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Review

Bioinvasion impacts on biodiversity, ecosystem services, and human health in the Mediterranean Sea

Konstantinos Tsirintanis[1], Ernesto Azzurro[2,3], Fabio Crocetta[3], Margarita Dimiza[4], Carlo Froglia[2], Vasilis Gerovasileiou[5,6], Joachim Langeneck[7], Giorgio Mancinelli[8,9,10], Antonietta Rosso[10,11], Nir Stern[12], Maria Triantaphyllou[4], Konstantinos Tsiamis[13], Xavier Turon[14], Marc Verlaque[15], Argyro Zenetos[16] and Stelios Katsanevakis[1,*]

[1]Department of Marine Sciences, University of the Aegean, Lofos Panepistimiou, 81100 Mytilene, Greece; [2]CNR-IRBIM, National Research Council. Institute of Biological Resources and Marine Biotechnologies, Ancona, Italy; [3]Department of Integrative Marine Ecology, Stazione Zoologica Anton Dohrn, I-80121 Naples, Italy; [4]Faculty of Geology & Geoenvironment, National and Kapodistrian University of Athens, Panepistimioupolis 15784, Athens, Greece; [5]Department of Environment, Faculty of Environment, Ionian University, 29100 Zakynthos, Greece; [6]Hellenic Centre for Marine Research (HCMR), Institute of Marine Biology, Biotechnology and Aquaculture (IMBBC), 71500 Heraklion, Greece; [7]Department of Biology, University of Pisa, 56126 Pisa, Italy; [8]Department of Biological and Environmental Sciences and Technologies (DiSTeBA), University of Salento, SP Lecce-Monteroni, 73100 Lecce, Italy; [9]National Research Council – Institute of Marine Biological Resources and Biotechnologies (CNR-IRBIM), 71010 Lesina (FG), Italy; [10]CoNISMa, Consorzio Nazionale Interuniversitario per le Scienze del Mare, 00196 Roma, Italy; [11]Department of Biological, Geological and Environmental Sciences, University of Catania, 95129 Catania, Italy; [12]Israel Oceanographic and Limnological Research, National Institute of Oceanography, Haifa 31080, Israel; [13]Vroutou 12 Athens, 11141, Greece; [14]Centre for Advanced Studies of Blanes (CEAB, CSIC), 17300 Blanes, Catalonia, Spain; [15]Aix Marseille University and Université de Toulon, CNRS, IRD, Mediterranean Institute of Oceanography (MIO), UM 110, Marseille, France; [16]Institute of Marine Biological Resources & Inland Waters (IMBRIW), Hellenic Centre for Marine Research (HCMR), 16452, Argyroupolis, Greece

**Corresponding author*
E-mail: *stelios@katsanevakis.com*

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Abstract

Biological invasions have become a defining feature of marine Mediterranean ecosystems with significant impacts on biodiversity, ecosystem services, and human health. We systematically reviewed the current knowledge on the impacts of marine biological invasions in the Mediterranean Sea. We screened relevant literature and applied a standardised framework that classifies mechanisms and magnitude of impacts and type of evidence. Overall, 103 alien and cryptogenic species were analysed, 59 of which were associated with both negative and positive impacts, 17 to only negative, and 13 to only positive; no impacts were found for 14 species. Evidence for most reported impacts (52%) was of medium strength, but for 32% of impact reports evidence was weak, based solely on expert judgement. Only 16% of the reported impacts were based on experimental studies. Our assessment allowed us to create an inventory of 88 alien and cryptogenic species from 16 different phyla with reported moderate to high impacts. The ten worst invasive species in terms of reported negative impacts on biodiversity include six algae, two fishes, and two molluscs, with the green alga *Caulerpa cylindracea* ranking first. Negative impacts on biodiversity prevailed over positive ones. Competition for resources, the creation of novel habitat through ecosystem engineering, and predation were the primary reported mechanisms of negative effects. Most cases of combined negative and positive impacts on biodiversity referred to community-level modifications. Overall, more positive than negative impacts were reported on ecosystem services, but this varied depending on the service. For human health, only negative impacts were recorded. Substantial variation was found among Mediterranean ecoregions in terms of mechanisms of impact and the taxonomic identity of impacting species. There was no evidence that the magnitude of impact increases with residence time. Holistic approaches and experimental research constitute the way forward to better understanding and managing biological invasions.

Key words: alien species, cryptogenic, effects, experiments, expert judgement, modelling, systematic review

Introduction

The rate of human-mediated introduction of species to new areas is high and accelerating all over the world (Seebens et al. 2017; Pyšek et al. 2020), with heavy and rising associated economic costs (Diagne et al. 2021). Modern biological invasions constitute a unique form of global environmental change, profound enough to surpass natural drivers of selection and dispersal, creating novel biological communities that would have never emerged through natural processes (Ricciardi 2007). In the ecological domain, the integration of novel species in the ecosystems can generate fundamental alterations to the structure of native communities and ecosystem functioning (e.g., Vitousek et al. 1996; Kideys 2002; Pranovi et al. 2006; Galil 2007; Ehrenfeld 2010; Vilà et al. 2011; Katsanevakis et al. 2014a; Howard et al. 2019), often with detrimental losses of native biodiversity (e.g., Clavero et al. 2009; Sala et al. 2011; Harper and Bunbury 2015; Bellard et al. 2016; Doherty et al. 2016; García-Gómez et al. 2020). The provision of ecosystem services can also be strongly affected by the impacts of biological invasions (Vilà et al. 2010; Katsanevakis et al. 2014a; Vilà and Hulme 2017; Castro-Díez et al. 2019). Furthermore, invasive species pose a threat to human health through a variety of mechanisms such as pathogen transmission, intoxication, and envenomation (Schaffner et al. 2013; Hulme 2014; Galil 2018; Peyton et al. 2019; Bédry et al. 2021).

Recent works highlighted that biological invasions can also have positive outcomes (Katsanevakis et al. 2014a; Vimercati et al. 2020), for example by creating novel ecosystems that may support native biodiversity and ecosystem functioning (Hobbs et al. 2009; Schlaepfer et al. 2011; Evers et al. 2018), providing ecosystem services (Katsanevakis et al. 2018; Apostolaki et al. 2019), and contributing to human well-being (Shackleton et al. 2019; Sfriso et al. 2020). The positive impacts of alien species are dependent on societal perception and different cultural values and motivations (Simberloff et al. 2013) and are commonly underestimated (Katsanevakis et al. 2014a). Nevertheless, their study is receiving increasing attention (Vimercati et al. 2020) and, in some cases, alien species can even constitute targets for protection and conservation (Schlaepfer et al. 2011; Mačić et al. 2018).

Impact assessment (including both negative and positive impacts of biological invasions) is an important but challenging process aiming to quantify the magnitude of changes and prioritise management and mitigation of undesired effects (Parker et al. 1999; Kumschick et al. 2012; Ricciardi et al. 2013; Simberloff et al. 2013; Ojaveer et al. 2015). The utilisation of conceptual frameworks that classify in a standard way the effects of alien species on ecosystems is essential in the process (Blackburn et al. 2011; Bacher et al. 2018). Katsanevakis et al. (2014a) assessed the impacts of marine alien species on biodiversity and ecosystem services utilising a framework that emphasised the robustness of the reported evidence and

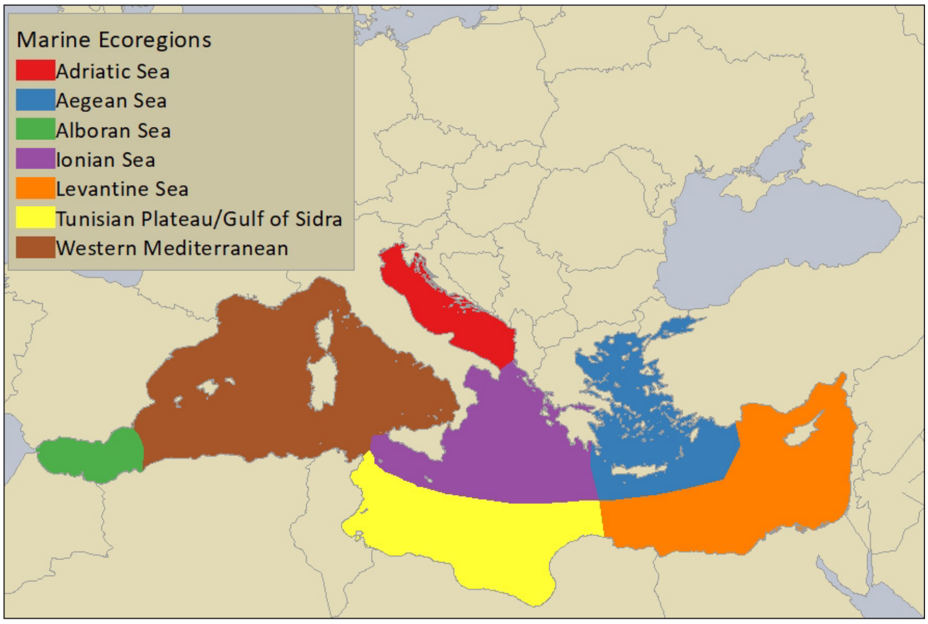


Figure 1. Mediterranean Sea ecoregions (*sensu* Spalding et al. 2007). The present review covered all seven Mediterranean ecoregions.

the ecological mechanisms of negative and positive impacts on both biodiversity and ecosystem services. Blackburn et al. (2014) proposed a classification framework of impact magnitude levels for a series of ecological mechanisms through which alien species impact individuals, populations, and communities. Difficulties that hinder impact assessments, such as a wide range of taxonomic groups, various types of affected habitats, estimation of impact magnitude, and spatial quantification of impacts, can be overcome through the application of such schemes (Kumschick et al. 2015; Katsanevakis et al. 2016; Nentwig et al. 2016; Galanidi et al. 2018).

The Mediterranean Sea is a hotspot of biodiversity with a high level of endemism (Coll et al. 2010). It is divided into seven marine ecoregions (Figure 1), each with a distinct suite of oceanographic and topographic features and relatively homogeneous species composition (Spalding et al. 2007). In addition, the Mediterranean is a hotspot of biological invasions, particularly throughout its eastern part, having the highest number of introduced species than any other sea region of the world (Costello et al. 2021). In the same easternmost sectors, under a rapid warming trend, many thermally-sensitive native populations have collapsed in the past few decades (Yeruham et al. 2015; Rilov 2016; Albano et al. 2021) and in some cases alien species are the only ones that can sustain ecosystem functions. Hence, a shift in conservation strategies from protecting native biodiversity to protecting ecosystem functions (thus also including some alien species as conservation targets) has been recently proposed (Katsanevakis et al. 2020a).

Approximately 1,000 species are estimated to have been introduced in Mediterranean ecoregions (Zenetos et al. 2010, 2012), with more than half having established populations (Galil et al. 2016; Zenetos et al. 2017; Zenetos and Galanidi 2020) and exhibiting an accelerating rate of establishment success during recent years (Zenetos et al. 2022). Biological invasions in the Mediterranean have caused large-scale biogeographic modifications, range shifts of native species, population declines or even local extinctions (Galil 2007; Edelist et al. 2013; Katsanevakis et al. 2014a). Previous assessments of the spatial variation of impacts in the Mediterranean Sea indicated strong spatial heterogeneity, not significantly correlated to alien species richness (Katsanevakis et al. 2016). As the situation changes fast, with many new alien species becoming invasive and expanding rapidly in the last few years (e.g., Dimitriadis et al. 2020; Zenetos and Galanidi 2020), and as new knowledge accumulates, a regular reassessment of impacts is important to adequately inform management measures.

With the purpose to update the current knowledge on invasive alien marine species' impacts on Mediterranean ecosystems, a new systematic literature review was conducted building upon the work of Katsanevakis et al. (2014a). To accomplish this, we compiled and assessed published available information on alien and cryptogenic species impacts to: (i) identify impactful species for biodiversity, ecosystem services, and human health, updating previous knowledge, (ii) assess the magnitude and mechanisms of their impacts, and their variability across Mediterranean Sea ecoregions, and (iii) propose an inventory of the impactful marine alien species of the Mediterranean Sea.

Materials and methods

List of assessed species

A list of targeted taxa for impact assessments was compiled, including marine alien and cryptogenic species flagged as of "High Impact" in the European Alien Species Information Network (EASIN; Katsanevakis et al. 2012) or as high-impact or invasive in recently published reviews (e.g. Otero et al. 2013; Katsanevakis et al. 2014a; Karachle et al. 2017; Galanidi et al. 2018; Zenetos et al. 2018; Peyton et al. 2019; Tsiamis et al. 2020). Based on their expert knowledge, the authors added to the list further invasive species not previously considered by EASIN or the aforementioned reviews. Diatoms, dinoflagellates and other microalgae were not included in the initial species list, based on Gómez (2008, 2019) who argued about the difficulties and uncertainties in defining the native distribution of such species. Tsiamis et al. (2021) have agreed that there are large gaps in knowledge on unicellular plankton species and that more work is needed on marine non-indigenous phytoplankton species in Europe before tagging any phytoplankton species as alien. In total, 103 alien and cryptogenic species belonging to 16 different taxonomic groups were assessed for their impacts on biodiversity, ecosystem services, and human health in the Mediterranean Sea.

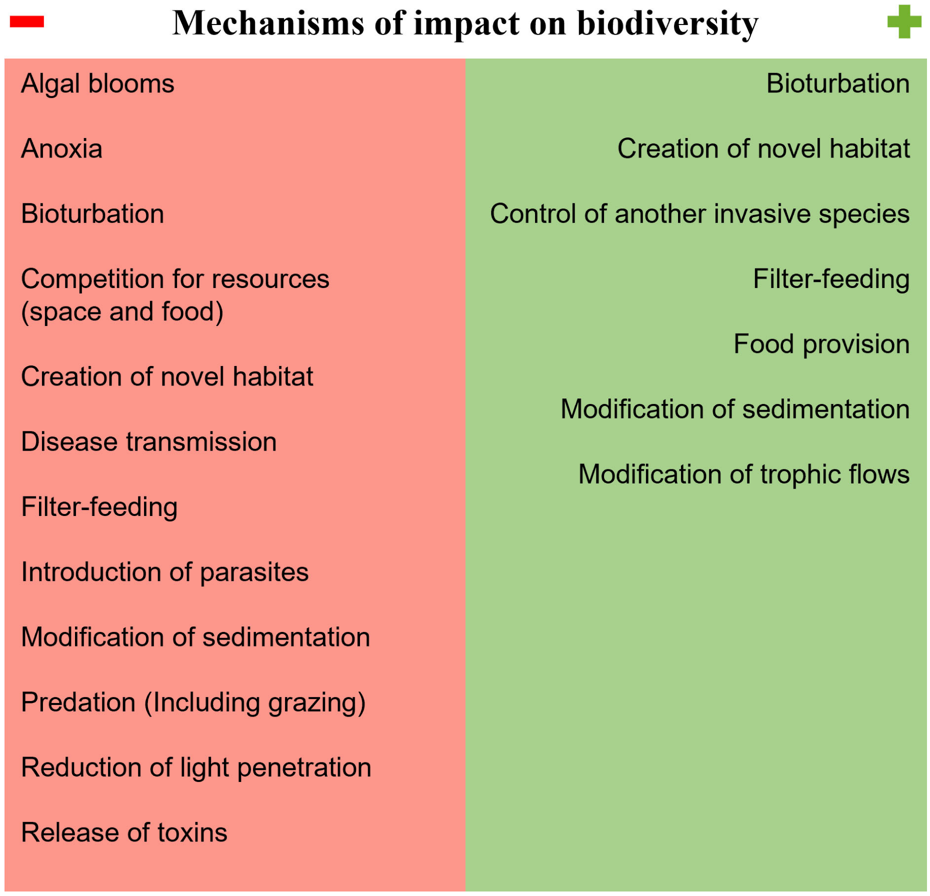
Literature review

A bibliographical review was performed for each targeted species, using the Scholar Google search engine, as it includes grey literature (i.e. technical reports, PhD and MSc theses, and conference proceedings) in addition to peer-reviewed journal articles. Species previously assessed by Katsanevakis et al. (2014a) were updated by searching for more recent publications (between 2013 and March 2021), whereas the bibliographic search was performed without chronological restrictions for those species not previously assessed. For each species, eligible documents were those with the following set of keywords (anywhere in the article): <species name> AND “impact” AND “Mediterranean”. The search provided 62,043 articles (sum of the articles found for each separate species search) but included duplicates as some articles covered more than one target species. Potentially eligible papers to be included in the review were initially screened based on their titles and abstracts; for those that passed the initial screening, the full text was reviewed. At a later stage, taxonomic experts further enriched the list of selected studies with additional documents that had not been found through the literature search. In total, 593 studies that included relevant information on negative or positive impacts of alien and cryptogenic species were retained for the analysis.

