

Review

Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review

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Abstract

A good understanding of the mechanisms and magnitude of the impact of invasive alien species on ecosystem services and biodiversity is a prerequisite for the efficient prioritisation of actions to prevent new invasions or for developing mitigation measures. In this review, we identified alien marine species that have a high impact on ecosystem services and biodiversity in European seas, classified the mechanisms of impact, commented on the methods applied for assessing the impact and the related inferential strength, and reported on gaps in available information. Furthermore, we have proposed an updated inventory of 87 marine species in Europe, representing 13 phyla, which have a documented high impact on ecosystem services or biodiversity.

Food provision was the ecosystem service that was impacted by the greatest number of alien species (in terms of both positive and negative impacts). Following food provision, the ecosystem services that were negatively affected by the highest number of alien species were ocean nourishment, recreation and tourism, and lifecycle maintenance, while the ecosystem services that were most often positively impacted were cognitive benefits, water purification, and climate regulation. In many cases, marine aliens were found to impact keystone/protected species and habitats. Thirty percent of the assessed species had an impact on entire ecosystem processes or wider ecosystem functioning, more often in a negative fashion. Forty-nine of the assessed species were reported as being ecosystem engineers, which fundamentally modify, create, or define habitats by altering their physical or chemical properties.

The positive impacts of alien species are probably underestimated, as there is often a perception bias against alien species. Among the species herein assessed as high-impact species, 17 had only negative and 7 only positive impacts; for the majority (63 species), both negative and positive impacts were reported; the overall balance was often unknown. Although there is no doubt that invasive species have modified marine ecosystems, evidence for most of the reported impacts is weak, as it is based on expert judgement or dubious correlations, while only 13% of the reported impacts were inferred via manipulative or natural experiments. A need for stronger inference is evident, to improve our knowledge base of marine biological invasions and better inform environmental managers.

Key words: biological invasions, evidence, impact assessment, high-impact aliens, provisioning services, regulating and maintenance

Introduction

Biological invasions severely challenge the conservation of biodiversity and natural resources. They are considered to be one of the most important direct drivers of biodiversity loss and a major pressure on several types of ecosystems,

with both ecological and economic impacts (MEA 2005). In marine ecosystems, alien marine species may become invasive and displace native species, cause the loss of native genotypes, modify habitats, change community structure, affect food-web properties and ecosystem processes, impede the provision of ecosystem services, impact

human health, and cause substantial economic losses (Grosholz 2002; Perrings 2002; Wallentinus and Nyberg 2007; Molnar et al. 2008; Vilà et al. 2010). The rapid globalisation and increasing trends of trade, travel, and transport in recent decades have accelerated marine biological invasions by increasing rates of new introductions through various pathways, such as shipping, navigational canals, aquaculture, and the aquarium trade (Hulme 2009; Katsanevakis et al. 2013).

Ecosystem services are the benefits people derive from natural ecosystems. The oceans, and especially coastal zones, have been estimated to contribute more than 60% of the total economic value of the biosphere (Costanza et al. 1997; Martínez et al. 2007). Research on marine ecosystem services has grown exponentially during the past decade, particularly following the Millennium Ecosystem Assessment (MEA 2005; Lique et al. 2013a). However, despite recent advances in the assessment and valuation of ecosystem services, many marine ecosystem services remain poorly assessed (Lique et al. 2013a). In particular, the loss or modification of marine ecosystem services by invasive species is often overlooked.

The Convention on Biological Diversity (CBD) recognised the need for the “compilation and dissemination of information on alien species that threaten ecosystems, habitats, or species to be used in the context of any prevention, introduction and mitigation activities”, and calls for “further research on the impact of alien invasive species on biological diversity” (CBD 2000). The objective set by Aichi Biodiversity Target 9 is that “by 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment”. This reflects Target 5 of the EU Biodiversity Strategy (EU 2011). In Europe, the Marine Strategy Framework Directive (MSFD; EU 2008) recognises alien marine species as a major threat to European biodiversity and ecosystem health, requiring Member States to develop strategies to reach the Good Environmental Status of the marine environment.

