offer advantages over traditional monitoring, including enhanced sensitivity and the ability to identify sparse NIS populations, even when visually challenging to identify life stages or when local taxonomic expertise is lacking (Bowers et al., 2021). Sample collection and preservation are relatively straightforward, requiring smaller sediment volumes, while eDNA can be directly extracted from water filters. In recent years, numerous evaluation and proof-of-concept studies have demonstrated the utility of both approaches for NIS monitoring in the environment and transportation vectors such as ballast water (e.g., Zaiko et al., 2015; Borrell et al., 2017; Rey et al., 2018; Holman et al., 2019; Rey et al., 2020; Bowers et al., 2021; Duarte et al., 2021; Knudsen et al., 2022).

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

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

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

In total, 1,671 alien and cryptogenic marine and oligohaline species are reported in the European Seas by EASIN (as of July 2023).

EASIN, European Alien Species Information Network.

NIS, non-indigenous species.

absolute abundance (McColl-Gausden et al., 2023; Sapkota et al., 2023). For successful NIS identification, both approaches rely on the availability of reference sequence data. The specificity of metabarcoding also depends on the phylogenetic resolution of the amplified taxonomic marker, which can be severely limited, e.g., when using partial sequences of the small subunit (18S) rRNA gene that may show little or no variation across metazoans, for which 12S or COI is commonly used. Insufficient database coverage can

severely limit the utility of metabarcoding, especially in regions where baseline biodiversity is poorly characterized. For example, Pearman et al. (2021) found that only 31% of 18S and 4% of the unique COI metabarcoding sequence variants obtained from a diversity survey of marinas in Tahiti could be assigned to species. Metabarcoding of eDNA is also dependent on the genetic reference sequences deposited on genetic databases that originate from vouchered museum specimens, as this makes species identification from sequence reads more reliable (Pleijel et al., 2008; Buckner et al., 2021). It is important that the bioinformatic handling of eDNA metabarcode sequence data includes a validation step that allows for identification being based on vouchered sequence data, rather than the most prevalent sequences. It also underlines the continuous importance of having taxonomic expertise in museum collections and the value of natural history collections at museums (Rocha et al., 2014).

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

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

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

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

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

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

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

3.5 Other technological tools

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

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

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

3.6 Citizen science

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

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

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

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

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

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

4 Predicting biological invasions

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

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

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

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

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

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

5 Pathways of marine IAS in Europe

The first large-scale assessment of marine NIS pathways of introduction was conducted a decade ago (Katsanevakis et al., 2013), based on the Hulme et al. (2008) pathway classification. With the use of the EASIN Catalogue (version 2.3), the assessment identified 1,369 marine NIS in European seas, with 1,257 associated with likely pathways of introduction. The study revealed a rising trend in new introductions, with shipping as the primary pathway for over half of the species. The second-most common pathway was marine and inland corridors, mainly the Suez Canal, with aquaculture and aquarium trade following in terms of the numbers of introduced species. Interestingly, aquaculture showed a notable decrease in new introductions from 2001 to 2010, attributed to regulatory measures at national and European levels (e.g., ICES, 2005; European Union (EU), 2007). In contrast,

introductions through other pathways, particularly aquarium trade, showed a consistent increase. The assessment underscored the ongoing expansion of the Suez Canal and the reduced barriers to the entry of Red Sea species as factors that are likely to facilitate the invasion of the Mediterranean Sea by additional Lessepsian species. These Lessepsian species have been greatly facilitated by climate change, and the increased temperatures of the eastern Mediterranean and currently dominate demersal communities (Box 1).

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

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

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

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

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

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

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



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

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

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

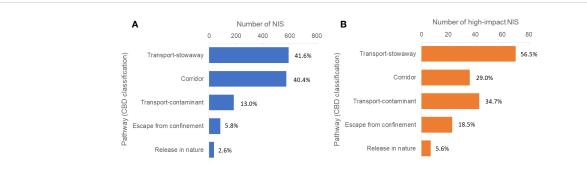
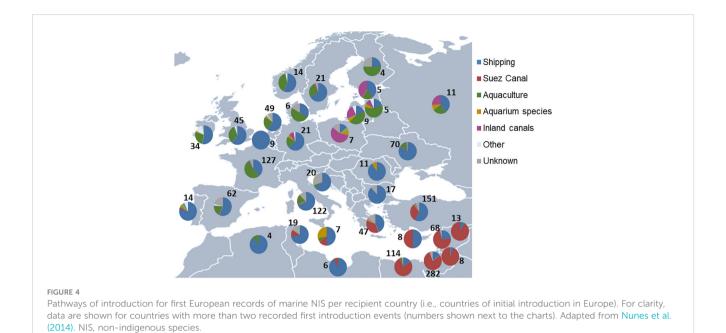


FIGURE 3

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



followed by "Transport-stowaway" (35%) (Katsanevakis et al., 2020). In the Baltic Sea, shipping and natural NIS spread from the North Sea dominate among the pathways for established NIS (Ojaveer et al., 2017).