From each retained paper, the following information was extracted and coded: DOI/link; short reference; year of publication; Mediterranean ecoregion (according to Spalding et al. 2007; Figure 1); species name and phylum following WoRMS (WoRMS Editorial Board 2021); and reported negative or positive impact on biodiversity, ecosystem services, and human health, type of evidence, mechanism of impact, magnitude of impact and ecosystem engineer type, if relevant (the latter two only for impacts on biodiversity). Only impacts referring to the Mediterranean Sea were included; potential impacts, e.g. based on evidence in non-Mediterranean regions, were not considered.

Framework for impact assessment

Type of evidence refers to the robustness of the methodological approach that was applied to assess the impact. As such, the robustness of the reported evidence was classified into six different types corresponding to three strength of evidence categories (Katsanevakis et al. 2014a, 2016). The six evidence types were: (i) manipulative experiments and (ii) natural experiments (high strength of evidence), (iii) direct observations, (iv) modelling, (v) non–experimental-based correlations (medium strength of evidence), and (vi) expert judgement (low strength of evidence). Manipulative experiments are field or laboratory experiments that include treatments/control and random selection of experimental units. In natural experiments, the experimental units (i.e. controls or impacted areas) are selected by nature



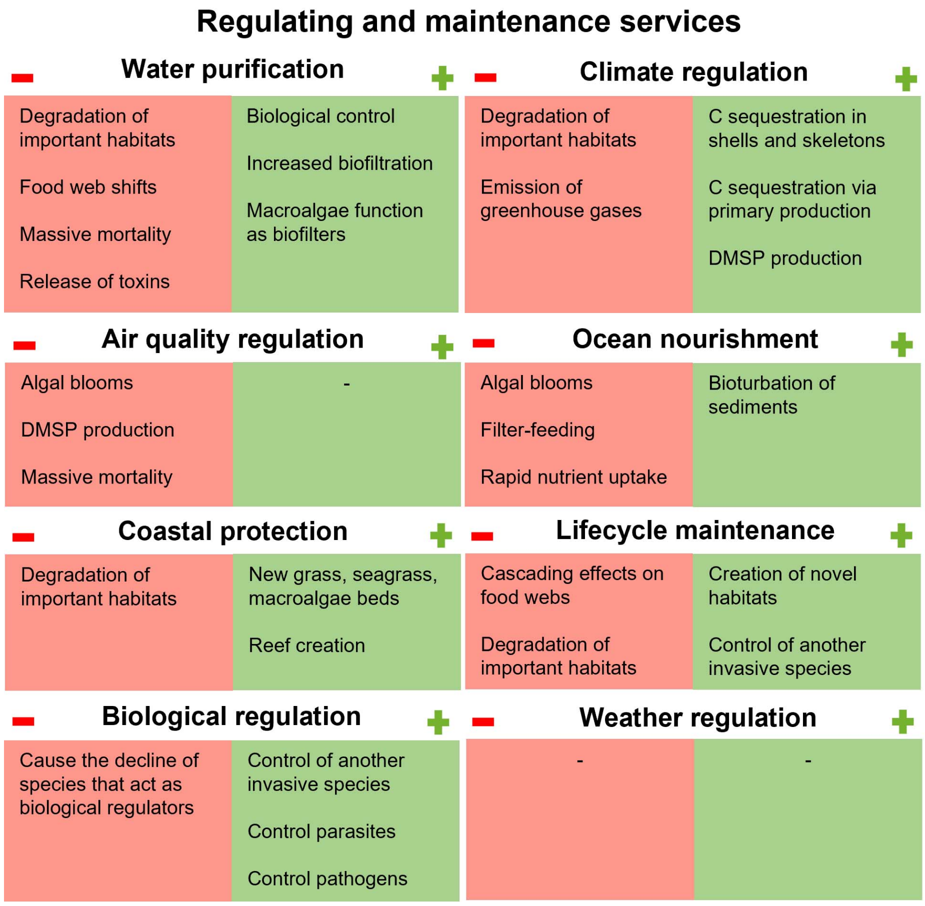
Mechanisms of impact on biodiversity

−	+
Algal blooms	Bioturbation
Anoxia	Creation of novel habitat
Bioturbation	Control of another invasive species
Competition for resources (space and food)	Filter-feeding
Creation of novel habitat	Food provision
Disease transmission	Modification of sedimentation
Filter-feeding	Modification of trophic flows
Introduction of parasites	
Modification of sedimentation	
Predation (Including grazing)	
Reduction of light penetration	
Release of toxins	

Figure 2. Main mechanisms through which marine alien species impact biodiversity (*sensu* Katsanevakis et al. 2014a). Red background refers to negative impacts and green background refers to positive impacts.

(i.e. not randomly). Direct observations are direct raw measurements of the impact about which there is no doubt (e.g. fouling in aquaculture or on fishing gear, new commodities in fish markets). Modelling refers to modelled consequences on biodiversity, ecosystem services and human health derived from ecosystem models. Non-experimental-based correlations refer to significant correlations between the targeted species and the investigated impact, but not based on an experimental design for data collection (e.g. there was a negative correlation between the biomass of an alien predator and the biomass of its native prey). Expert judgement is a qualitative or semi-quantitative assessment that relies on the empirical knowledge of experts based on the species' traits or the reported impact of similar or the same species in a different geographical region.

Each reported impact was linked to the underlying mechanism. Mechanisms of impact were classified according to Katsanevakis et al. (2014a), with some additions (see Figure 2 for biodiversity; Figure 3 for regulating and maintenance ecosystem services; Figure 4 for cultural, provisioning ecosystem services, and human health). The impact magnitude was classified following the five-level classification proposed by Blackburn et al. (2014), i.e. minimal, minor, moderate, major, and massive (Table 1),



Regulating and maintenance services

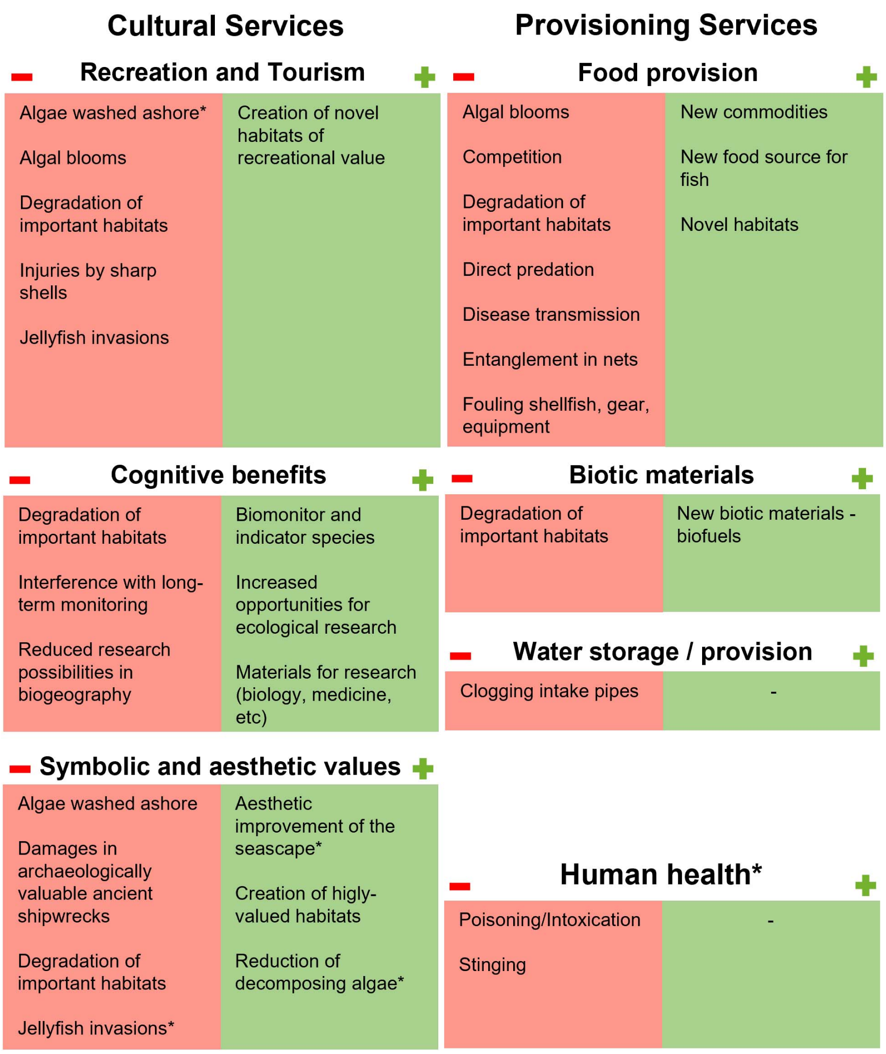
	−	+
Water purification	Degradation of important habitats Food web shifts Massive mortality Release of toxins	Biological control Increased biofiltration Macroalgae function as biofilters
Climate regulation	Degradation of important habitats Emission of greenhouse gases	C sequestration in shells and skeletons C sequestration via primary production DMSP production
Air quality regulation	Algal blooms DMSP production Massive mortality	-
Ocean nourishment	Algal blooms Filter-feeding Rapid nutrient uptake	Bioturbation of sediments
Coastal protection	Degradation of important habitats	New grass, seagrass, macroalgae beds Reef creation
Lifecycle maintenance	Cascading effects on food webs Degradation of important habitats	Creation of novel habitats Control of another invasive species
Biological regulation	Cause the decline of species that act as biological regulators	Control of another invasive species Control parasites Control pathogens
Weather regulation	-	-

Figure 3. Main mechanisms through which marine alien species impact regulating and maintenance ecosystem services (*sensu* Liquete et al. 2013). Red background refers to negative impacts while green background refers to positive impacts. The classification of impacts on ecosystem services was based on Katsanevakis et al. (2014a).

considering also Volery et al. (2020). The selection of marine ecosystem services classification was based on Liquete et al. (2013), who proposed a classification of 14 marine ecosystem services grouped as "provisioning", "regulating and maintenance", and "cultural" (Table 2). Ecosystem engineers were categorised into four different types: structural, chemical, light engineers, and bioturbators (Wallentinus and Nyberg 2007; Berke 2010; Katsanevakis et al. 2014a; Figure 5).

Analyses

In addition to descriptive statistics, contingency table analyses were conducted to quantify the degree of association between selected pairs of variables. The hypothesis of independence between such pairs was tested via chi-square tests. To avoid having cells with < 5 observations, certain categories within each variable were grouped. Hierarchical cluster analysis, using Euclidean distance and square-root transformation of the number of impact records by each mechanism for each species, was performed to determine the similarities of the analysed species in terms of the mechanisms of their impacts for both negative and positive records.



Cultural Services

Recreation and Tourism

−	+
Algae washed ashore* Algal blooms Degradation of important habitats Injuries by sharp shells Jellyfish invasions	Creation of novel habitats of recreational value

Cognitive benefits

−	+
Degradation of important habitats Interference with long-term monitoring Reduced research possibilities in biogeography	Biomonitor and indicator species Increased opportunities for ecological research Materials for research (biology, medicine, etc)

Symbolic and aesthetic values

−	+
Algae washed ashore Damages in archaeologically valuable ancient shipwrecks Degradation of important habitats Jellyfish invasions*	Aesthetic improvement of the seascape* Creation of higly-valued habitats Reduction of decomposing algae*

Provisioning Services

Food provision

−	+
Algal blooms Competition Degradation of important habitats Direct predation Disease transmission Entanglement in nets Fouling shellfish, gear, equipment	New commodities New food source for fish Novel habitats

Biotic materials

−	+
Degradation of important habitats	New biotic materials - biofuels

Water storage / provision

−	+
Clogging intake pipes	-

Human health*

−	+
Poisoning/Intoxication Stinging	-

Figure 4. Main mechanisms through which marine alien species impact provisioning, cultural ecosystem services (*sensu* Liquete et al. 2013) and human health. Red background refers to negative impacts while green background refers to positive impacts. The classification of impacts on ecosystem services was based on Katsanevakis et al. (2014a), with the exception of categories marked with an asterisk (*) that are new.

To test the hypothesis that the magnitude of reported impacts on biodiversity increases with the residence time, i.e. the number of years passed since the first detection of the species in the Mediterranean Sea, we followed two different approaches. In the first approach, a one-way ANOVA was conducted with the maximum reported magnitude of impact on biodiversity for each species as the categorical factor and the residence time as the dependent variable. Levene's test was applied to test homogeneity of variances, and Tukey's honestly significant difference (HSD) procedure for multiple range tests. In the second approach, we created an impact score in which for each species all reports of impacts were summed up in a weighted sum with varying weights depending on the magnitude of impact: massive 4; major 3; moderate 2; minor 1; minimal 0. The relationship between the impact score and the residence time of each species was investigated with a linear regression approach. All analyses were conducted using Statgraphics Centurion XVI.

Table 1. Impact magnitude classification levels with criteria description (adapted from Blackburn et al. 2014, considering also Volery et al. 2020), referring to both negative and positive impacts.

Impact magnitude	Criteria description
Minimal	No effect on fitness of native species; negligible impact on native species due to competition, predation, parasitism, toxicity, bio-fouling, food provision or control of another invasive species; no effects on ecosystem processes and ecosystem functioning; no chemical, physical or structural impact on the ecosystem (not an ecosystem engineer).
Minor	Impact on individual of a native species due to competition, predation, parasitism, toxicity, bio-fouling, food provision, or control of another invasive species without substantial population changes; minor impact on ecosystem processes and ecosystem functioning with no related population changes; any environmental or habitat alterations in chemical, physical or structural characteristics do not result in population changes.
Moderate	Native species population changes due to competition, predation, parasitism, toxicity, bio-fouling, food provision or control of another invasive species but without changes in community composition; or impact on ecosystem processes and ecosystem functioning resulting in population declines/increases but no substantial change in species composition; or ecological engineering, resulting in population declines/increases but no substantial change in community composition.
Major	Changes in community composition through local or global extinction (negative) or re-establishment (positive) of at least one native species, because of competition, predation, parasitism, toxicity, bio-fouling, food provision or control of another invasive species; impact on ecosystem processes and ecosystem functioning resulting in species composition changes; or ecological engineering, resulting in change in community composition. Major magnitude applies when under the hypothetical scenario of the alien species extinction, the induced changes are considered as reversible within 10 years or within 3 generations of the extinct/re-established native taxon/ -a, whichever is longer.
Massive	Same conditions as in "major" magnitude, but changes are considered as irreversible under the hypothetical scenario of the alien species extinction, within 10 years or within 3 generations of the extinct/re-established native taxon/-a.