With limited funding, it is necessary to prioritise actions for the prevention of new invasions and for the development of mitigation measures. This requires a good knowledge of the impact of invasive species on ecosystem services and biodiversity, their current distributions, and the pathways of their introduction (Molnar et al. 2008; Katsanevakis et al. 2013; Galil et al. 2014).

Here, we provide a comprehensive review of the impacts of alien marine species on the ecosystem services and biodiversity of European seas (including the entire Mediterranean and Black Seas), with the aim of (1) identifying high-impact species for each ecosystem service and for biodiversity; (2) classifying mechanisms of impact; (3) proposing an updated inventory of high-impact alien marine species for Europe; (4) commenting on the methods applied for assessing impact and their inferential strength; and (5) reporting gaps in available information.

Methods

Selection of list of species

Our list of target species was compiled by combining and updating the ‘100 of The Worst’ list of DAISIE (Delivering Alien Invasive Species Inventories for Europe; <http://www.europe-aliens.org/speciesTheWorst.do>), the NOBANIS fact sheets on Invasive Alien Species (European Network on Invasive Alien Species; <http://www.nobanis.org/FactSheets.asp>), the SEBI ‘List of worst invasive alien species threatening biodiversity in Europe’ (Streamlining European 2010 Biodiversity Indicators; <http://biodiversity.europa.eu/topics/sebi-indicators>), and the datasheets of CABI’s Invasive Species Compendium (CABI-ISC; <http://www.cabi.org/isc/>). These lists cover all environments (terrestrial, freshwater, marine), and thus we selected only those species that have been classified as marine by the European Alien Species Information Network (EASIN; Katsanevakis et al. 2012), excluding predominantly freshwater species that might also appear in oligohaline environments (i.e. with salinities < 5).

Based on our critical review of the aforementioned lists (DAISIE, NOBANIS, SEBI, CABI-ISC), review publications that report the impact of alien marine species in European or regional seas (e.g. Streftaris and Zenetos 2006; Otero et al. 2013), the authors’ data and expertise, and our review of the scientific and grey literature, an updated European list of high-impact marine species is proposed. There are many reasons why such a list is needed: (1) some of the existing lists are general (covering all environments) and restrictive (e.g. ‘100’ worst invasives; the magic number ‘100’ is not scientifically derived); (2) some lists do not have a European focus but are either global (CABI-ISC) or sub-European (NOBANIS); in the former case they might include species that are high-impact elsewhere



Figure 1. Europe and the surrounding seas. The present review covered all surrounding seas, including those that are not entirely European, i.e the entire Mediterranean and Black Seas.

but not in Europe, while in the latter case they exclude by definition species that are invasive in the Mediterranean or the Black Sea and not in the North or the Baltic Seas; (3) these lists are not always regularly updated and re-evaluated and might miss newly established high-impact species; (4) some species that had been considered high-impact in the past, might have later passed into a non-invasive phase.

Literature search – selection criteria – expert review

An initial bibliographic search was performed with the Scholar Google search engine, which, apart from peer-reviewed articles, also includes technical reports, PhD theses, and conference proceedings. For each species on our list, eligibility criteria included any document with the following keywords anywhere in the article:

<species name> AND “alien” AND “impact” AND (“Mediterranean” OR “Black Sea” OR “North Sea” OR “Baltic”). The results amounted to 20,843 articles, including duplicates (i.e. this is the sum of the articles found for each separate search for all the species of our initial high-impact list).

The process of selecting papers to include in the review started with a screening on the basis of the titles (2,506 papers including duplicates). Non-English publications were excluded, and full-text articles were not available for a number of records (266). The full text of the remaining articles (2,046) was screened and after excluding non-relevant articles, 329 papers were included in the review. These papers reported the impacts of one or more of the target marine species on one or more ecosystem services and/or biodiversity. Both positive and negative impacts were recorded.

At a second stage, we additionally retrieved information from the DAISIE, NOBANIS, and CABI-ISC factsheets and from additional sources suggested by the co-authors that had not been found through the systematic search described above.