6 Impacts on biodiversity, ecosystem services, and human health: assessing and mapping impacts

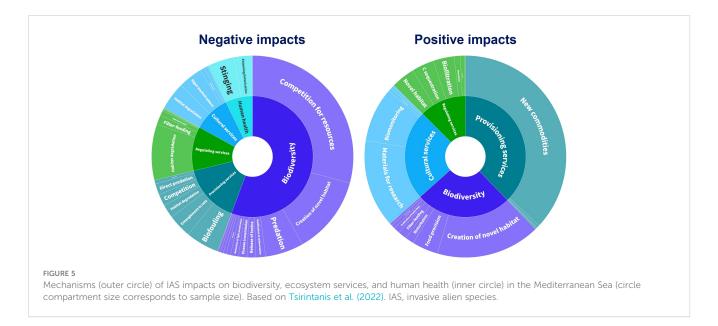
IAS impact and risk assessments are increasingly demanded by managers for informed decision-making. Risk screening can help identify species with invasive potential in the area of interest, requiring further analysis of their potential impacts (Ricciardi and Rasmussen, 1998; Copp et al., 2005). IAS often share life-history traits, such as frequent reproduction, large body size, long life span, high degree of omnivory, and a climate match with the area of interest (Statzner et al., 2008; Chan et al., 2021). Moreover, invasive species tend to have broad tolerance to abiotic conditions (Leuven et al., 2009) and a history of being invasive in other regions.

Several protocols exist for IAS impact and risk assessment, such as BPL/BINPAS (Olenin et al., 2007; Narščius et al., 2012), EICAT (Hawkins et al., 2015), SEICAT (Bacher et al., 2018), FISK and related tools (Copp et al., 2005; Copp, 2013), GABLIS (Essl et al., 2011), GB-NNRA (Baker et al., 2008), GISS (Nentwig et al., 2016), Harmonia+ (D'hondt et al., 2015), ISEIA (Branquart, 2009), and NGEIAAS (Sandvik et al., 2013). These tools rank taxa based on their threat level in the risk assessment area at a specified spatial scale. Until recently, there was no standardized and evidence-based system to classify the positive impacts of alien species; EICAT+covered this gap by offering a protocol to categorize the magnitude of positive NIS impacts (Vimercati et al., 2022). The screening tools vary in objectives, taxonomic resolution, and target (e.g., specific habitats or pathways), as well as complexity, approaches to assess

uncertainty, and scoring systems used. These variations may result in significant differences and inconsistencies in the assessment outcomes; selection of assessors, clear assessment guidelines, and adequate training are important in addition to arriving at final decisions collaboratively by consensus (González-Moreno et al., 2019).

A pan-European systematic review of NIS impacts (Katsanevakis et al., 2014b) identified 87 marine species in Europe with documented high impacts on biodiversity or ecosystem services. The study revealed that food provision was the most affected ecosystem service both positively and negatively. Other services negatively affected included ocean nourishment, recreation and tourism, and life cycle maintenance, while cognitive benefits, water purification, and climate regulation were among the services often positively impacted. Additionally, 49 assessed species were considered ecosystem engineers, altering habitats through physical or chemical modifications. The study acknowledged a potential bias against NIS, suggesting that positive impacts might be underestimated.

Tsirintanis et al. (2022) studied the impacts of biological invasions on biodiversity, ecosystem services, and human health in the Mediterranean Sea. They identified various biological mechanisms through which NIS affect Mediterranean ecosystems, resulting in both negative and positive impacts (Figures 5, S1; Table S1). Negative impacts on biodiversity were primarily due to competition for resources, followed by the creation of novel habitats and predation (Figure 5; Table S1). NIS structural ecosystem engineers can completely transform seascapes and substantially change community composition, leading to the loss of native species (García-Gómez et al., 2021; Mancuso et al., 2022). Alien predators and grazers cause significant negative impacts on Mediterranean ecosystems by consuming native biota (Sala et al., 2011; Kampouris et al., 2019).



Predator-prey interactions in the marine environment are dynamic ecosystem processes influenced by local environmental factors and species' ecological features, capable of affecting multiple food-web levels (Rilov, 2009).

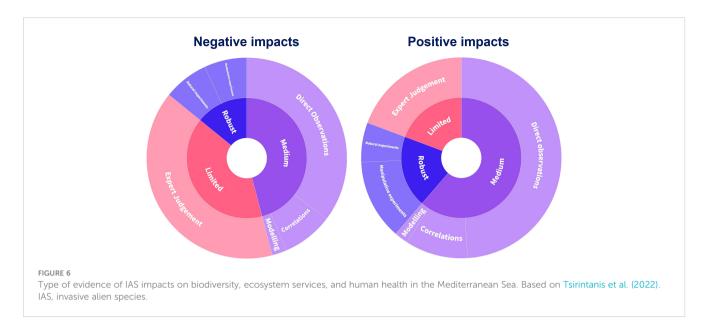
Biofouling is the primary mechanism of negative impacts on provisioning services, with many IAS densely colonizing aquaculture facilities and reared species, leading to significant economic losses (Tsotsios et al., 2023). IAS also greatly impact cultural services through the degradation of highly valued habitats, algae massively washed ashore, and jellyfish blooms reaching coastal waters, negatively affecting tourism (e.g., Ghermandi et al., 2015; Ruitton et al., 2021). Habitat degradation is the primary mechanism through which IAS negatively impact regulating services. Regarding human health, IAS primarily cause negative impacts through stinging or poisonings/intoxications (Galil, 2018; Bédry et al., 2021) (Figure 5; Table S1).