Results

Impact matrix

The 593 studies on the 103 alien and cryptogenic species resulted in 1,343 records of negative and positive impacts on biodiversity, ecosystem services, and human health (Table 3). A detailed description of impacts for each species is given in the online Supplementary material Appendix 1. Among the analysed taxa, Osteichthyes was the most numerous group (24 species), followed by Mollusca (17 species), and Arthropoda (Crustacea) (14 species), whereas 25 macroalgae were analysed, belonging to Rhodophyta (12 species), Chlorophyta (8 species), and Ochrophyta (5 species). Biodiversity was impacted by 70% of the studied species (72 taxa; Table 3), whereas the remaining ones (30%) showed no reported impacts on biodiversity. Only 3% of the studied species had only positive effects on biodiversity, whereas 27% had only negative ones. In most cases (40%) the studied species impacted biodiversity both negatively and positively.

Among the 72 species impacting biodiversity, 38 represented ecosystem engineers that caused alterations to the studied ecosystem as bioconstructors (structural engineers), regulators of light penetration (light engineers), modifiers of the chemical matrix of the environment (chemical engineers), and bioturbators (Table 3). Most ecosystem engineers were macroalgae (phyla Ochrophyta, Chlorophyta, and Rhodophyta) and Mollusca.

Table 2. The applied marine ecosystem services classification scheme, with a description of each service (*sensu* Liquete et al. 2013).

Ecosystem service	Category	Description
Food provision	Provisioning	Provision of biomass from the marine environment for human consumption. This includes all industrial, artisanal and recreational fishing activities and aquaculture.
Water storage and provision	Provisioning	Provision of water for human consumption and other uses. In the marine environment, these uses are mainly associated with coastal lakes, deltaic aquifers, desalination plants, industrial cooling processes, and coastal aquaculture in ponds and raceways.
Biotic materials and biofuels	Provisioning	Provision of biomass or biotic elements for non-food purposes, including medicinal (e.g. drugs, cosmetics), ornamental (e.g. corals, shells) and other commercial or industrial purposes, such as fishmeal, algal or plant fertilisers, and biomass to produce energy or biogas from decomposing material.
Water purification	Regulating and maintenance	Biochemical and physicochemical processes involved in the removal of wastes and pollutants from the aquatic environment, including treatment of human waste, dilution, sedimentation, trapping or sequestration (e.g. of pesticide residues or industrial pollution); bioremediation; oxygenation of “dead zones”, filtration and absorption; remineralisation; and decomposition.
Air quality regulation	Regulating and maintenance	Regulation of air pollutant concentrations in the lower atmosphere.
Coastal protection	Regulating and maintenance	Natural protection of the coastal zone against inundation and erosion from waves, storms or sea level rise by biogenic and geologic structures that disrupt water movement and thus stabilise sediments or create protective buffer zones.
Climate regulation	Regulating and maintenance	The ocean acts as a sink for greenhouse and climate active gasses, as inorganic carbon is dissolved into the seawater and used by marine organisms, a percentage of which is sequestered; perennial large algae and higher plants can store carbon for longer periods.
Weather regulation	Regulating and maintenance	Influence on the local weather conditions, e.g. the influence of coastal vegetation and wetlands on air moisture and, eventually, on the saturation point and cloud formation.
Ocean nourishment	Regulating and maintenance	Natural cycling processes leading to the availability of nutrients in seawater for the production of organic matter.
Lifecycle maintenance	Regulating and maintenance	The biological and physical support to facilitate the healthy and diverse reproduction of species; this mainly refers to the maintenance of key habitats that act as nurseries, spawning areas or migratory routes.
Biological regulation	Regulating and maintenance	Biological control of pests. The control of pathogens especially in aquaculture installations, the role of cleaner fish in reefs, biological control on the spread of vector borne human diseases, and the control of invasive species.
Symbolic and aesthetic values	Cultural	This is about the exaltation of senses and emotions by seascapes, habitats or species, and values put on coastal natural and cultural sites, and on the existence and beauty of charismatic habitats and species such as corals or marine mammals.
Recreation and tourism	Cultural	Opportunities that the marine environment provides for relaxation and entertainment, including coastal activities such as bathing, sunbathing, snorkelling, SCUBA diving, and offshore activities such as sailing, recreational fishing, and whale watching.
Cognitive effects	Cultural	Inspiration for arts and applications (e.g. architectural designs inspired by marine shells, medical applications replicating marine organic compounds), material for research and education (e.g. as test organisms for biological experiments), information and awareness (e.g. respect for nature through the observation of marine wild life).

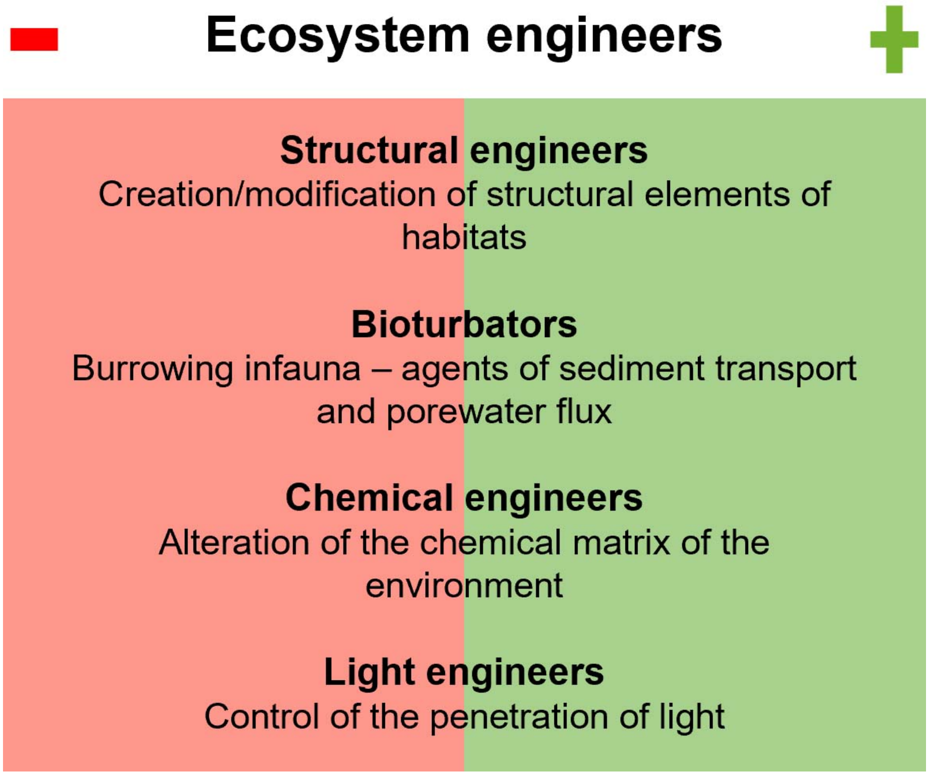


Figure 5. Ecosystem engineer types with impacts on biodiversity (both negative and positive).

Food provision (commercial and recreational fishing, aquaculture) was the most impacted ecosystem service, with 33 species causing negative impacts, 18 positive impacts, and 14 both (Table 3). Osteichthyes were the taxonomic group including the highest number of species with an impact on food provision (19 species). All impacts caused by macroalgae (in total 15 species) on this service were negative. The cultural ecosystem service of "cognitive effects" had the second-highest number of impactful species, with most of the studied taxa affecting this service positively, as they constituted model species for biomonitoring or *in vitro* research studies. Among regulating and maintenance services, "life-cycle maintenance" and "climate regulation" were affected by the highest number of species. Human health impacts were all negative, caused by 9 species.

Impacts on biodiversity

More negative than positive impacts on biodiversity were reported, with 468 records (78%) against 129 (22%) (Figure 6A). *Caulerpa cylindracea* was the invasive species for which most negative impacts on biodiversity were reported, with 53 cases. This chlorophyte of Australian origin thrives in a variety of habitats, depths and environmental conditions, and negatively affects species and communities in multiple ways (see Appendix 1). The species is widespread in the Mediterranean and so are its effects on biodiversity. *Womersleyella setacea* and *Lophocladia lallemandii* followed in terms of negative impact records. These invasive rhodophytes form dense

Table 3. Impact Matrix: Negative (red) and positive (green) impacts of marine alien and cryptogenic species on biodiversity and ecosystem services of the Mediterranean. Colour indicates strength of evidence (vivid colours for high strength of evidence, medium for medium strength, pale colours for low strength). For species without reported impacts or minimal impacts grey cells are depicted for biodiversity and blank cells for ecosystem services and human health. Type of evidence is indicated for each impact: Manipulative Experiments, E; Natural Experiments, N; Direct Observations of impact, O; Modelling, M; non-experimental-based Correlations, C; Expert Judgement, J. (Cr): Cryptogenic species.

	Impact on biodiversity			Impact on marine ecosystem services and human health														
				Provisioning			Regulating and maintenance								Cultural			Health
Alien Species	Minimal / No impact	Impact on species / communities	Ecosystem engineer	Food provision	Water Storage and provision	Biotic materials and biofuels	Water purification	Air quality regulation	Coastal protection	Climate regulation	Weather regulation	Ocean nourishment	Lifecycle maintenance	Biological regulation	Symbolic and aesthetic values	Recreation and tourism	Cognitive benefits	Human health
Cercozoa																		
Haplosporidium pinnae (Cr)		NOJ																
Foraminifera																		
Amphistegina lobifera		CJ J	O						J	J							NJ	
Ochrophyta																		
Chrysonephos lewisii		O	O												O	O		
Rugulopteryx okamurae		NOCJ	NO N	O					O				NO		O	O	O	
Sargassum muticum		J	OCJ O	O	J	J	J		J				J J		O	O	J EJ	
Stypopodium schimperi		OJ	OJ O									J			O	OJ	EJ	
Undaria pinnatifida		J	O O	O			J					J				O	EJ	
Chlorophyta																		
Caulerpa cylindracea		ENOMCJ	NOCJ ENOJ	J		J			EJ			J	ENOMJ EJ		J	J	J EOCJ	
Caulerpa taxifolia		ENOJ	ENOJ NO	OJ		J			J EJ				NJ		J	J	J J	
Caulerpa taxifolia var. *distichophylla*		EJ	N N	O									J					
Cladophora patentiramea															O	O		
Codium arabicum		J													O	O		
Codium fragile subsp. *fragile*		OJ O	OJ EO	O		J		J		J			J		O	O	J C	
Codium parvulum		J		O											O	O		
Halimeda incrassata		N	N N															
Rhodophyta																		
Acrothamnion preissii		ENOCJ	OJ O	O									J		J	J	J	
Agarophyton vermiculophyllum		CJ	NOJ NO	O		J							J		O O	O	J CJ	
Antithamnion nipponicum		J		O														
Asparagopsis armata		EJ O	OCJ OC	O								J			J	J	J EJ	
Asparagopsis taxiformis		EOCJ	N									J	J				EJ	
Bonnemaisonia hamifera																		
Galaxaura rugosa		J													O	O		
Ganonema farinosum (Cr)																		
Grateloupia turuturu		J	OJ O	O														
Lophocladia lallemandii		ENOCJ	NOCJ NO	J		J			J J			J	J		OJ	J	J	
Polysiphonia morrowii																		
Womersleyella setacea		ENOCJ	NOC OC	OJ		J	J		J J			J	ENOJ		J	J	J	
Tracheophyta																		
Halophila stipulacea		C O	O OC	J			J		J	NJ		J	J				C	
Porifera																		
Paraleucilla magna		EJ		O														
Cnidaria																		
Macrorhynchia philippina																		OJ
Oculina patagonica (Cr)		OCJ	O O	J		J							J		J	J	J E	
Rhopilema nomadica		OJ	E	O	O										O	OCJ	CJ	OJ
Ctenophora																		
Mnemiopsis leidyi		ENC J		O														

Table 3. (continued).

Bryozoa																		
Amathia verticillata (Cr)		E	O O	O														
Tricellaria inopinata		J		OJ														
Mollusca																		
Anadara kagoshimensis		J	OJ OJ	J						J		J J						
Anadara transversa		ECJ	OJ OJ	EOJ						J		J J						
Arcuatula senhousia		EOCJ	EOCJ EOCJ	OJ			J			O J		EJ						
Brachidontes pharaonis		ECJ ECJ	NOCJ OCJ		O		J			J		J	O					
Bursatella leachii (Cr)				O													E	
Chama pacifica		J	OJ OJ			O	J			J		J	J				CJ	
Conomurex persicus		J	C	O						J							EC	
Crepidula fornicata																		
Dendostrea cf. *folium*																		
Fulvia fragilis		J								J							N	
Magallana/Crassostrea species		EOJ	OJ OCJ	O			EJ ECJ		J	J		J	J J		J J	J J	J	
Mya arenaria																		
Petricolaria pholadiformis																		
Pinctada radiata		O	O O	O O			J			J		J	J				EC	
Rapana venosa				O														
Ruditapes philippinarum		CJ	ENOCJ EOCJ	O			MJ			M MJ		J					ENJ	
Spondylus spinosus		CJ	OJ OJ	O		O	J			J		J	J				NC	
Annelida: Polychaeta																		
Ficopomatus enigmaticus			O OJ														EN	
Hydroides elegans		EOJ	EO EO	O												O		
Arthropoda: Crustacea																		
Acartia (Acanthacartia) tonsa (Cr)		C															N	
Callinectes sapidus		EOCJ		OJ O													CJ	
Dyspanopeus sayi		E																
Erugosquilla massavensis		CJ		OJ O													E	
Matuta victor																		
Metapenaeus monoceros		MCJ M		CJ O													EC	
Metapenaeus stebbingi		O		O													E	
Paracerceis sculpta		J																
Penaeus aztecus				O														
Penaeus pulchricaudatus		OMJ M		J O													EC	
Penaeus semisulcatus		OM M		O													NCJ	
Percnon gibbesi (Cr)		O																
Portunus segnis		OJ		OC O													EC	
Rhithropanopeus harrisii																		
Echinodermata																		
Diadema setosum																		J
Synaptula reciprocans																		
Chordata: Ascidiacea																		
Botrylloides violaceus																		
Botrylloides diegensis																		
Ciona robusta				O													EC	
Clavelina oblonga				O														
Didemnum vexillum		O		O														
Herdmania momus																	CJ	
Microcosmus squamiger		OC C		O														
Polyandrocarpa zorritensis							E							E				
Styela plicata		E		OJ			E							E			ENC	
Chordata: Osteichthyes																		
Alepes djedaba				O														
Apogonichthyoides pharaonis																		
Atherinomorus forskalii		OJ		O														
Decapterus russelli				O														
Dussumieria elopsoides				O														
Etrumeus golanii				O														
Fistularia commersonii		NOM M		MJ OM														

Table 3. (continued).