Ecosystem Services classification

The marine ecosystem services classification recently proposed by Lique et al. (2013a) was followed. This classification included the following categories of ecosystem services: (1) food provision; (2) water storage and provision; (3) biotic materials and biofuels; (4) water purification; (5) air quality regulation; (6) coastal protection; (7) climate regulation; (8) weather regulation; (9) ocean nourishment; (10) lifecycle maintenance; (11) biological regulation; (12) symbolic and aesthetic values; (13) recreation and tourism; and (14) cognitive benefits. A detailed description of each category and the correspondence with other classifications can be found in Lique et al. (2013a) and is herein summarised in Table 1. In some of the reviewed papers, different categories of ecosystem services were used, but we adapted them accordingly.

Types of evidence

When assessing the impact of alien species on ecosystem services and biodiversity, the aim was to evaluate induced changes in the capacity of an ecosystem to provide services, in the flow and societal benefit of such services, and in the status of biodiversity at any level (species, habitat, ecosystem), including single-species impacts. In such assessments there is often more than one hypothesis that can explain an observed change. Evidence of an effect is herein defined as the information needed to separate hypotheses and exclude some as implausible. Strong evidence for an impact of an alien species excludes all other alternative hypotheses but that which states that the observed change came about as an effect of the introduced species. Weak evidence leaves us with other plausible hypotheses to explain an observed change, and thus no certainty of any effect caused by the introduced species.

To assess the strength of documented evidence of the impacts of alien species, we categorised 'evidence' into the following six categories: Manipulative Experiments, Direct Observations of impact, Natural Experiments, Modelling, non-experimental-based Correlations, and Expert

Judgement. By 'Manipulative Experiments' (marked with a superscript 'E' in text) we mean field or laboratory experiments that include treatments/control and random selection of experimental units. In Natural Experiments (marked with a superscript 'N' in text), one of the elements of manipulative experiments is missing and the experimental units (i.e. controls or impacted areas) are selected by nature (i.e. not randomly). Natural Experiments include Before-After, Control-Impact, and Before-After Control-Impact (BACI) or beyond BACI designs. 'Modelling' refers to presumed impacts as derived from ecosystem models. 'Non-experimental-based Correlation' herein refers to inference based on an observed correlation between the species' presence/abundance and the impact, but not based on an experimental design for data collection (e.g. when invasive species X appeared, native species Y started to decline; or the time series of abundance of invasive species X is negatively correlated with the time series of the catches of commercial species Y). 'Expert judgment' refers to statements of impact that are based not on experiments or correlations but on expert opinion, usually based on the species traits or the documented impact of similar species. 'Direct Observation of impact' is herein defined as an observation or direct measurement of the impact about which there is no doubt (e.g. the clogging of fishing nets by jellyfish; large-scale mortality events).

Only real impacts that exist in European seas have been included in this assessment; potential/future impacts, e.g. based on evidence in other marine areas outside Europe, have not been included. The only exception was for the assessments of cognitive benefits for which the geographic dimension is often less relevant. The evidence for stated impacts on ecosystem services or biodiversity in European seas was categorised as 'Manipulative Experiment', 'Natural Experiment', 'Direct Observation of impact', 'Modelling', or 'non-experimental-based Correlation' only if the experiment, observation, or sampling was conducted in European waters. Otherwise, where an impact in European waters is inferred in the literature based on a study conducted elsewhere, the evidence was categorised as 'Expert Judgement', even if the original study reports an experiment, direct observation of impact, or non-experimental-based correlation. The magnitude of reported impacts was not taken into account; i.e., local, small-scale, and large-scale impacts were all treated equally.

Table 1. List and description of marine ecosystem services, adapted from Lique et al. (2013a)

Ecosystem service	Description
Provisional services	
Food provision	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	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	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.
Regulating and maintenance services	
Water purification	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	Regulation of air pollutant concentrations in the lower atmosphere.
Coastal protection	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	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	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	Natural cycling processes leading to the availability of nutrients in seawater for the production of organic matter.
Lifecycle 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	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.
Cultural services	
Symbolic and aesthetic values	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	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	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).

Results and discussion

Impact Matrix – Overview

One hundred and one marine or euryhaline species listed as invasive in DAISIE, NOBANIS, SEBI, and CABI, were included in the present assessment (Table 2). Nine additional species (in bold in Table 2) were included, as their high

impact on ecosystem services or biodiversity has been well documented. The dominant groups in the assessed list of species were Crustacea (23 species), followed by Mollusca (20 species), and macroalgae (16 species). Details on the literature review and the impact assessment of each species of the list can be found in the online supplementary material (Supplement 1).