Many positive NIS impacts have been reported in the European Seas (Katsanevakis et al., 2014b; Tsirintanis et al., 2022). In the Mediterranean, provisioning services benefit the most from NIS introductions through the provision of new commodities. Various fish, mollusks, and crustaceans have proven a boon for the fisheries and aquaculture sector, especially in the Levantine Sea (e.g., Katsanevakis et al., 2018). The creation of novel habitats is the most important mechanism of positive effects on biodiversity, as alien structural ecosystem engineers provide new habitats and shelter for various species through the formations they create (Katsanevakis et al., 2014b; Guy-Haim et al., 2018; Figure 5). Cultural services are positively affected by research conducted on NIS specimens for future potential exploitation of molecules for pharmaceutical or industrial applications (e.g., Genovese et al., 2012; Nekvapil et al., 2019). Regarding regulating services, the creation of novel habitats, carbon sequestration, and biofiltration are the most important mechanisms contributing to positive impacts (Figure 5; Table S1).

Evidence of reported impacts is mostly of medium strength (Figure 6; Table S1), predominantly from direct observations (e.g., novel habitat creation, competitive overgrowth of sessile organisms, or predation effects derived through stomach content analysis), followed by non-experimental-based correlations between a species presence/abundance and an impact, and modeling to project impact consequences (Figure 6; Table S1). Many reported impacts are only based on expert judgment. Only a small percentage of NIS impacts are supported by robust evidence from manipulative or natural experiments (Katsanevakis et al., 2014b; Tsirintanis et al., 2022; Figure 6).

Several indices have been developed to assess NIS ecological impacts and ecological status considering NIS presence. ALEX (ALien biotic indEX; Çinar and Bakir, 2014) evaluates NIS impacts on benthic communities, aligning with the EU Water Framework Directive classification system; Piazzi et al. (2015) also recommended its application. ECOfast, an ecological evaluation index for shallow rocky reefs, was recently developed (Kytinou et al., 2023). ECOfast-NIS, a variant of this index, penalizes the presence of certain NIS that have negative impacts on local food webs. CIMPAL (Cumulative IMPacts of invasive ALien species) is a conservative additive model based on IAS and habitat distributions, reported magnitude of ecological impacts, and the strength of such evidence (Katsanevakis et al., 2016). CIMPAL has been implemented for the Mediterranean Sea (Katsanevakis et al., 2016), the European scale (Teixeira et al., 2019), and other marine regions like Maltese waters (Bartolo et al., 2021) and the Aegean Sea (Tsirintanis et al., 2023).

Despite extensive negative impacts, global documentation of marine IAS-related extinctions remains scarce. A recent global review on drivers of marine extinctions reported IAS as responsible for 27 out of 786 extinction cases (seven global and 20 local extinctions) (Nikolaou and Katsanevakis, 2023). Among the seven globally extinct species due to IAS, six were seabirds and one was a diadromous fish, while the invasive species causing the



extinctions were not marine (e.g., invasive rats). In many reported extinctions, IAS were not the sole driver, and their contribution was often unknown, introducing uncertainty about their actual role as the cause of extinctions. The Mediterranean-endemic fan mussel *Pinna nobilis* is an example of IAS-related local extinctions in Europe. It experienced extensive local extinctions due to infection by the newly described protozoan *Haplosporidium pinnae* (likely introduced by shipping), putting the species at risk of global extinction (Katsanevakis et al., 2022). It is now critically endangered in the Red List (Kersting et al., 2019).

Although complete species extinction due to biological invasions is rare in the marine environment, dramatic declines in populations caused by predation or parasitism can lead to functional extinction (Boero et al., 2013). For instance, in the Baltic Sea, the invasion of the round goby *Neogobius melanostomus* resulted in a significant decline in the population of blue mussels (*Mytilus edulis trossulus*), leading to the disappearance of the mussel-created biotope, which served as a crucial habitat for wintering bird populations (Skabeikis et al., 2019).

The predatory impacts of IAS are often focused on, with most studies emphasizing the top-down predatory effects of invaders on native prey, although many species play both predator and prey roles in the ecosystem. The prey role is particularly interesting since nearly all NIS eventually become subject to predation by native predators, which can even lead to the control of IAS populations (e.g., Hunt and Yamada, 2003; Jensen et al., 2007), a process that often takes time (Santamaría et al., 2022). For example, in the Chesapeake Bay, USA, native blue crabs exert predation pressure on the invasive green crab to the point where there are no green crab populations left (DeRivera et al., 2005). In many cases, native predators may even benefit from the new prey (Crane et al., 2015; Pintor and Byers, 2015). Conversely, there are instances where the increased invasive resource leads to an increase in predator populations and results in increased predation on native species (Noonburg and Byers, 2005).

Prey naivety toward invasive predators has been extensively studied and documented (e.g., Sih et al., 2010; Anton et al., 2020). However, less focus has been given to the naivety of predators, although similar naivety may occur, especially toward novel prey (Reid et al., 2010; Santamaría et al., 2022). This can be particularly noticeable during the early stages of invasion, resulting in lower predation pressure on the novel species compared to native, more familiar prey (e.g., Carlsson et al., 2009; Santamaría et al., 2022).