Herklotsichthys punctatus	▨						O														
Lagocephalus sceleratus		OMJ				OMJ															OJ
Nemipterus randalli		CJ				J	O													NC	
Parexocoetus mento	▨																				
Parupeneus forsskali		C				C	O														
Pempheris rhomboidea		OMJ		J	J																
Plotosus lineatus		CJ				O															OJ
Pterois miles		O																J			OJ
Sargocentron rubrum		OC		J	J		O														
Saurida lessepsianus		MJ				J	O													N	
Scomberomorus commerson	▨						O														
Siganus luridus		ENMCJ	MJ	J	J	J	O		J	J			J			EJ		J	J	J	OJ
Siganus rivulatus		ENMCJ	MJ	J	J	J	O		J	J			J			EJ		J	J	J	J
Sphyraena chrysotaenia		C					O														
Torquigener flavimaculosus	▨																				J
Upeneus moluccensis		NC				C	O														
Upeneus pori		NC				C	O														

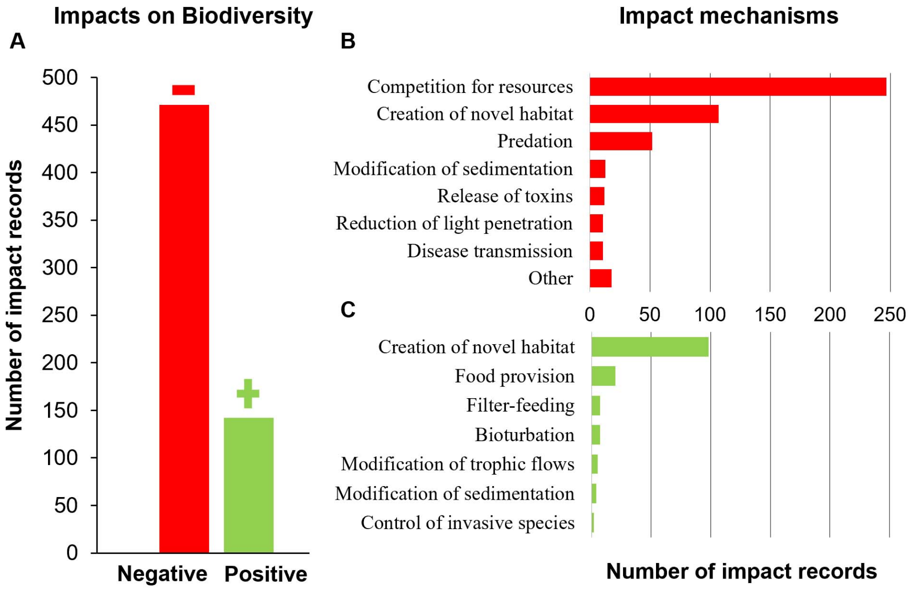


Figure 6. A) Number of impact records that resulted from the review analysis to impact biodiversity. Number of impact records by mechanism through which alien species impacted biodiversity B) negatively or/ and C) positively.

algal turfs that overgrow other species and alter ecologically important habitats, with negative implications in benthic communities. Although widespread in the Mediterranean, their effects were mainly reported from the western Mediterranean ecoregion. Apart from macroalgae, the mollusc *Brachidontes pharaonis* and the fishes *Siganus luridus* and *Siganus rivulatus* were the species with most negative impact records among the studied taxa. The Erythrean *B. pharaonis* is an old invader of the Mediterranean, with a wide range of distribution, but it did not exhibit an alarming invasive behaviour until the late 1990s. Subsequently, its populations exploded in many eastern Mediterranean localities, becoming dominant in shallow rocky reef platforms with extremely high densities, outcompeting native species and shaping community composition (see Appendix 1). The

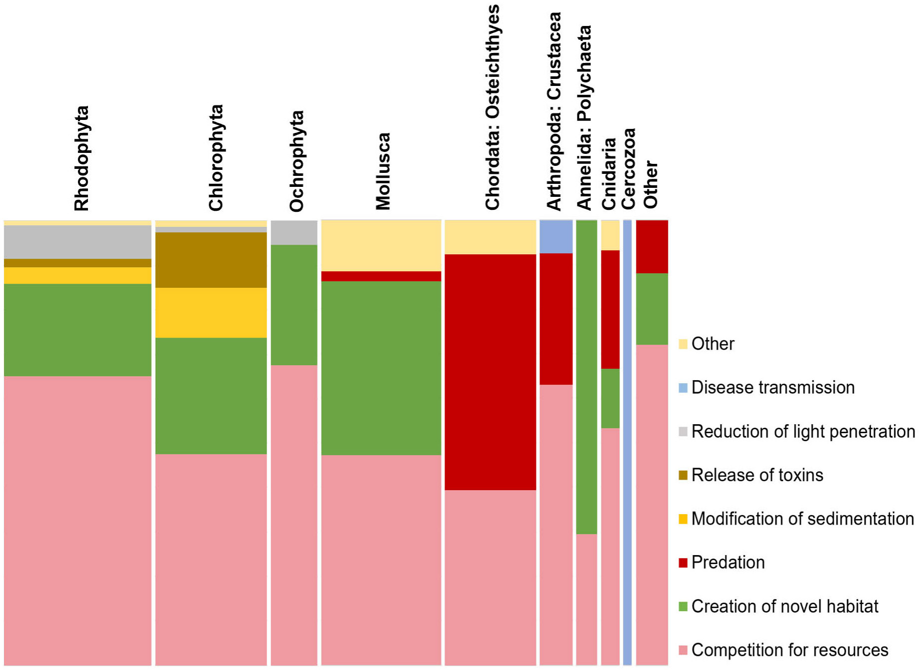


Figure 7. Mosaic chart of mechanisms of negative impacts on biodiversity for the studied different phyla.

Lessepsian invaders *Siganus* spp. dominate fish communities in many parts of the eastern Mediterranean and have caused detrimental losses on Mediterranean macroalgal communities through their herbivory (see Appendix 1 for more information).

Caulerpa cylindracea was also the species most reported for its positive impacts, with 12 records, followed by *B. pharaonis* and the serpulid *Ficopomatus enigmaticus*. Although the dense populations of *C. cylindracea* constitute a nuisance for the majority of native biota, it can also facilitate several other species, from seagrasses to invertebrates. *Brachidontes pharaonis* has acquired a functional role in Mediterranean ecosystems and contributes significantly as a structural ecosystem engineer, as a filter-feeder that reduces turbidity and increases light penetration, and as a food source for native biota. *Ficopomatus enigmaticus* is a reef-building structural engineer that provides novel habitat for many benthic taxa.

Negative impacts were caused by a variety of mechanisms (Figure 6B, C; Figure 7), significantly differing in frequency by taxonomic group (chi-square test; keeping the three most frequent mechanisms and grouping all others; keeping the six most frequent taxonomic groups and grouping all others; $p < 0.001$). Competition for resources was the most reported mechanism of negative impacts with almost 250 records, followed by the creation of novel habitat, and predation (Figure 6B). This was the case for most studied phyla except Chordata (Osteichthyes), Annelida (Polychaeta), and Cercozoa (Figure 7). Osteichthyes caused negative impacts mostly by preying on native biota. *Hydroides elegans* and *F. enigmaticus*, the two studied alien polychaetes, mainly affected other species through the creation of novel

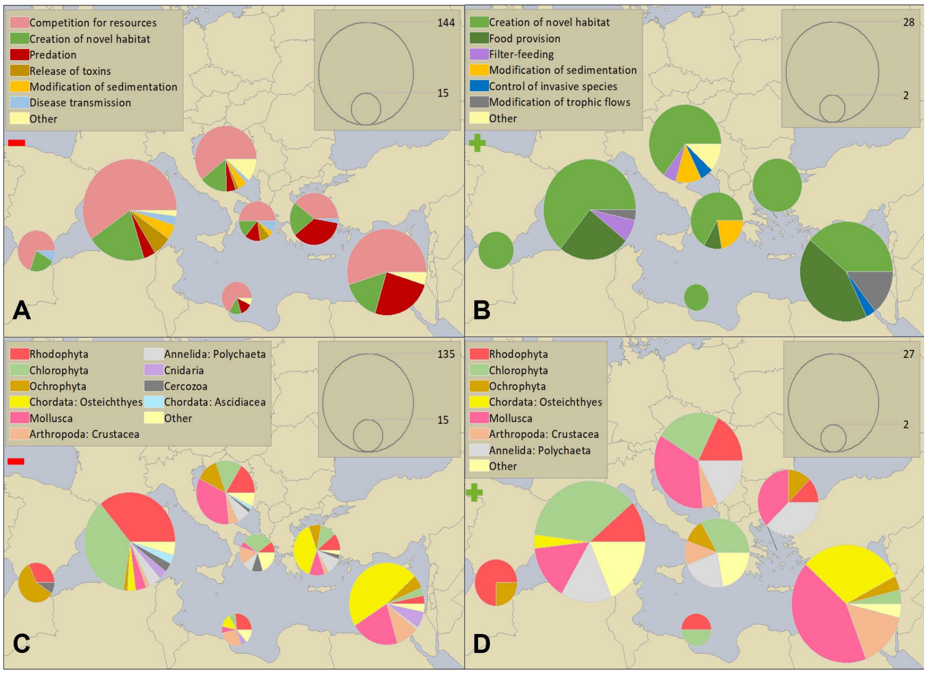


Figure 8. Geographical variation of the A) negative and B) positive mechanisms of impact on biodiversity by Mediterranean ecoregion and of analyzed alien phyla with C) negative and D) positive impacts on biodiversity per Mediterranean ecoregion. The size of the pie charts reflects the number of reported cases (the inset indicates the minimum and maximum sizes).

habitat. This was also an important mechanism of negative impacts for macroalgae such as *L. lallemandii*, *C. cylindracea*, *Caulerpa taxifolia* and molluscs such as *B. pharaonis*, and *Spondylus spinosus*. *Haplosporidium pinnae*, the sole representative of Cercozoa, has been associated with the disease that has caused the extinction of the endemic bivalve *Pinna nobilis* from almost the entire Mediterranean Sea, except for a small number of refugia. The creation of novel habitat was the most common mechanism of positive impacts on biodiversity accounting for 65% of the reported positive cases (Figure 6C). Species such as *F. enigmaticus*, *S. spinosus*, the bivalves of the genus *Magallana/Crassostrea* (see the notes in the Appendix 1 for the taxonomic status of the genus), and the rhodophyte *Asparagopsis armata* create novel habitats that support a variety of species.

Analysis of impacts by ecoregion revealed that interspecific competition is the most important mechanism generating negative impacts on biodiversity in all Mediterranean ecoregions (Figure 8A); nevertheless, the frequency of the various mechanisms significantly differed by ecoregion (chi-square test; keeping the three most frequent mechanisms—competition, creation of novel habitat, predation—and grouping all others; $p < 0.001$). The creation of novel habitat was the second most reported negative impact mechanism in western and central Mediterranean ecoregions. On the contrary, predation was the second most impactful mechanism in the eastern Mediterranean ecoregions (Figure 8A). The frequency of the mechanisms of reported positive impacts also differed by ecoregion (chi-square test; keeping the two most frequent mechanisms and grouping all others; excluding ecoregions with < 5 records; p = 0.008). Structural ecosystem engineers that create novel habitats were the main contributors to positive impacts in all Mediterranean ecoregions, except for the Levantine Sea where positive impacts of food provision slightly exceeded the creation of novel habitat (Figure 8B). Food provision to native biodiversity was also important in the western Mediterranean and the Ionian Sea (Figure 8B).

There was significant variation in the taxonomic composition of the species that caused negative impacts on biodiversity among ecoregions (chi-square test; keeping the five most reported phyla and grouping all others; p < 0.001) (Figure 8C). In the western Mediterranean, the most reported negative impacts were caused by invasive Rhodophyta and Chlorophyta, whereas in the Levantine and the Aegean Sea by Osteichthyes, and in the Adriatic Sea by Mollusca (Figure 8C). *Caulerpa cylindracea*, *L. lallemandii*, *W. setacea*, *C. taxifolia*, and *Acrothamnion preissii* were among the chlorophytes and rhodophytes with negative effects in the western Mediterranean whereas, in the Levantine Sea, *B. pharaonis*, *S. luridus* and *S. rivulatus* were the species with the most recorded impacts. *Siganus luridus* was also the species that accounted for most of the recorded negative impacts in the Aegean Sea. Negative impacts caused by Crustacea had an important share of total impacts in the Tunisian plateau/Gulf of Sidra, the Levantine, and the Ionian Sea, but they had little relevance in the western Mediterranean and the Alboran Sea (Figure 8C). The Alboran Sea has been plagued by the negative impacts of the brown alga *Rugulopteryx okamurae*, a recent invader that has caused detrimental effects on local ecosystems (see Appendix 1 for more information).

There was also significant variation in the taxonomic composition of the species that caused positive impacts on biodiversity among ecoregions (chi-square test; keeping only the three ecoregions with the highest number of records and the four mostly reported phyla, grouping all others; p = 0.01). Macroalgae constituted the bulk of positive impact records for the western Mediterranean, the Alboran Sea, and the Tunisian plateau/Gulf of Sidra and had an important share in total reported positive impacts from the Adriatic and the Ionian Sea (Figure 8D). Mollusca ranked first in terms of reported positive impacts in the Levantine and the Adriatic Sea and had an important share in the western Mediterranean and the Aegean Sea. As creators of novel habitats, Polychaeta contributed to positive impacts in the Aegean, Ionian, Adriatic Sea, and western Mediterranean (Figure 8D). Furthermore, some Osteichthyes were reported to have positive impacts on biodiversity, because of their role in the novel trophic webs, but only in the Levantine Sea.

“Major” was the most reported impact magnitude category for both negative and positive impact records (Figure 9). Nevertheless, the frequency of impact magnitudes substantially differed between negative and positive impacts, with “major” impacts having a significantly higher frequency in

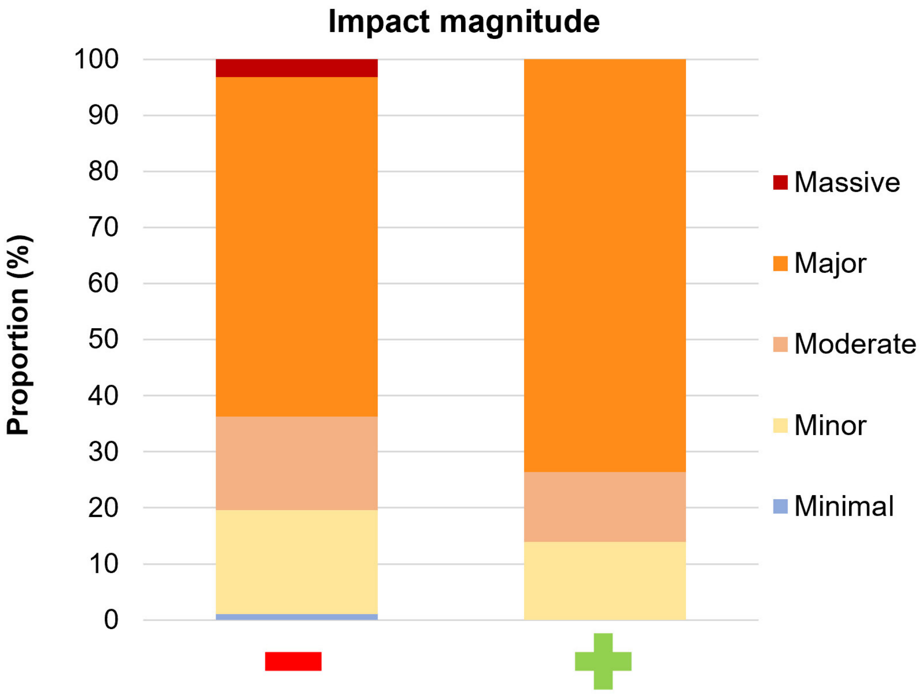


Figure 9. Proportion of impact magnitude categories of negative (left column) and positive (right column) impacts on biodiversity.

positive than negative impacts (chi-square test; excluding minimal and massive magnitude categories due to their low frequencies; p = 0.011). Overall, 61% of negative impacts and 74% of positive impacts were classified as major; no positive impacts of massive magnitude were reported. The frequency of the categories of magnitude of impact significantly differed among taxonomic groups (chi-square test; disregarding minimal and massive magnitude categories due to their low frequencies, combining phyla with a small number of records together; p < 0.001). Major negative impacts were the primary magnitude category recorded for Rhodophyta, Chlorophyta, Ochrophyta, Mollusca, Polychaeta, Cnidaria, Foraminifera, Ascidiacea, and Bryozoa (Figure 10A). Massive negative impacts were only recorded for Osteichthyes (*Siganus* spp.), Cercozoa (*H. pinnae*), and Ochrophyta (*R. okamurae*) (Figure 10A). Moderate and minor impacts were the most reported for Crustacea. Although the number of records of positive impacts was lower than that of negative impacts, they followed a similar pattern regarding impact magnitude (Figure 10B), with significant differences among taxonomic groups (chi-square test; combining phyla with a small number of records together; p = 0.011).

There was no evidence that the magnitude of impact increases with residence time. The average residence time of introduced species did not differ by the maximum reported magnitude of negative (ANOVA; p = 0.947) or positive (ANOVA; p = 0.300) impacts. The slope of the linear regression between the residence time of introduced species and the negative impact score did not differ significantly from zero (p = 0.985), and the intercept (i.e. the average score ± S.E.) was 11.3 ± 3.3 (Figure 11). The slope remained

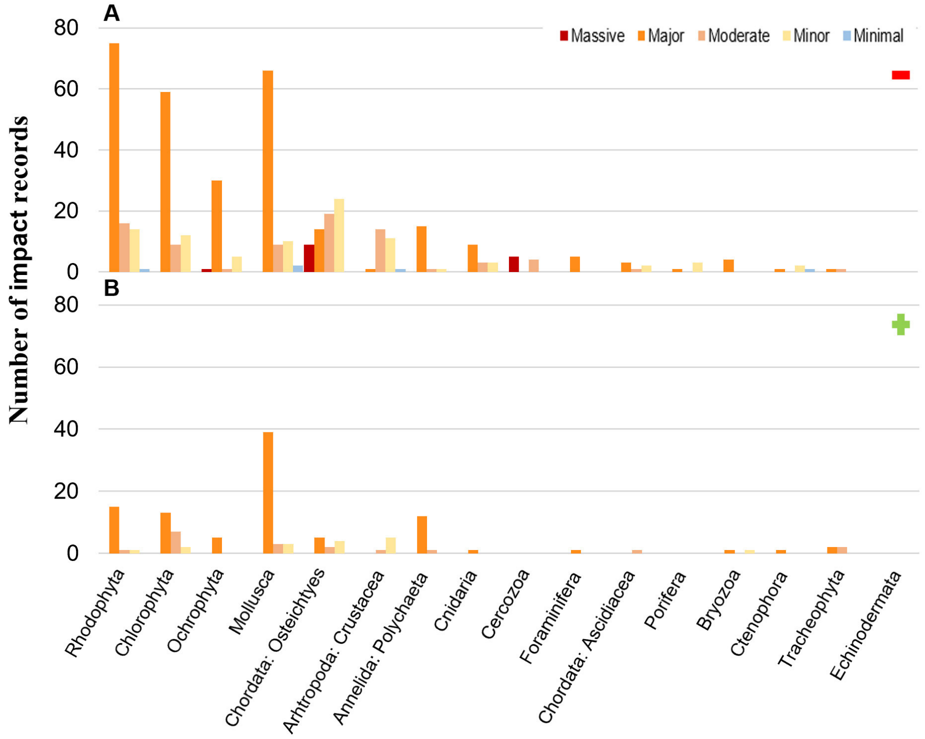


Figure 10. Impact magnitude of A) negative and B) positive impacts on biodiversity per phylum of alien species analysed..

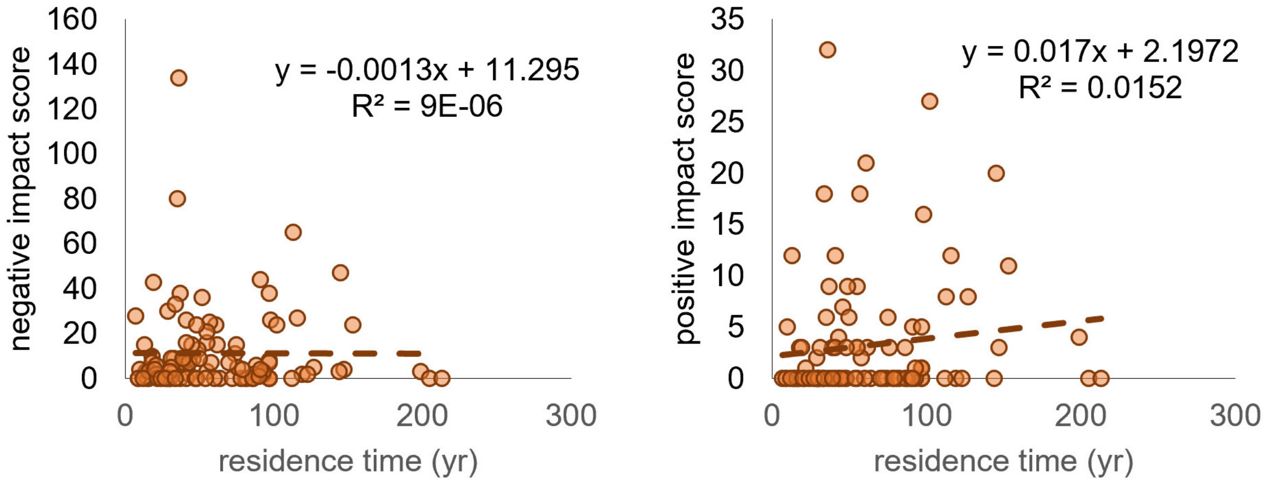


Figure 11. Regressions of negative (left) or positive (right) impact scores in relation to residence time (years since first detection) for each of the assessed species.

statistically not different from zero even when three influential points (with leverage values greater than five times that of an average data point) were removed (p = 0.529). Similarly, the slope of the linear regression between the residence time of introduced species and the positive impact score did not significantly differ from zero (p = 0.215), and the intercept (i.e. the average score ± S.E.) was 2.2 ± 1.0 (Figure 11). The slope remained statistically not different from zero even when three influential points (with leverage values greater than five times that of an average data point) were removed (p = 0.057).

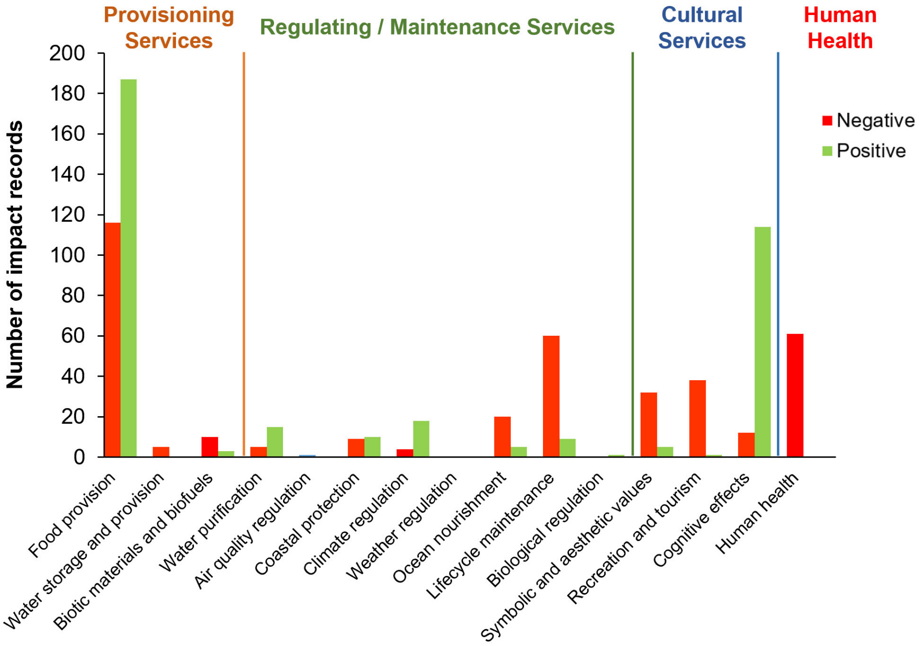


Figure 12. Overview of negative and positive impacts on ecosystem services and human health.

Impacts on ecosystem services

Overall, 685 negative and positive impact records were found to affect provisioning, regulating/maintenance, and cultural ecosystem services, with 312 negative and 373 positive records in total, whereas for human health 61 negative and no positive impacts were recorded. Most impact records on provisioning services were recorded for food provision, with 116 negative and 188 positive records (Figure 12). Negative impacts prevailed over positive for regulating/maintenance services. Still, for several regulating and maintenance services (climate regulation, water purification, coastal protection, and biological regulation) more positive than negative impacts were reported (Figure 12). Among regulating/maintenance services, lifecycle maintenance was the one with the highest number of recorded negative impacts. No impact records were found for weather regulation. For the cultural services "aesthetic values" and "recreation and tourism", 70 negative and only 6 positive impact records were reported. On the other hand, for "cognitive effects" records, positive impacts prevailed by 114 records against only 12 cases of negative impacts.

The frequency of the mechanisms of reported negative impacts on provisioning ecosystem services significantly differed by ecoregion (chi-square test; keeping the four most frequent mechanisms and excluding the Alboran Sea; $p < 0.001$). Fouling shellfish, gear, and equipment of aquaculture facilities was the primary mechanism of negative impacts on provisioning services in the Adriatic Sea, the Ionian Sea, and the western Mediterranean (Figure 13A). Entanglement in nets was the most important mechanism in the Levantine and the Alboran Sea, with a considerable contribution to negative impacts on provisioning services throughout the Mediterranean

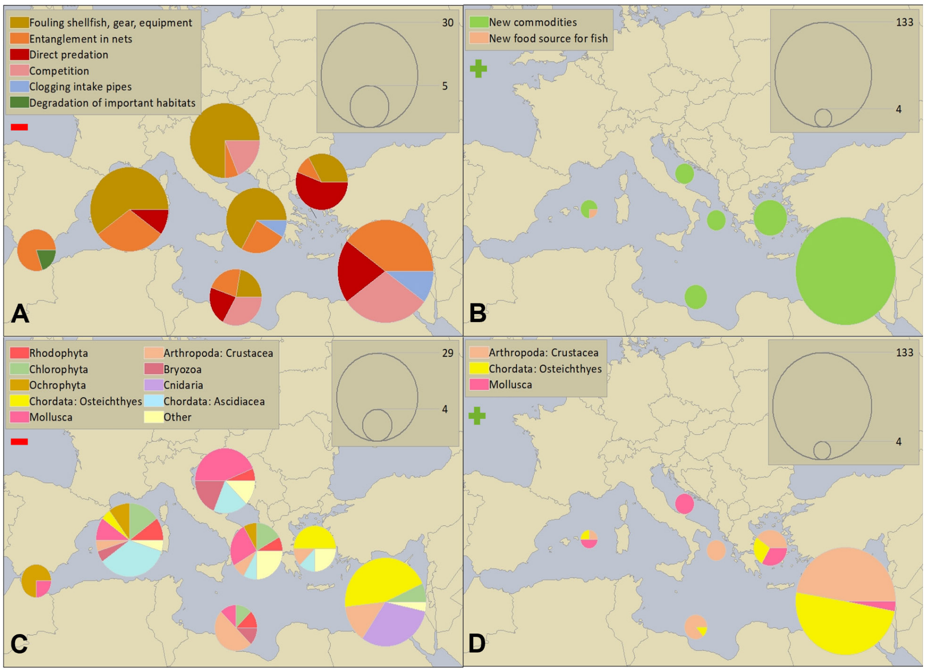


Figure 13. Geographical variation of the A) negative and B) positive mechanisms of impact on provisioning ecosystem services by Mediterranean ecoregion and of analyzed alien species phyla with C) negative and D) positive impacts on provisioning services per Mediterranean ecoregion. The size of the pie charts reflects the number of reported cases (the inset indicates the minimum and maximum sizes).

(Figure 13A). Predation was also a primary mechanism of negative impacts, especially in the eastern Mediterranean. From the analysis of positive impacts by ecoregion on provisioning services (Figure 13B), it became obvious that the Levantine Sea was the main beneficiary, due to new commodities for local fisheries. Most positive impacts were recorded in this ecoregion and significantly declined westwards (Figure 13B). Among all mechanisms positively impacting provisioning services across Mediterranean ecoregions, "new commodities" were by far the most important.

The taxonomic synthesis of the species that negatively impacted provisioning services differed significantly among ecoregions (chi-square test; keeping the four most frequent phyla and merging all the others; excluding the Alboran Sea; $p < 0.001$) (Figure 13C). Ascidians were the major group of negative impacts in the western Mediterranean, with an important contribution also in the Adriatic Sea (Figure 13C). This is due to species such as the alien ascidians *Styela plicata* and *Clavelina oblonga* that commonly foul farmed shellfish and aquaculture equipment. Molluscs (*Pinctada radiata*), bryozoans (*Tricellaria inopinata*), and sponges (*Paraleucilla magna*) also foul aquaculture facilities, introducing negative effects on production. Cnidaria and Osteichthyes were the main groups that impacted provisioning services in the Levantine Sea (Figure 13C). The invasive jellyfish *Rhopilema nomadica* formed massive swarms that became a nuisance for the local fisheries due to entanglement in nets and for water supply for local power plants and desalination facilities due to blocking of intake pipes. The fish *Lagocephalus sceleratus* was also a major pest for fisheries in the Levantine and the Aegean Sea due to its predation on the catch and the damage caused to fishing gear. Alien crustacean species were also reported to negatively impact the provision of food across multiple ecoregions (Figure 13C). The alien crabs *Callinectes sapidus* and *Portunus segnis* interfered with local fisheries in multiple Mediterranean ecoregions by preying on the catches and by getting entangled in nets. Alien shrimps such as *Metapenaeus monoceros* and *Penaeus pulchricaudatus* have been associated with population declines of the commercially important native shrimp *Penaeus kerathurus* (see Appendix 1).

The main contributors of positive impacts on food provision were alien Osteichthyes and Crustacea, with positive impact records substantially increasing eastwards (Figure 13D). Several alien fish such as *Nemipterus randalli*, *Scomberomorus commerson*, *Sphyraena chrysotaenia*, *Saurida lessepsianus*, *Upeneus* spp., *Siganus* spp. and crustaceans such as *P. pulchricaudatus*, and *Metapenaeus* spp. are marketed in many Mediterranean countries. *Callinectes sapidus* is collected and sold in the northern Adriatic and Ebro Delta (Spain) where it is an appreciated shellfish. Mollusc species, such as those of the genus *Magallana/Crassostrea*, *Ruditapes philippinarum*, and *Conomurex persicus* have historically contributed to food provision as new commodities in various Mediterranean ecoregions.

Degradation of habitats was the primary mechanism of negative impacts on regulating services, mainly recorded in the western Mediterranean and affecting life-cycle maintenance (Figure 14A). *Posidonia oceanica* meadows and coralligenous communities are marine habitats with a fundamental role in the functioning of Mediterranean ecosystems and the conservation of marine life. Invasive Rhodophyta such as *W. setacea*, *A. preissii*, and *L. lallemandii* have the potential to degrade such ecosystems (Figure 14C) through the formation of dense algal turfs that epiphytise *Posidonia* meadows and homogenise the diversity and complexity of coralligenous communities, degrading their state and negatively affecting the life they support (see Appendix 1). Such habitats are also vulnerable to the invasion by *C. cylindracea* that negatively affects many keystone species. Furthermore, the recent Ochrophyta invader *R. okamurae* can displace native species, monopolise shallow communities, and even cause community shifts in coralligenous communities.