7 Management options: lessons learned from the implementation of management measures

7.1 Prevention: pathway management

Prevention of IAS introductions is the first line of defense (Olenin et al., 2011; Katsanevakis, 2022). According to Article 13 of the IAS Regulation, EU Member States need to "carry out a comprehensive analysis of the pathways of unintentional introduction and spread of invasive alien species of Union concern" in their marine waters and "establish and implement one single action plan or a set of action plans to address the priority pathways".

To prevent introductions through shipping (Transportstowaway), the most important pathway of marine introductions in the EU (Figure 3), a critical development was the entry into force of the IMO BWMC in 2017. The BWMC mandates all ships to adopt a ballast water management plan and, by September 2024, treat their ballast waters with an approved ballast water treatment system to diminish the survival probabilities of ballast water-transferred marine organisms. Although enforcement of the BWMC is challenging, it is expected to substantially reduce new introductions *via* ballast waters. In contrast, biofouling is currently regulated only voluntarily. The IMO's Biofouling Guidelines (Resolution MEPC.207(62)2011) aim to establish a globally

consistent approach to biofouling management. However, there is growing support for a new Biofouling IMO Convention, with intensive research focusing on efficient biofouling systems, including surveillance optimization (e.g., Abdo et al., 2018; Luoma et al., 2022) and hull cleaning (e.g., Morrisey and Woods, 2015; Zabin et al., 2016).

Corridors, particularly the Suez Canal, rank as the second-most significant introduction pathway in Europe (Figure 3). However, managing the Suez Canal to control invasions (e.g., implementing a salinity barrier or establishing locks to reduce current movement) falls beyond EU jurisdiction, and there is no political will from Egypt or the Barcelona Convention to undertake such measures (Galil et al., 2017). Nonetheless, there are arguments that consider climate change impacts in the eastern Mediterranean, Lessepsian species may not pose the primary threat to biodiversity and ecosystem services; instead, they could potentially play a role in securing ecosystem functions and services (see Box 1).

Regulation 708/2007 "concerning the use of alien and locally absent species in aquaculture" (European Union (EU), 2007) has been an important instrument for reducing aquaculture-introduced species. It was implemented well before the IAS Regulation, based on the ICES Code of Practice on the Introductions and Transfers of Marine Organisms (ICES, 2005), and resulted in a noticeable decline in new introductions (Katsanevakis et al., 2013). In contrast, the aquarium trade, a lesser but growing pathway (Zenetos and Galanidi, 2020), lacks EU-level regulation, leading to continued risks of new introductions. Numerous potentially invasive marine species are traded in EU markets (e.g., Mazza et al., 2015; Vranken et al., 2018).

7.2 Implemented eradication and control measures for marine IAS (physical, chemical, and biological approaches): lessons learned

In a recent systematic review of implemented species-specific eradication and control measures for marine IAS, only 31 studies covering 40 cases were found, of which 11 failed to achieve eradication or control targets (Table S2; Katsanevakis, 2022). These studies mainly focused on macroalgae (10), ascidians (7), and fish (seven; all related to lionfish). Physical methods were most commonly used (e.g., removal by divers, mechanical removal by trawling, dredging, or suction, jute matting, heat treatment, using traps, or promoting targeted fisheries), followed by chemical (using various chemicals such as bleach, herbicides, salt, acetic acid, copper sulfate, and sodium hypochlorite) and biological methods (using native predators or parasites).

Only six successful eradication cases have been reported in the global literature (Table S2): sodium hypochlorite used to eradicate the green alga *Caulerpa taxifolia* from California, USA (Anderson, 2005); physical removal by divers to eradicate the brown alga *Ascophyllum nodosum* from Redwood City, California, USA (Miller et al., 2004); a combination of physical removal by divers and heat treatment to eradicate the brown alga *Undaria pinnatifida* from a sunken trawler in Chatham Islands,

New Zealand (Wotton et al., 2004); eradication of the sabellid polychaete *Terebrasabella heterouncinata* from an intertidal site in California, USA, by removing its main native host (Culver and Kuris, 2000); extensive chemical treatment with 187 tonnes of liquid sodium hypochlorite and 7.5 tonnes of copper sulfate to eradicate the mussel *M. sallei* from three sheltered marinas in the Darwin Harbour Estuary (Northern Territory, Australia) (Bax et al., 2002); and dredging to eradicate the invasive mussel *Perna perna* from a subtidal soft-sediment habitat in central New Zealand (Hopkins et al., 2011). Remarkably, successful eradication efforts have been reported only from the USA, New Zealand, and Australia; no successful eradication of a marine IAS from the EU has been reported.

In the EU, only four related studies appear in the literature (Uchimura et al., 2000; Žuljevic et al., 2001; Mancinelli et al., 2017; Kleitou et al., 2021). The first three are experimental investigations or proposals of control approaches, lacking large-scale implementation. Only the latter (Kleitou et al., 2021) made an effort to control lionfish populations in Cyprus, with partial success; lionfish removals significantly decreased its density and biomass (by >50%) in the short term, but long-term suppression requires repeated removals due to rapid population recovery. Another unpublished control effort in the EU (also from Cyprus) is the case of the silver-cheeked toad-fish Lagocephalus sceleratus, a toxic predatory fish with serious impacts on fisheries and human health. A targeted fishery by the small-scale fleet was promoted through fishers' compensation based on the fished and incinerated biomass (Table S3). Although there has been no targeted monitoring to assess the measure's effectiveness, empirical evidence from fishers supports its success in reducing the species' biomass and mitigating its impacts; food web modeling indicates that *L*. sceleratus populations could have been higher without any measures, and continuous management is necessary to prevent the population's rebound at high levels (Michailidis et al., 2023).

The only two species for which large-scale control efforts have been implemented in the EU (*Pterois miles* and *L. sceleratus*) have not been included in the IAS list of Union Concern of the IAS Regulation. Both species were proposed, but their inclusion in the latest (2022) update of the list was not approved. Conversely, there are no known successful control efforts for the only two marine species included in the Union List, i.e., the fish *P. lineatus* and the alga *R. okamurae* (Supplementary Text 1; Table S4). This highlights an inconsistency between the criteria for inclusion in the Union List (which may secure EU or national funding for management efforts) and existing applicable management options for specific marine IAS.

Reported successful eradication or control efforts globally (Katsanevakis, 2022) have highlighted several best practices (Table S2). The most critical factor for eradication success is a rapid response after detection (e.g., Bax et al., 2002; Miller et al., 2004; Anderson, 2005; Hopkins et al., 2011); delayed responses compromised many eradication efforts (e.g., Read et al., 2011; Sambrook et al., 2014). Developing rapid response mechanisms among EU member states (largely missing) is essential for successful eradication. Missing the critical time window for a

rapid response makes eradication from the marine environment practically impossible. Once an IAS is established, alternative management strategies beyond eradication should be explored, essentially focusing on control (see Section 7.3) or considering the option of non-intervention (ignore).

Other best practices for successful eradication or control include flexibility in amending existing legislation (Bax et al., 2002); good coordination among local, regional, and national authorities and stakeholders (Anderson, 2005); effective communication with stakeholders and the local community to gain public support (Bax et al., 2002; Wotton et al., 2004); adequate and continuous funding (Wotton et al., 2004; Anderson, 2005; Hopkins et al., 2011; Sambrook et al., 2014); continuous monitoring (Culver and Kuris, 2000; Miller et al., 2004; Wotton et al., 2004; Anderson, 2005; Kleitou et al., 2021); and a good knowledge of biology and ecology of the IAS and underlying ecological theory to select appropriate eradication/control methods (Culver and Kuris, 2000; Wotton et al., 2004; Anderson, 2005; Hopkins et al., 2011; Green et al., 2014; Harris et al., 2020).

7.3 Management options for established IAS populations

Managing marine IAS is more challenging than terrestrial and freshwater species due to the increased functional connectivity of the oceans (Kinlan and Gaines, 2003; Katsanevakis, 2022). Nevertheless, several management measures have been implemented (Section 7.2; Table S2), and potential additional options have been investigated (e.g., Thresher and Kuris, 2004; Giakoumi et al., 2019; Katsanevakis, 2022) (Table 6). The applicability of these measures depends on factors, such as effectiveness, technical feasibility, social acceptability, side impacts on native communities, and cost (Giakoumi et al., 2019). Some options, such as biological control using alien predators, parasites, or viral diseases, are strongly opposed by experts and stakeholders due to fears of irreversible detrimental side effects on native biodiversity. Despite their low expected effectiveness, soft measures like "education and awareness" or "environmental rehabilitation", and inaction were ranked high by experts (Thresher and Kuris, 2004; Giakoumi et al., 2019). Commercial utilization of IAS has been widely suggested as a means of turning mitigation costs into profits for local populations (Mancinelli et al., 2017). Targeting and eating invaders, such as the lionfish (Kleitou et al., 2022), offers several supplementary advantages, such as raising public awareness about IAS and encouraging citizen participation in identifying new populations and engaging in other control measures (Nuñez et al., 2012).

A striking result reported by Thresher and Kuris (2004) was that the perceived likelihood of success of management options was negatively correlated with their acceptability. This suggests the need to enhance the effectiveness of existing techniques or increase the acceptability of potentially effective techniques (e.g., biological control and genetic technology to decrease pest viability) or

TABLE 6 Management options for controlling established marine IAS populations.

Physical measures

Physically remove IAS-culling efforts.

Encourage targeted removal and commercial or recreational utilization (excluding trading of live individuals).

Chemical measures

Deploy pest-specific biocides, reproductive inhibitors, etc.

Deploy non-specific biocides, tactically applied.

Biological/ecological measures

Rehabilitate the environment in the belief that resistance to IAS impacts will increase.

Promote native consumers (predators or grazers) that attack the IAS.

Promote native diseases and parasites that attack the IAS

Apply biological control using alien consumers (predators or grazers).

Apply biological control using alien parasites and/or diseases.

Apply biological control using alien viruses.

Genetically modify native species (i.e., to use them as vectors for physiological inhibitors).

Genetically modify disease/virus to increase pathogenicity against pests.

Apply genetic approaches that affect only the IAS.

Other

Education and public awareness.

Do nothing in the belief that the problem might go away.

Adapted from Thresher and Kuris (2004); Giakoumi et al. (2019), and Katsanevakis (2022). IAS, invasive alien species.

develop new techniques that are both acceptable and effective (Thresher and Kuris, 2004).