Positive mechanisms of impact on “regulating and maintenance” ecosystem services were much less reported (Figure 14B). Carbon sequestration overall accounted for most positive impacts either through the formation of shells or via primary production. Such positive contributions to climate change were attributed to Mollusca, Foraminifera, and Tracheophyta (Figure 14D). Shell-forming organisms such as the foraminiferan *Amphistegina*

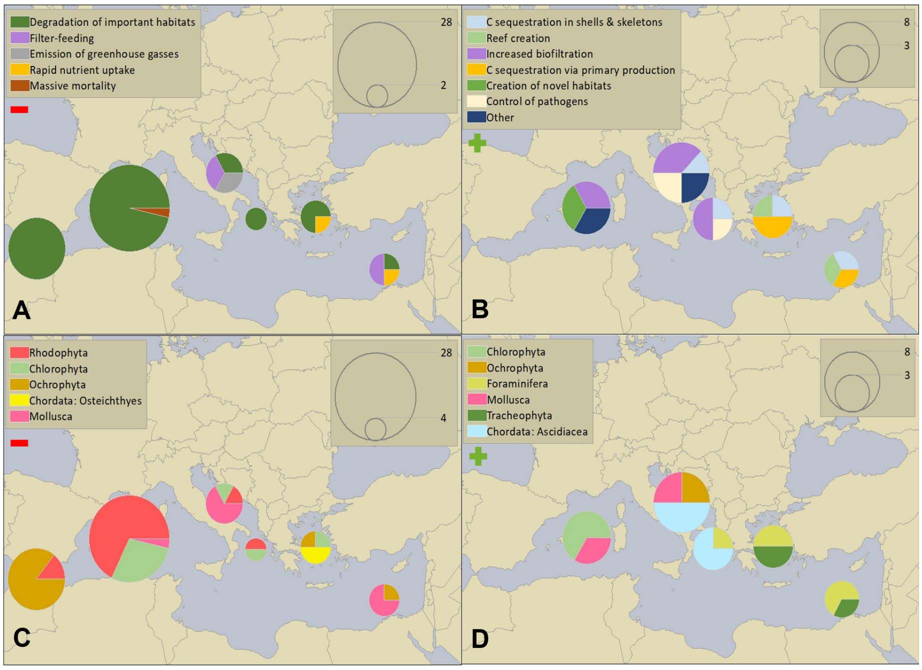


Figure 14. Geographical variation of the A) negative and B) positive mechanisms of impact on regulating and maintenance ecosystem services by Mediterranean ecoregion and of analyzed alien species phyla with C) negative and D) positive impacts on regulating and maintenance services per Mediterranean ecoregion. The size of the pie charts reflects the number of reported cases (the inset indicates the minimum and maximum sizes).

lobifera or the bivalves *R. philippinarum* and *Arcuatula senhousia* form dense aggregations that constitute banks of carbon storage in the marine environment, since their shells contain carbonate. Meadows of the alien seagrass *Halophila stipulacea* are also considered carbon sinks (see Appendix 1).

The Levantine Sea was the Mediterranean ecoregion with most studies of impacts on cultural ecosystem services (Figure 15A, B). The negative effects in the Levantine were primarily caused by Chlorophyta, Ochrophyta, and Rhodophyta (Figure 15C) through decomposing macroalgal material that washed ashore. Seaweed drifts of *Codium parvulum*, *Codium arabicum*, *Galaxaura rugosa*, and *Stypopodium schimperi* have regularly occurred in the eastern Mediterranean during recent decades, disturbing local activities and tourism and degrading the aesthetic value of the coast. Large and dense macroalgal thalli of *Sargassum muticum* and *Undaria pinnatifida* have sometimes become a nuisance in Adriatic lagoons, hindering navigation. In the Levantine Sea, *R. nomadica* massive swarms have also hindered tourism profits as they pose a threat to swimmers and deter tourists from visiting the coast.

On the other hand, alien species have offered materials for research on potential pharmaceutical products and biomonitoring services, which are the main positive impacts reported on cultural services (Figure 15B), with frequencies that were not found to differ significantly among ecoregions (chi-square test; excluding the Alboran Sea; p = 0.136). Many molluscs and

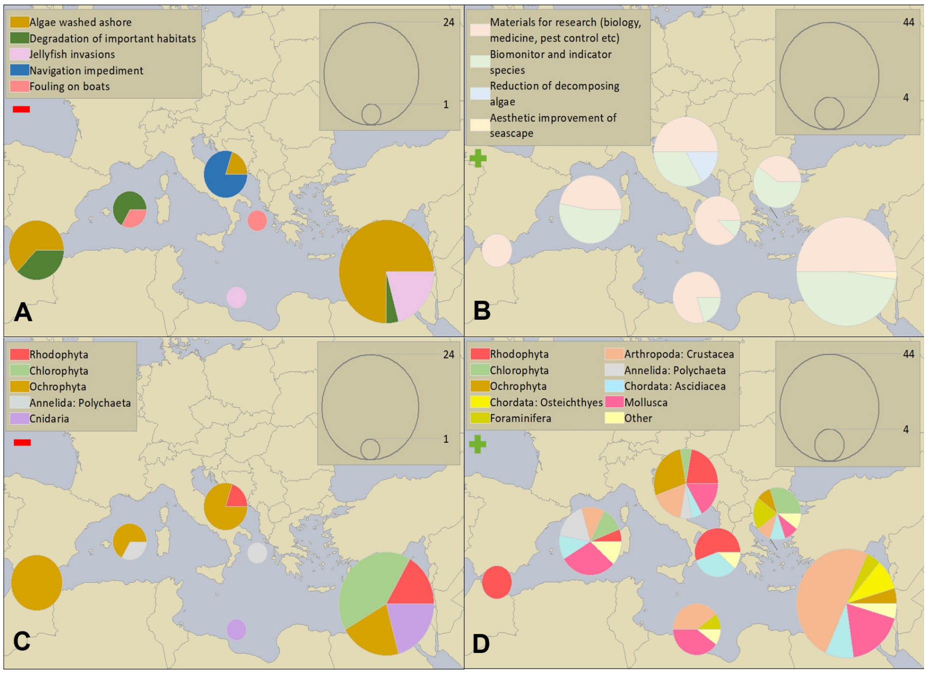


Figure 15. Geographical variation of the **A)** negative and **B)** positive mechanisms of impact on cultural ecosystem services by Mediterranean ecoregion and of analyzed alien species phyla with **C)** negative and **D)** positive impacts on cultural services per Mediterranean ecoregion. The size of the pie charts reflects the number of reported cases (the inset indicates the minimum and maximum sizes).

crustaceans such as *S. spinosus*, *P. radiata*, and *Penaeus semisulcatus*, and the foraminiferan *A. lobifera*, have been used effectively as biomonitoring species for marine pollution (Figure 15D; see Appendix 1).

Impacts on human health

Reported impacts on human health were only negative. The great majority of this evidence came from the Levantine Sea (Figure 16A) and was primarily related to stinging and poisoning/intoxication caused by only 9 species belonging to Osteichthyes, Cnidaria, and Echinodermata (Figure 16B), namely: *L. sceleratus*, *Torquigener flavimaculosus*, *Plotosus lineatus*, *P. miles*, *S. luridus*, *S. rivulatus*, *Macrorhynchia philippina*, *R. nomadica*, and *Diadema setosum*. Such unwanted accidents are sometimes described in the scientific literature. For example, in the eastern Mediterranean, severe intoxications and cases of death were attributed to the consumption of *L. sceleratus,* which contains in its tissues a paralytic neurotoxin called tetrodotoxin that can be lethal for humans. *Rhopilema nomadica* has caused a vast number of hospitalizations of swimmers and fishers in the Levantine Sea due to its painful stings. The long-spined sea urchin *D. setosum* poses a threat for swimmers in the eastern Mediterranean where it can be found at high densities in shallow waters, as its spines contain venom and may inflict painful stings.

Grouping of species according to the mechanisms of their impacts

Species with impacts on biodiversity, ecosystem services, and human health were grouped by hierarchical cluster analysis according to their

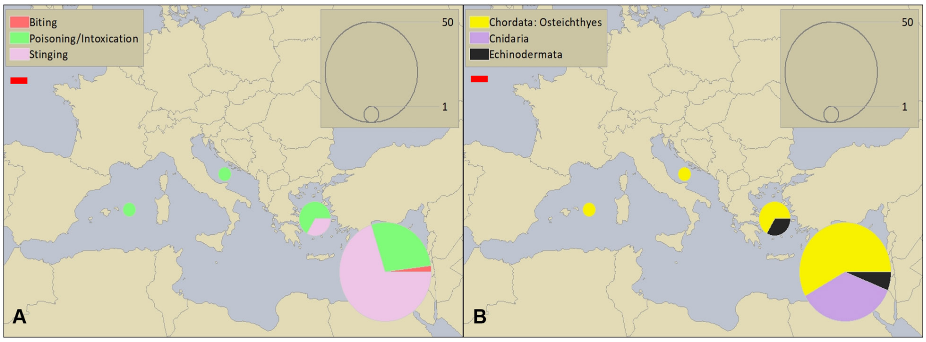


Figure 16. Geographical variation of **A)** mechanisms of negative impact and the responsible **B)** phyla causing the impacts on human health by Mediterranean ecoregion.

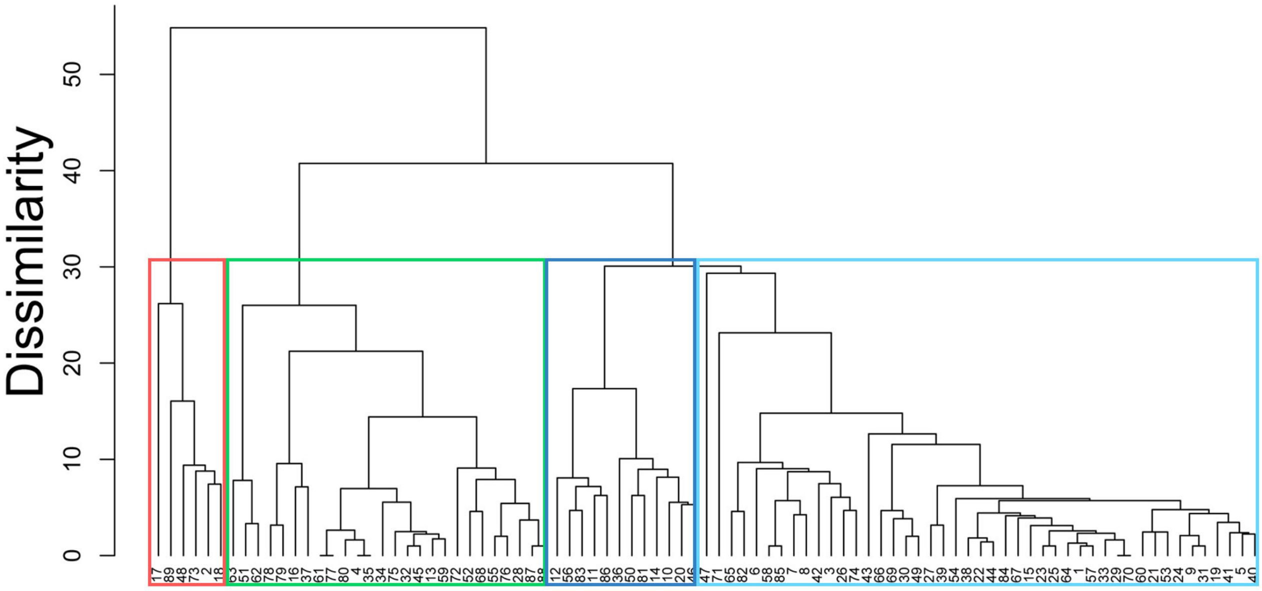


Figure 17. Hierarchical cluster dendrogram of alien and cryptogenic species (Cr: cryptogenic) based on the mechanisms of reported impacts on biodiversity, ecosystem services and human health. Coloured frames (red, green, blue, light blue) indicate the four major groups species of the dendrogram. Included species are numbered as follows: 1) *Acartia (Acanthacartia) tonsa* (Cr), 2) *Acrothamnion preissii*, 3) *Agarophyton vermiculophyllum*, 4) *Alepes djedaba*, 5) *Amathia verticillata* (Cr), 6) *Amphistegina lobifera*, 7) *Anadara kagoshimensis*, 8) *Anadara transversa*, 9) *Antithamnion nipponicum*, 10) *Arcuatula senhousia*, 11) *Asparagopsis armata* , 12) *Asparagopsis taxiformis*, 13) *Atherinomorus forskalii*, 14) *Brachidontes pharaonis*, 15) *Bursatella leachii* (Cr), 16) *Callinectes sapidus*, 17) *Caulerpa cylindracea*, 18) *Caulerpa taxifolia*, 19) *Caulerpa taxifolia* var. *distichophylla*, 20) *Chama pacifica*, 21) *Chrysonephos lewisii*, 22) *Ciona robusta*, 23) *Cladophora patentiramea*, 24) *Clavelina oblonga*, 25) *Codium arabicum*, 26) *Codium fragile* subsp. *fragile*, 27) *Codium parvulum*, 28) *Conomurex persicus*, 29) *Decapterus russelli*, 30) *Diadema setosum*, 31) *Didemnum vexillum*, 32) *Dussumieria elopsoides*, 33) *Dyspanopeus sayi*, 34) *Erugosquilla massavensis*, 35) *Etrumeus golanii*, 36) *Ficopomatus enigmaticus*, 37) *Fistularia commersonii*, 38) *Fulvia fragilis*, 39) *Galaxaura rugosa*, 40) *Grateloupia turuturu*, 41) *Halimeda incrassata*, 42) *Halophila stipulacea*, 43) *Haplosporidium pinnae* (Cr), 44) *Herdmania momus*, 45) *Herklotsichthys punctatus*, 46) *Hydroides elegans*, 47) *Lagocephalus sceleratus*, 48) *Lophocladia lallemandii*, 49) *Macrorhynchia philippina*, 50) *Magallana/Crassostrea* species, 51) *Metapenaeus monoceros*, 52) *Metapenaeus stebbingi*, 53) *Microcosmus squamiger*, 54) *Mnemiopsis leidyi*, 55) *Nemipterus randalli*, 56) *Oculina patagonica* (Cr), 57) *Paracerceis sculpta*, 58) *Paraleucilla magna*, 59) *Parupeneus forsskali*, 60) *Pempheris rhomboidea*, 61) *Penaeus aztecus*, 62) *Penaeus pulchricaudatus*, 63) *Penaeus semisulcatus*, 64) *Percnon gibbesi* (Cr), 65) *Pinctada radiata*, 66) *Plotosus lineatus*, 67) *Polyandrocarpa zorritensis*, 68) *Portunus segnis*, 69) *Pterois miles*, 70) *Rapana venosa*, 71) *Rhopilema nomadica*, 72) *Ruditapes philippinarum*, 73) *Rugulopteryx okamurae*, 74) *Sargassum muticum*, 75) *Sargocentron rubrum*, 76) *Saurida lessepsianus*, 77) *Scomberomorus commerson*, 78) *Siganus luridus*, 79) *Siganus rivulatus*, 80) *Sphyraena chrysotaenia*, 81) *Spondylus spinosus*, 82) *Styela plicata*, 83) *Stypopodium schimperi*, 84) *Torquigener flavimaculosus*, 85) *Tricellaria inopinata*, 86) *Undaria pinnatifida*, 87) *Upeneus moluccensis*, 88) *Upeneus pori*, 89) *Womersleyella setacea*.

similarity of mechanisms of reported impacts, resulting in 4 major groups (Figure 17).

The first cluster (red colour in Figure 17) included six alien macroalgae, namely *C. cylindracea*, *W. setacea*, *L. lallemandii*, *R. okamurae*, *A. preissii*, and *C. taxifolia*. A high number of negative impact records was reported for each of these species, with competition for resources being the most common mechanism of impact. A high number of impact records was also reported on ecosystem services through the mechanism of degradation of important habitats, with 84 negative cases on 8 different services. These species also constitute ecosystem engineers that mainly impacted other species negatively (34 records) rather than positively (21 records) through the creation of novel habitat.