8 IAS and climate change

Climate change, primarily ocean temperature increases, may facilitate the introduction and establishment of thermophilic NIS. It can also amplify the impacts associated with IAS, reducing the fitness of thermally sensitive species and thereby decreasing the resilience of native species, habitats, and ecosystems (Birchenough et al., 2015). The Mediterranean Sea, a semi-enclosed basin experiencing rapid warming compared to other marine regions (Schroeder et al., 2016), is a hotspot for bioinvasions by thermophilic Red Sea species (Costello et al., 2021; Box 1). In the Mediterranean, it was shown that an alien intertidal gastropod is much more resilient to warming than three native gastropod species, which may disappear in the future, leaving it the only large mollusk grazer in the region (Rilov et al., 2022).

Higher rates of between-continent dispersal events due to increasing international trade and human traveling are expected (Hewitt et al., 2018; Sardain et al., 2019; Roura-Pascual et al., 2021).

For marine ecosystems, trade/transport and climate change are considered by invasion scientists as the primary drivers of IAS impacts until 2050 (Essl et al., 2020). The combined effects of climate and rapid transport could result in large-scale biotic homogenization, potentially exceeding the impact of either climate change or IAS acting alone due to context-dependent interactions (Gissi et al., 2021). Despite global climate change often facilitating IAS (Dukes and Mooney, 1999), these two issues are mostly treated independently (Pyke et al., 2008).

Climate change may affect IAS introduction pathways and vectors (Robinson et al., 2020). Melting Arctic ice caps have already facilitated new, faster shipping routes, connecting previously isolated ports and regions and increasing the chances of propagules surviving transit (Pyke et al., 2008; Miller and Ruiz, 2014; McCarthy et al., 2022). Climate change can also alter shipping connectivity by affecting trading patterns and tourism destinations, leading to increased propagule pressure in some locations and decreased pressure in others.

The effects of ocean climate change and acidification on NIS introductions and impacts are frequently discussed in the literature (Occhipinti-Ambrogi, 2021). However, causal effects are not well-documented. Studies that aimed to elucidate the influence of climate change on NIS tend to focus on the impact of increasing ocean temperature, with less attention to non-thermal factors associated with climate change (e.g., ocean acidification, salinity, dissolved oxygen, weather events, and hydrodynamic changes). Furthermore, limited research evaluates the effects of multiple factors and their interactions (Gissi et al., 2021), restricting our ability to robustly predict future IAS impacts.

Marine species are expected to undergo a general poleward expansion due to seawater warming (Pinsky et al., 2013; Poloczanska et al., 2016; Essl et al., 2019). Some evidence suggests that climate-related changes are increasing IAS abundances in marine systems (Sorte et al., 2010; García-Gómez et al., 2020; Stæhr et al., 2020). Among the different pathways of NIS introductions, the poleward expansion linked to ocean warming would be most relevant for secondary introductions. This is because southern seas, as hotspots of NIS introductions, could serve as source populations for further introductions to northerly regions as temperature conditions gradually become favorable there.

The rate of new NIS has significantly increased since the early 1980s (e.g., Zenetos et al., 2022; Jensen et al., 2023) possibly influenced by climate change-induced warming of the sea. Recent studies suggest a higher rate of new NIS arrivals in southern seas (Tsiamis et al., 2018; Tsiamis et al., 2019; Zenetos et al., 2022), with up to 76% of all NIS primary introductions in Europe originating from the Mediterranean Sea. This suggests the importance of secondary non-assisted dispersal for many observed NIS species in northern regions. In the OSPAR regions, secondary introductions accounted for only 5% of NIS introductions (Stæhr et al., 2022). The influence of climate-related warming on NIS introductions is not generally strongly supported by data and

requires targeted species-specific analysis for the different European regions.

Climate change can alter the effectiveness of IAS management. Temperature dictates the life cycle of many IAS, influencing maturation, reproduction, establishment, and persistence (e.g., King et al., 2021; Teixeira Alves et al., 2021), with implications for eradication and population control under climate change. Some studies suggest that mechanical control of IAS becomes less efficient under climate change pressure (Hellmann et al., 2008; Pyke et al., 2008; Kernan, 2015), necessitating increased management efforts to achieve the same management goals (Teixeira Alves and Tidbury, 2022). Further research is needed to understand how both thermal and non-thermal factors of climate change influence IAS management.

In climate change hotspots, particularly in land-locked basins, such as the Mediterranean Sea, native biodiversity decline due to climate change may compromise ecosystem functioning and services (see Box 1). In such cases, thermophilic NIS could play a significant role in sustaining ecosystem functioning and services. As a result, a change in conservation goals has been proposed, moving from protecting native biodiversity to protecting functions and services (Rilov et al., 2019a; Rilov et al., 2020). Similarly, Reise et al. (2023) highlighted that some NIS in the Wadden Sea positively contributes to sediment stabilization, mud accretion, and diversification of lower food web levels, potentially benefiting foraging birds. They argued that these NIS have raised the tidal ecosystem's capacity to adapt to environmental change rather than degrade it.

9 Recommendations: how to improve the management of IAS in Europe

9.1 Costs of biological invasions and funding

Global damage and management costs associated with biological invasions have exponentially increased in the last 50 years (Diagne et al., 2020). However, the allocation of economic resources toward invasive species prevention, control, research, long-term management, and eradication measures needs a substantial increase to offset the economic losses caused by direct and/or indirect impacts of invaders (Diagne et al., 2021).

The extensive economic impacts of invasions, reaching beyond administrative and national scales, highlight a clear discrepancy between the implementation of international agreements (Table 1) by local authorities and the achievement of broad policy objectives. Enhancing governance, encompassing the capacity to implement policies through expertise and resources, is crucial for preventing and managing biological invasions and their impacts. International initiatives and European Institutions play a critical role in supporting and expediting measures that require local implementation but rely on effective global and regional coordination. Strategic planning and securing adequate funding will be central to addressing many of the challenges raised in this review.

9.2 Inadequate coverage of marine biological invasions by the IAS Regulation

Currently, only two marine species (P. lineatus and R. okamurae) are included in the List of Invasive Alien Species of Union Concern, which does not reflect the status of marine biological invasions in the EU. Marine NIS thrive in the European seas, with EASIN listing 1,602 alien or cryptogenic species, while globally, WRiMS and AquaNIS currently report 2,781 and 2,028 species, respectively. The Mediterranean Sea, in particular, is a hotspot of biological invasions, harboring more NIS than any other sea globally (Costello et al., 2021). Many of these species are invasive, significantly impacting biodiversity, ecosystem services, and human health (Katsanevakis et al., 2014b; Tsirintanis et al., 2022). An EU horizon scanning exercise identified 18 marine species absent from or with a limited distribution in EU marine waters as potential candidates for inclusion in the list based on their impacts and management feasibility (Tsiamis et al., 2020). However, it seems that member states hesitate to include marine species in the list of IAS of Union Concern, assuming that management of marine IAS is impossible. As indicated in previous sections, managing marine IAS is more challenging than terrestrial or freshwater species, but it is not impossible. Hence, the current list of IAS of Union Concern does not fully acknowledge the threat marine IAS pose to the EU marine environment, and it needs to be supplemented based on current scientific advice and risk assessments (as per Article 5 of the IAS Regulation).

9.3 Learning from countries with high biosecurity: take stock of good practices

Ideally, a robust biosecurity system should encompass all three steps of the invasion process (pre-border, border, and post-border) and implement effective and timely interventions, drawing from countries with established cutting-edge biosecurity programs (Carvalho et al., 2023). New Zealand, Australia, and the USA have well-established biosecurity systems, as evidenced by their successful cases of marine IAS eradication or control (Table S2). For example, New Zealand's Marine Biosecurity Team, operating under the Ministry of Fisheries since 1998, conducts various activities such as quarantine, surveillance, response to incidents, long-term control of established pests, and enforcement of legislation (Hewitt et al., 2004). Europe could benefit from the experience, learning from both successes and failures in managing IAS in these countries. Organizing workshops and meetings involving high-level policymakers, marine scientists, managers, and officials from various countries can promote collaborative knowledge sharing and mutual learning to enhance global marine IAS management.

9.4 Creating an EU funding mechanism to secure the sustainability of important information systems

Adequate EU funding is crucial to sustain key databases and online information systems. EASIN plays a central role in harmonizing and integrating information on NIS in Europe. It primarily acts as an aggregator that gathers data from various

sources and provides efficient tools and services for access to harmonized datasets. However, the foundation of the European infrastructure relies on national institutions, local and regional networks, and online databases and initiatives. These entities are essential data suppliers to centralized systems like EASIN. Therefore, it is critical to financially support and sustain national institutions and scientific networks to ensure the continuous flow of information, knowledge, and expertise to EASIN and the scientific community.

NIS information systems should be multipurpose, following the principle of "gather data once, utilize it many times". In addition to operational usage, these systems should continuously accumulate data for analysis and forecasting. Ideally, this should not only include information on species occurrences but also offer search functions for NIS biological traits, environmental tolerance limits, and their impacts on native biodiversity, ecosystem functioning, economy, and public health.

9.5 Improving monitoring and early warning systems

Continued efforts to increase the spatial and temporal coverage of marine IAS monitoring, as well as transboundary cooperation, are required. Aligned with the ethos of "take once, use many" and driven by the application of novel techniques such as eDNA, automated monitoring, and even citizen science, integration of NIS monitoring with other biodiversity monitoring programs, where applicable, is an opportunity to balance data collection against increasing costs/ declining budgets. Automated eDNA monitoring (Hansen et al., 2020; Preston et al., 2023) and using citizen science for monitoring eDNA also have associated difficulties (Agersnap et al., 2022; Knudsen et al., 2023), and the eDNA metabarcoding itself (Fonseca, 2018) and species-specific eDNA detection are not without pitfalls and problems with interpretation (Klymus et al., 2019). The data analysis required when eDNA is to be interpreted is often complicated and is better off being aided by taxonomic experts who are familiar with the organisms known to inhabit the sampled area. Further, streamlining marine NIS data flow and reducing data time lags will enhance early warning systems and facilitate rapid response. Understanding introduction pathways is also crucial for implementing effective prevention measures and reducing new introductions.

Several studies have considered how man-made structures (offshore wind farms, wrecks, and oil and gas platforms) could act as *de facto* MPAs, facilitating colonization by both native and NIS (Birchenough and Degraer, 2020). It is important to highlight that the presence of these man-made structures will alter the species pool, with repercussions for trophic interactions (Mavraki et al., 2019) and secondary production, and may also serve as stepping stones for range-expanding (sometimes non-indigenous; Kerckhof et al., 2011) species altering population connectivity patterns (Henry et al., 2018; Coolen et al., 2020).