The second cluster (green colour in Figure 17) was formed by 26 species that were grouped together primarily due to their positive impact on food provision, being new commodities. All these species, mainly crustaceans, fishes, and two molluscs, contributed to 91% of the overall positive impacts on food provision by new commodities. Among them, the alien shrimps *M. monoceros*, *P. pulchricaudatus*, and *P. semisulcatus* were the species with the highest number of positive reports as new commodities, but also some competitive negative impacts on native shrimp species and thus exhibited a high similarity. The alien fishes *N. randalli*, *Saurida lessepsianus*, *Upeneus* spp., the alien molluscs *C. persicus* and *R. philippinarum*, and the alien crab *P. segnis* formed a subgroup within this cluster following the same pattern of reported mechanisms of impact but with a lower frequency. Predation (including grazing) was also a mechanism of negative impact characteristic for some species of this cluster, such as the herbivorous fish *Siganus* spp., the omnivorous crab *C. sapidus*, and the piscivorous fish *F. commersonii.*

The third major cluster (blue colour in Figure 17) included alien molluscs such as *B. pharaonis*, *Chama pacifica*, and *Magallana/Crassostrea* species, the alien polychaetes *F. enigmaticus* and *H. elegans*, the alien macroalgae *Asparagopsis* spp. and *U. pinnatifida*, and the cryptogenic hexacoral *Oculina patagonica*. A high number of impacts on biodiversity was recorded for these species, mainly through the mechanisms of competition and the creation of novel habitat (both negative and positive for the latter) as structural ecosystem engineers.

The final cluster (light blue colour) was delineated by 45 species with 394 impact records. Thirty-six species of this cluster had less than 10 records each. Competition for resources was the most common mechanism of impact with 59 records, caused by 33 of the 46 species of the cluster. Fouling species with negative impacts on aquaculture followed as the second most common mechanism. Such species with both competition and fouling impacts were the ascidians *Styela plicata*, *Clavelina oblonga*, and *Didemnum vexillum*, the bivalve *P. radiata*, the sponge *P. magna*, and the bryozoan *T. inopinata.* Most species with negative impacts on human health were also included in this cluster. *Diadema setosum*, *M. philippina*, *P. lineatus*, and *P. miles* were grouped together with high similarity as stinging species.

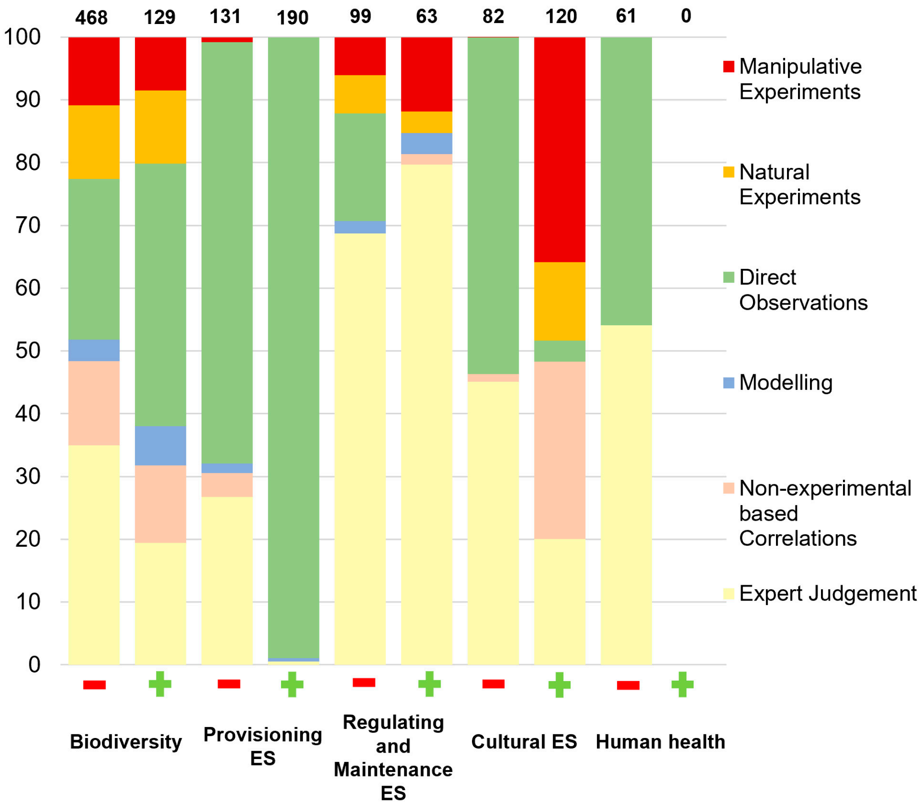


Figure 18. Type of evidence of the analysed impact records on biodiversity, ecosystem services and human health. The numbers on top of the bars indicate the sample size (number of reported cases) for each category.

Type of evidence

Only 16% of impact records were experimental (9% were based on manipulative and 7% on natural experiments; Figure 18). Moreover, many of the experimental studies were *in vitro* experiments on alien species extracts and compounds. Most of the taxa studied by experimental studies were Chlorophyta and Rhodophyta. Overall, direct observation was the most common type of evidence accounting for 40% of all records. Reported impacts on provisioning ecosystem services were almost exclusively based on direct observations (Figure 18). Fouling on aquaculture facilities, entanglement in nets, and new commodities in the fisheries and fish markets are undoubtedly direct impacts and as such were classified as direct observations. For biodiversity records, direct observations referred to the creation of novel habitat, apparent competitive interactions such as overgrowth of sessile organisms, predation impacts derived from stomach content analysis, and massive mortalities. Expert judgement and non-experimentally based correlations accounted for 32% and 9% of impact records, respectively (Figure 18), the former being dominant for “regulating and maintenance” ecosystem services. Modelling overall accounted for only 2% of the records.

The western Mediterranean and the Alboran Sea exhibited the highest percentages of experimental studies assessing negative impacts on biodiversity,

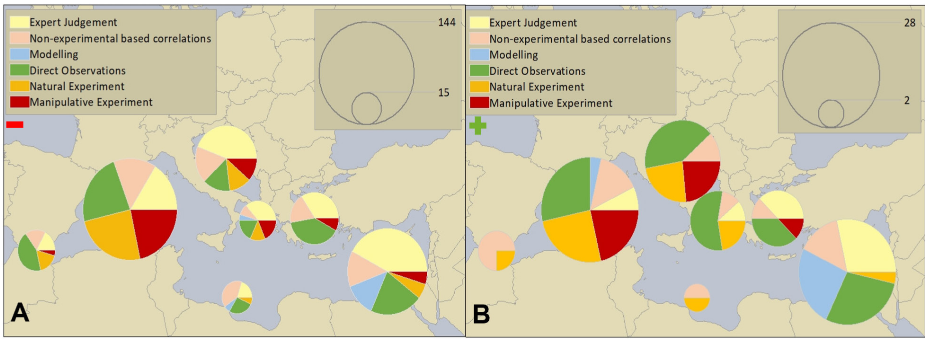


Figure 19. Geographical variation of type of evidence for negative (A) and (B) positive impacts on biodiversity across Mediterranean ecoregions.

followed by the Adriatic and the Ionian Sea (Figure 19A). Much less experimental studies were recorded in the Aegean and the Levantine Sea. Instead, expert judgement was the main type of evidence in these ecoregions, as well as in the Adriatic and the Ionian Sea. The western Mediterranean and the Adriatic Sea were the ecoregions with the highest proportion of experimental studies for positive impacts on biodiversity (Figure 19B). Most impact reporting through modelling studies for both negative and positive impacts was from the Levantine Sea (Figure 19A, B).

Inventory of high impact species in the Mediterranean Sea

An inventory of impactful species, based on both negative and positive reported impacts on biodiversity, ecosystem services and human health, is proposed in Table 4 and includes 88 species. Of the 103 assessed species, 15 were excluded from this inventory due to the complete absence of impact records or the reporting of only minor impacts. For three included species there was only weak evidence for their impact, based on expert judgement. Based on their negative impacts score on biodiversity, a list of the ten worst invasive species was compiled (Table 5). *Caulerpa cylindracea* ranked first, followed by *W. setacea* and *L. lallemandii*. Macroalgae dominated in the list of the ten worst invasives (6 species), followed by fishes and bivalve molluscs (2 species each).

Discussion

The number of reported negative impact records on biodiversity was approximately four times higher than the number of positive ones. Analysing the mechanisms of these effects, it was revealed that many alien species strongly compete for space and resources with native biota (e.g., Turon et al. 2007; Fanelli et al. 2015; Manconi et al. 2020) whereas others act as ecosystem engineers and alter the structure of habitats causing major negative effects on the local communities (e.g., Rilov et al. 2004; Bedini et al. 2014). Furthermore, intense feeding activities of invasive species can cause the decline of native populations (e.g., Kampouris et al. 2019), with alien grazers even being able to cause massive negative impacts in eastern

Table 4. Proposed inventory of alien and cryptogenic marine species with reported moderate to high impacts on biodiversity or ecosystem services or human health. Species whose impact was only reported by expert judgement are marked in light yellow (weak evidence); Cr: For cryptogenic species.

Cercozoa
Haplosporidium pinnae (Cr)
Foraminifera
Amphistegina lobifera
Ochrophyta
Chrysonephos lewisii
Rugulopteryx okamurae
Sargassum muticum
Stypopodium schimperi
Undaria pinnatifida
Chlorophyta
Caulerpa cylindracea
Caulerpa taxifolia
Caulerpa taxifolia var. *distichophylla*
Cladophora patentiramea
Codium arabicum
Codium fragile subsp. *fragile*
Codium parvulum
Halimeda incrassata
Rhodophyta
Acrothamnion preissii
Agarophyton vermiculophyllum
Antithamnion nipponicum
Asparagopsis armata
Asparagopsis taxiformis
Galaxaura rugosa
Grateloupia turuturu
Lophocladia lallemandii
Womersleyella setacea

Tracheohyta
Halophila stipulacea
Porifera
Paraleucilla magna
Cnidaria
Macrorhynchia philippina
Oculina patagonica (Cr)
Rhopilema nomadica
Ctenophora
Mnemiopsis leidyi
Bryozoa
Amathia verticillata (Cr)
Tricellaria inopinata
Mollusca
Anadara kagoshimensis
Anadara transversa
Arcuatula senhousia
Brachidontes pharaonis
Bursatella leachii (Cr)
Chama pacifica
Conomurex persicus
Fulvia fragilis
Magallana/Crassostrea species
Pinctada radiata
Rapana venosa
Ruditapes philippinarum
Spondylus spinosus

Annelida: Polychaeta
Ficopomatus enigmaticus
Hydroides elegans
Arthropoda: Crustacea
Acartia (Acanthacartia) tonsa (Cr)
Callinectes sapidus
Dyspanopeus sayi
Erugosquilla massavensis
Metapenaeus monoceros
Metapenaeus stebbingi
Paracerceis sculpta
Penaeus aztecus
Penaeus pulchricaudatus
Penaeus semisulcatus
Portunus segnis
Echinodermata
Diadema setosum
Chordata: Ascidiacea
Ciona robusta
Clavelina oblonga
Didemnum vexillum
Herdmania momus
Microcosmus squamiger
Polyandrocarpa zorritensis
Styela plicata

Chordata: Osteichthyes
Alepes djedaba
Atherinomorus forskalii
Decapterus russelli
Dussumieria elopsoides
Etrumeus golanii
Fistularia commersonii
Herklotsichthys punctatus
Lagocephalus sceleratus
Nemipterus randalli
Parupeneus forsskali
Pempheris rhomboidea
Plotosus lineatus
Pterois miles
Sargocentron rubrum
Saurida lessepsianus
Scomberomorus commerson
Siganus luridus
Siganus rivulatus
Sphyraena chrysotaenia
Torquigener flavimaculosus
Upeneus moluccensis
Upeneus pori

Table 5. The ten worst invasive species, based on their negative impact score (accounting only for impacts on biodiversity). This ranking does not account for the spatial extent of impacts but is based on a sum of all reported impacts in the literature, weighted by their magnitudes.

Species	Negative Impacts Score
Caulerpa cylindracea	134
Womersleyella setacea	80
Lophocladia lallemandii	65
Brachidontes pharaonis	47
Siganus luridus	44
Rugulopteryx okamurae	43
Caulerpa taxifolia	38
Siganus rivulatus	38
Acrothamnion preissii	36
Spondylus spinosus	33

Mediterranean ecoregions by depleting rocky reef algal biomass (e.g., Sala et al. 2011). At the same time, some alien species create novel habitats that offer shelter to many other native organisms (e.g., Di Martino et al. 2007; Munari et al. 2015), constitute new food sources for native predators (e.g., Giacoletti et al. 2016; Tiralongo et al. 2021), and contribute to other ecological functions of the recipient ecosystem (e.g., Sarà et al. 2021).

It is noteworthy that a higher number of positive than negative impacts were recorded affecting the flow of ecosystem services. Food provision appears as the most affected ecosystem service by both positive and negative impacts. Invasive fish have significantly increased their numbers in the last thirty years, representing today more than half of the total abundance and biomass of the Levantine fish (Katsanevakis et al. 2018). Simultaneously, severe population declines in some native fish populations occurred (Edelist et al. 2013). All surveys that indicated a competitive effect of alien species on commercial native species stocks were supported by weak or modest strength of evidence. There is no strong evidence supporting the hypothesis of native species population declines exclusively or largely due to competition with alien species. On the other hand, research has demonstrated that many species have declined in the Levantine Sea due to climate change, as the new temperature regime is beyond their thermal niche (Rilov 2016). Climate change is an important stressor for native biota and has negatively affected the Mediterranean Sea (Marbà et al. 2015; Rilov 2016; Albano et al. 2021). In the western Mediterranean, shallow waters have been warming for more than a century with more abrupt positive trends during the recent decades that have resulted in local sea surface temperature increases that even exceed 1 °C (Lejeusne et al. 2010) and deleterious marine heatwaves (Garrabou et al. 2009, 2019, 2022). The eastern basin was shown to be warming faster (Pisano et al. 2020; Novi et al. 2021), with surface water temperature even exceeding a 3 °C increase during the period 1978–2014 in the southeastern regions (Ozer et al. 2017). Climate change has played a crucial role in the alteration of eastern Mediterranean ecosystems and the collapse of several species (Rilov 2016; Albano et al. 2021), but these dramatic changes are better explained as a result of the combined effects of climate change and biological invasions (Marras et al. 2015; Azzurro et al. 2019; Yeruham et al. 2020). Indeed, multiple stressors often act in synergy, leading to multiplicative effects (Korpinen et al. 2019; Gissi et al. 2021).

A progressive transition towards a more thermophilic biota is reported for the global fishery catch for most marine ecosystems (Cheung et al. 2013), and also in the Mediterranean Sea (Tsikliras and Stergiou 2014), where warm adapted invaders of Indo-Pacific origin are already replacing native biota (Stergiou et al. 2016 and references therein; Katsanevakis et al. 2018; Albano et al. 2021). Yet, to date many alien species contribute to food provision as new commodities (Katsanevakis et al. 2018), especially in the eastern Mediterranean where alien fishes and crustaceans are more abundant in comparison to the western basin (Katsanevakis et al. 2014b). Levantine fisheries have even begun to shift their target from deeper to shallower waters where they can catch larger quantities of thermophilic alien species (van Rijn et al. 2020).

Contrary to the general idea that invading alien species are inherently "bad", a view that is often dependent on social perceptions (Katsanevakis et al. 2014a), the positive effects of tropical invaders are worth exploring in detail, especially in the current climate change context. In the Levantine Sea, the ecological space made available by the shift of temperate species towards higher latitudes and greater depths cannot be covered by neonatives (*sensu* Essl et al. 2019) from southern regions, as this is a land-locked basin. In that sense, it can be argued that thermophilic Lessepsian immigrants entering the Mediterranean through the Suez Canal may contribute to limiting the loss of ecosystem functions and services. Restoring the Levantine Sea ecosystems to their previous state before climate change and massive biological invasions is unrealistic. Except for targeted management actions for specific species (e.g. *P. miles* and *L. sceleratus*), marine managers in the region need to be adaptive and realistic, understanding and accepting the role of alien species in the novel marine ecosystems.