9.6 Improving predictions

Accurately predicting the potential distribution of invasive species is crucial for global marine conservation. To improve

predictions, it is imperative to consider the biological characteristics and distribution of the species, biotic interactions, and environmental conditions. Incorporating intrinsic traits in modeling can prove advantageous, as these traits can either facilitate higher adaptation rates or impose limitations on the invasion process (Gamliel et al., 2020). More data from both native and invaded ranges enhance prediction accuracy, allowing for a better assessment of the role of environmental factors in distribution and expansion potential. Removing noisy or uncertain predictors can further increase model accuracy. Integrating invasion dynamics like biotic interactions, dispersal limitations, and adaptation potential can inform potential niche conservatism violations (D'Amen and Azzurro, 2020b; Liu et al., 2020). As a final note, when selecting modeling approaches (e.g., correlative, mechanistic, and process-oriented), careful consideration of available input data accompanied by rigorous validation is essential (Melo-Merino et al., 2020).

9.7 Improving integrated impact assessments: cumulative impact mapping to prioritize actions

Cumulative impact assessments of invasive species are valuable for several reasons. They offer a comprehensive understanding of the combined effects of multiple IAS on marine ecosystems, aiding policymakers and managers in understanding the extent and severity of ecological disturbances. This knowledge is crucial for devising effective strategies to prevent new invasions and mitigate existing impacts. As marine management shifts toward ecosystem-based spatial approaches, cumulative impact assessments become essential tools. They facilitate the integration of spatial information into environmental decisions and the setting of specific operational objectives. By identifying highly impacted areas, resources can be directed toward priority zones or targeted management actions for IAS.

Comprehensive large-scale analyses of the impacts of all alien marine species are urgently needed. Policymakers and managers, particularly in regions like the European Union, require a better understanding of invasive species' impacts to meet environmental protection goals. Despite limitations and uncertainties in impact assessments, the adaptive management approach, involving monitoring, filling data gaps, and learning from management actions, offers a way to address and manage IAS impacts over time. In a limited-funding environment, decision-makers can efficiently allocate resources by focusing on sites, pathways, and species with high impacts and low uncertainty, increasing the chances of success in mitigating IAS effects. These initial successes can motivate further efforts to address biological invasions.

9.8 Assessing positive impacts and exploiting NIS

NIS have become a permanent component of contemporary ecosystems, and their potential benefits on ecosystem services,

human wellbeing, and biodiversity should be thoroughly investigated (Schlaepfer et al., 2011; Vimercati et al., 2020; Vimercati et al., 2022). Many invasion studies are biased toward perceiving alien species as harmful due to their history of detrimental effects on ecosystems. Some reported negative impacts supported by limited strength of evidence may be influenced by this bias (Katsanevakis et al., 2014b; Tsirintanis et al., 2022), affecting impact assessments (e.g., compare Figures 5 and Figure S1). Scientists should adopt holistic approaches, considering both the negative and positive consequences of IAS on recipient ecosystems, relying on substantial evidence. The role of NIS in marine conservation, restoration, and securing ecosystem functioning and services, particularly in climate change hotspots, deserves serious consideration (see Box 1) (Mačić et al., 2018; Rilov et al., 2019a; Rilov et al., 2020).

In such regions heavily impacted by climate change, such as the eastern Mediterranean, IAS commercial exploitation becomes not merely a management choice but an essential measure to ensure the fishing industry's viability and safeguard seafood supply from the ocean (Katsanevakis, 2022). However, in other regions, there are risks associated with promoting commercial utilization of IAS, and initiatives aimed at controlling IAS through human consumption should be carefully evaluated, as they could produce unintended outcomes contrary to their goals (Nuñez et al., 2012; Katsanevakis, 2022). This shift in perception could lead to illicit attempts to spread IAS to new areas, ultimately exacerbating their invasive potential (Mancinelli et al., 2017). Furthermore, it might create pressure to maintain and sustainably exploit these problematic species (Nuñez et al., 2012), as has happened in the cases of Rapana venosa in the Black Sea (Demirel et al., 2021) and the invasive red (Kamchatka) king crab (Paralithodes camtschaticus) fishery in the Barents Sea (Spiridonov, 2018).

Bioprospecting involves identifying and extracting new bioactive compounds with various potential applications, such as biomedicine, human health, food provision, nutraceuticals, cosmeceuticals, and the search for anti-fouling and antimicrobial agents. Managing IAS through prospecting can turn a threat into a resource, as demonstrated by growing research on invasive species, e.g., alien or native jellyfish (see Leone et al., 2015; Leone et al., 2019; De Domenico et al., 2023, and references therein), alien macroalgae (Misal and Sabale, 2016; Vitale et al., 2018; Cherry et al., 2019; Meinita et al., 2022), and even the poisonous *L. sceleratus* (Çavaş et al., 2020).

Author contributions

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Writing – review & editing. KT: Visualization, Writing – original draft, Writing – review & editing. SB: Conceptualization, Writing – original draft, Writing – review & editing. HJ: Conceptualization, Writing – original draft, Writing – review & editing. SWK: Writing – original draft, Writing – review & editing. AL: Data curation, Writing – original draft, Writing – review & editing. AM: Writing – original draft, Writing – review & editing. SP: Writing – original draft, Writing – review & editing. HTi: Writing – original draft, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

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