Regarding the impacts of invasive species on human health, we observed that these are mostly limited to the eastern basin. Among the nine species, only *L. sceleratus* was found to have an impact in locations west of the Aegean Sea, and the species has already reached the westernmost end of the Mediterranean (Azzurro et al. 2020). The actual number of negative impact cases on human health is probably underestimated because many non-life-threatening episodes do not require hospitalisation and are treated by first aid. Such cases are most often not officially reported (Bédry et al. 2021), especially not by scientific literature. Bédry et al. (2021) proposed a series of actions to manage the effects of marine biological invasions on human health: i) to reinforce public awareness of the potential dangers that specific alien species may pose to human health, ii) to train and prepare professional medical personnel on the physiological effects of toxic alien species, iii) to establish a regional warning and monitoring system. In this review, we did not record positive impacts of alien or cryptogenic species on human health but future research on alien species is expected to disclose their potential as providers of biomolecules, to be used by the pharmaceutical industry (e.g. Genovese et al. 2009; Minicante et al. 2016; Dhahri et al. 2020). However, the discovery of new potentially active molecules is a well-worn argument very often put forward to minimise the problem of species introductions (a “chestnut” in journalistic terms), but its validity has only rarely, if ever, been demonstrated and evaluated. Marine species capable of producing active metabolites are well known around the world and invasions are not necessary to initiate research and exploitation. The industrial exploitation of such molecules often requires either aquaculture production or chemical synthesis. So far, to the best of our knowledge, there are no examples of industrial exploitation of Mediterranean invaders for active molecules.

Biological invasions remain one of the most catastrophic threats to global biodiversity, but the complexity of their impacts along with their ecological, and socio-economic dimensions are worth exploring in detail and at different scales. Some scientists consider that the origin of a species does not make it *de facto* responsible for negative consequences (Davis et al. 2011) since native species also possess the ecological ability to affect ecosystems and cause deleterious impacts under certain conditions. For example, the coastal rocky reefs of the eastern Mediterranean are overgrazed by the invasive rabbitfishes *Siganus luridus* and *S. rivulatus* (Sala et al. 2011; Giakoumi 2014; Vergés et al. 2014; Yeruham et al. 2020) but under certain conditions, similar effects can be provoked by native grazers (Hereu 2006; Vergés et al. 2009; Bonaviri et al. 2011; Gianni et al. 2017; Tsirintanis et al. 2018; Papadakis et al. 2021), often due to cascading effects caused by the loss of overfished native predators (Sala et al. 1998). It should also be highlighted that some of the high-impact species of the current proposed inventory are cryptogenic, meaning that their origin cannot be completely ascertained. Non-factual perception of alien species as invasive (i.e. negatively impacting ecosystems and human well-being) neglects a holistic approach to impact assessment and can lead to bias (Goodenough 2010; Katsanevakis et al. 2014a). Commonly the same species have both negative and positive impacts on biodiversity, and the overall balance is hard to assess. For example, the possible facilitation of the restoration of a degraded ecosystem by an invasive alien species like the facilitation of seagrass seedlings by *C. cylindracea* in degraded meadows (Ceccherelli and Campo 2002; Pereda-Briones et al. 2018) deserves further consideration and confirmation by long-term studies evaluating the survival rate of germlings in dense *C. cylindracea* meadows. This brings up ecological, cultural, and socio-economic considerations that complicate decision making in invasive species management, as changes in host communities are not always perceived as harmful (Bonanno 2016), and management decisions need to account for conflicts and trade-offs (Mason et al. 2017).

In this study, we found a clear geographic differentiation in the distribution of reported impacts. For example, predation as a mechanism of impact was more important in the Levantine Sea than in the rest of the basin. This is following the higher richness and abundance of invasive fishes that characterise the eastern sectors of the Mediterranean, being introduced from the Red Sea through the Suez Canal and favoured by the higher temperatures of the eastern Mediterranean (Katsanevakis et al. 2014b). The great taxonomic differences of alien species among ecoregions (Zenetos et al. 2012; Katsanevakis et al. 2014b), as well as the significant differences in impacts among taxonomic groups, revealed in this study, partly explain the variation detected among Mediterranean ecoregions.

A global effect of alien species invasions is biotic homogenization, the process of native biodiversity impoverishment happening simultaneously with a proliferation of alien species that results in the expansion of homogeneity in terms of genetic, taxonomic and functional diversity with unclear biodiversity distinctions (Olden et al. 2004 and references therein). Signs of biotic homogenization are evident in the marine ecosystems of the

Mediterranean Sea, as the establishment and advancement of biological invasions in the basin have occurred alongside native biota impoverishment and losses (Galil 2007 and references therein). In many cases, an impoverished homogeneous state has been spread within the Mediterranean basin, through the spread and dominance of some alien structural ecosystem engineers (Navarro-Barranco et al. 2018; Morri et al. 2019). The increasing rate of biological invasions in the Mediterranean and the continuing seawater warming led to the replacement of endemic populations by mostly thermophilic Lessepsian species. Hence, the "Mediterranean character" of the marine biota progressively declines, contributing to the breakdown of the regional distinctiveness of the Mediterranean Sea (Ben Rais Lasram and Mouillot 2009).

In the current literature review, most studies on impacts on biodiversity were based on medium and low strength of evidence. In agreement with Katsanevakis et al. (2014a), the proportion of reported impacts with high strength of evidence (i.e. manipulative and natural experiments) was low. These studies were conducted in 13 out of the 22 Mediterranean countries, with most cases (84%) reported from Italy, Spain, and France (Figure 20A). The latter are the Mediterranean countries with the higher budget for research and development (UNESCO 2021) (Figure 20B), reflecting the connection between research robustness, number of experimental studies, and investment in research and development. Indeed, several studies relate scientific output to national spending on research and development, the number of universities in a country, GDP, and English proficiency (Man et al. 2004; Meo et al. 2013; Jamjoom and Jamjoom 2016; Mueller 2016).

Another possible reason for the higher inferential strength of impact assessment studies in the western Mediterranean countries could be related to the taxonomic distribution of alien species within the Mediterranean. There is a higher species richness of alien macroalgae in the western Mediterranean in comparison to the eastern basin, and the opposite pattern for alien fish species, which have primarily invaded the eastern Mediterranean (Katsanevakis et al. 2014b). Our analysis revealed that the vast majority (90%, n = 76) of experimental impact cases on biodiversity reported from the western Mediterranean and the Alboran Sea assess impacts caused by alien macroalgae, whereas no experimental study investigates impacts caused by alien fish. At the same time, experimental impact records are significantly lower in numbers in the Levantine and the Aegean Sea and mainly refer to alien fish effects (71%; n = 14). Macroalgae are sessile organisms, easier to be controlled in confined experimental treatments, in contrast to mobile organisms such as fish. There is already a high level of difficulty in performing underwater experiments to investigate ecological interactions due to the various factors that affect a diver's awareness such as visibility and temperature (O'Brien and Caramanna 2017). In addition, species mobility may interfere with the success of an

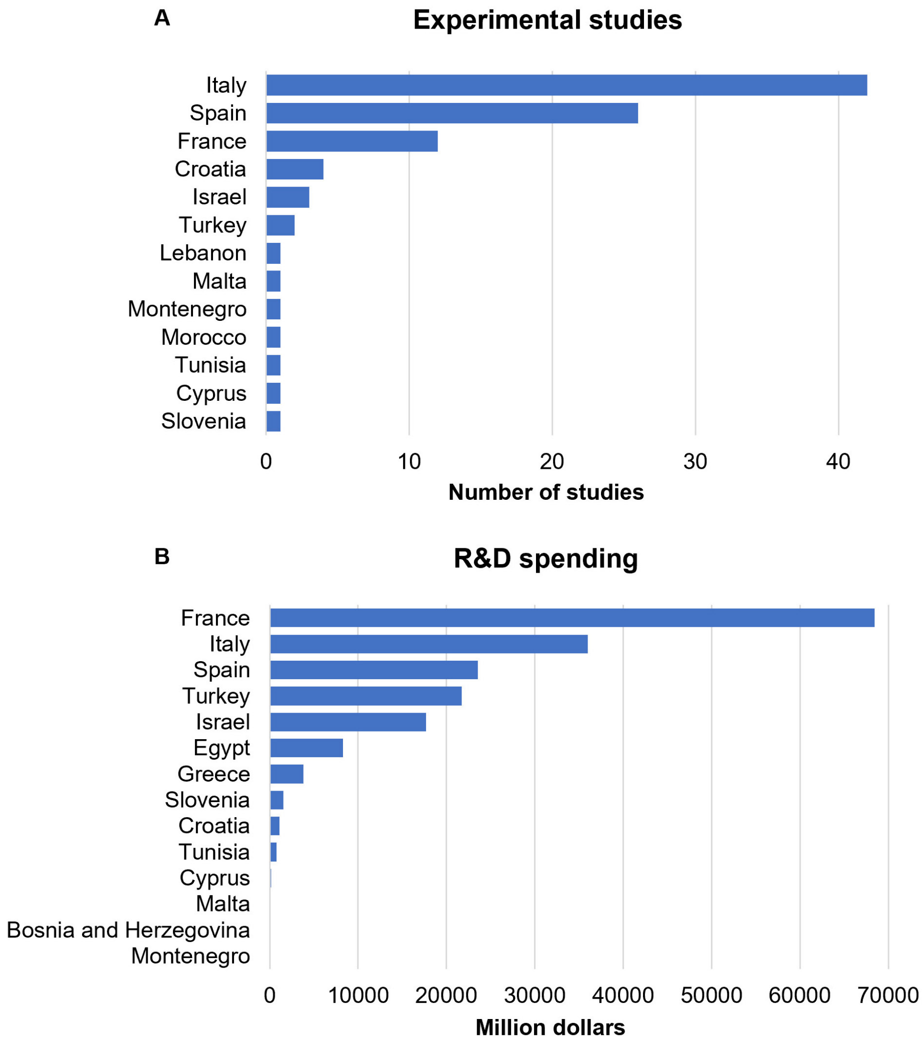


Figure 20. A) Number of reported experimental studies included in this review assessing impacts on biodiversity, per Mediterranean country, B) Total intramural expenditure on Research and Development (R&D), performed by some Mediterranean countries during 2018, expressed in Purchasing Power Parity dollars (UNESCO 2021).

applied underwater experiment and this fact can explain why experimental research on alien species is more limited in the eastern Mediterranean, dominated by mobile species invasions. Similar results were reported by Kytinou et al. (2020), who reviewed methodological approaches globally that analyse coastal shelf food webs, and concluded that only 14% of the reviewed studies conducted manipulative or natural experiments, and most of the studies focused on benthic species and much less on fish. Also, Thomsen et al. (2014) reviewed aquatic alien species' experimental impact assessment surveys within forty years (1972–2012) and found only one alien marine fish species studied by experiments among more than a hundred different species. The species mobility hypothesis is further supported by the fact that in the Levantine and the Aegean Sea most of the impacts were reported by experimental studies on the herbivorous fishes *Siganus* spp. with assessments based on the effects on macroalgal communities, i.e. the sessile food of siganids.

Furthermore, there are several additional confounding factors that distort the actual impact patterns, such as paucity of data (Ojaveer et al. 2015), taxonomic impediment (Engel et al. 2021), challenges for assessing and quantifying the actual impact of particular alien taxa (Carlton 2002; Simberloff 2011; Davidson and Hewitt 2014; Strayer et al. 2017), and weak inferential strength of evidence (Katsanevakis et al. 2014a). Another aspect to consider is that the current analysis examines impacts caused by each alien species separately. But species do interact, and their cumulative impacts are not necessarily additive but can be multiplicative or mitigative (Katsanevakis et al. 2016), also often interacting with other local or global stressors such as climate change (Gissi et al. 2021). Hence, impacts by alien species reported in a specific location are not necessarily representative of the entire ecoregion. As a consequence, spatial patterns herein reported should be interpreted with caution, as highlighted in other studies reporting spatial patterns in biological invasions (e.g. Pyšek et al. 2008; Stranga and Katsanevakis 2021).

In addition, the methodological approach of the current impact assessment framework is performed without chronological restrictions and depicts the effects of alien and cryptogenic species on biodiversity, ecosystem services and human health from the moment of the first impact report of each targeted species until 2021. The temporal variation of impacts was not taken into account. Still, invasive alien species can regress after an invasion phase, following a so-called "boom and bust" invasion pattern, as has been reported for *Caulerpa cylindracea*, *C. taxifolia*, *L. lallemandii* and *S. schimperi* (Iveša et al. 2006; Montefalcone et al. 2015; Dimitriadis et al. 2021; Santamaría 2021). Unfortunately, the literature of marine invasions sorely lacks scientific articles showing the evolution of invaded sites over several decades (Strayer et al. 2017; Ojaveer et al. 2018). The reason may be due to the functioning of scientific research, i.e. the short duration of doctoral thesis projects, short-term funding, the need to publish quickly, the lack of interest of scientific journals and reviewers in what seems routine monitoring, and probably also the fact that spectacular bad news is easier to publish than good news. Hence, it is possible that some of the published impacts later declined in magnitude, due to the "boom-and-bust" dynamics of biological invasions. This stresses the need for repetitive assessments and regular re-evaluation of the impacts of alien species.

We have provided a list of the "ten worst invasive species" in the Mediterranean, based on reported impacts. Similar lists have been compiled in the past (e.g. see Streftaris and Zenetos 2006; Katsanevakis et al. 2016) based on different approaches and metrics. Depending on the criteria applied for impact assessment, different schemes can lead to strikingly different outcomes (González-Moreno et al. 2019). Hence, any such ranking of invasive species should be perceived under the limitations and assumptions of the analysis that produced it. For example, the present study did not account for the spatial distribution of impactful species and the geographical extent of reported impacts, which for some species can be quite small (i.e. high impact but in a restricted area). Nevertheless, it is remarkable that our inventory of the ten worst invasive species is quite similar to the respective ranking in Katsanevakis et al. (2016) [their indicator D3], produced by a quite different approach, i.e. the sum of cumulative impact scores of the species on marine habitats based on a conservative additive model (CIMPAL) across all 10 × 10 km cells that cover the entire Mediterranean Sea. Eight of the ten top species are shared by the two rankings.

We recorded a variety of impacts on biodiversity, ecosystem services and human health caused by alien and cryptogenic species. Without forgetting that all introduced species represent a disturbance to nature by modifying native ecosystems (Ricciardi et al. 2013), management choices need to be based on robust evidence. This remains a primary need in the process of evaluating the effects of alien species in ecosystems. The way forward to interpret biological invasions and prioritise management actions is to incorporate holistic approaches to alien species impact assessments, accounting for both positive and negative impacts and socio-ecological tradeoffs, and increase the strength of evidence through the implementation of more experimental studies.

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Authors’ contribution

KTs: research conceptualization, design and methodology, review and data collection, data analysis, writing the first draft of the manuscript; SK: research conceptualization, design and methodology, data analysis, supervision, editing and writing; all authors: validating data, contribution with additional data and taxonomic expertise, interpretation, editing and writing.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Species-specific review of the impacts of alien and cryptogenic species on biodiversity, ecosystem services and human health in the Mediterranean Sea, and other related information.

This material is available as part of online article from:
http://www.reabic.net/aquaticinvasions/2022/Supplements/AI_2022_Tsirintanis_etal_Appendix.pdf