Food provision was the ecosystem service that was impacted by the highest number of alien

Table 2. Impact Matrix: Negative (red) and positive (green) impacts of alien marine species in European waters on ecosystem services (sensu Lique et al. 2013a) and biodiversity. Species that have not been previously listed as high-impact species in DAISIE, NOBANIS, SEBI, or CABI are indicated in bold. 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.

Alien species	Impact on marine ecosystem services (<i>sensu</i> Lique et al. 2013)													Impact on biodiversity					
	Provisioning		Regulating and maintenance								Cultural			Little/Unknown	Single-species impact	Multiple-species impact	Impact on keystone species or species of high conservation value	Affects entire ecosystem processes / wider ecosystem functioning	Ecosystem engineer - creator of novel habitat
	Food (fisheries, aquaculture etc)	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						
Dinophyta (Myxozoa)																			
Alexandrium minutum (Cr)	O								J			J	J			O		OJ	
Alexandrium monilatum	O								J	J						O		OJ	
Karenia mikimotoi (Cr)	O				O				J	J		O				O	OJ	OJ	
Gymnodinium catenatum (Cr)	O			O					J			J				EOC	J	OJ	
Haptophyta																			
Phaeocystis pouchetii (Cr)	EN			O	J		J		J	J		J				EJ	J	OJ O	
Ochromytha																			
Coscinodiscus wailesii (Cr)	O			J					J			J	J			J	J	OJ	
Fibrocapsa japonica (Cr)	J								J	J		J				EJ		J	
Odontella sinensis (Cr)																			
Pseudochattonella verruculosa (Cr)	EO								J	J		J				EO		OJ	
Macroalgae																			
Acrothamnion preissii	OJ		J		J	J			J	EJ		J	J	J		ENJ	EJ	OJ O O	
Asparagopsis armata	O		O	EO					J	J			J	J		J		O O	
Asparagopsis taxiformis (Cr)				J					J				J			J		O O	
Bonnemaisonia hamifera									J				J			ECJ		O O	
Caulerpa cylindracea	J		J			E			J	J		J	J	J		ENC	EN E	NJ NO NO	
Caulerpa taxifolia	J		J			J E			J	J		J	J	J		EN	EN	J O O	
Codium fragile subsp. fragile	O J		J		J		J		J	J		J	J	J		OJ	EN	O O	
Gracilaria vermiculophylla	O J		J O	EO		J J			J	J	J	OJ	OJ	J		EC	EJ EC	NJ O O	
Grateloupia turuturu	O O													J				O O	
Lophocladia lallemandii	J		J			J J			J	J		J	J	J		NC	N	ENJ O O	
Polysiphonia morrowii	J								J				J					J J	
Sargassum muticum	OJ J	O	J	NO J		J J			J	J	J	OJ	OJ	J		NC	ENOC	J NO NJ	
Stypopodium schimperi									J			O	J	J		J	J	O O	
Ulva australis																			
Undaria pinnatifida	O O			EO					J	J		OJ	OJ	J		CJ	J	O O	
Womersleyella setacea	OJ		J J		J J				J	ENJ	J	J	J	J		ENC	CJ	ENC NOJ O O	
Tracheophyta																			
Halophila stipulacea	J			J		J J			J	OJ			J			OJ		O	
Spartina alterniflora	O		O J	J	O J J				J J	J J		OJ	J			OC	J	O O	
Spartina anglica	O		O J	J	O J J				J J	J J		OJ	J			OC	J	EO EO	
Polychaeta																			
Ficopomatus enigmaticus	O	O		ECO					J	OJ						J	O	O O	
Hydroides dianthus	O			J												CO	CO	O O	
Hydroides elegans	O			J									J			CO	CO	O O	
Hydroides ezoensis	J			J												J	JO	O O	
Marenzelleria spp. (neglecta & viridis)	J			J J					J				J			ECO	CO	E EO EO	
Pileolaria berkeleyana																			
Spirorbis (Dexiospira) marioni																			
Crustacea																			
Acartia (Acanthacartia) tonsa (Cr)	J			J						J						CJ	J	J J	
Amphibalanus improvisus (Cr)	O	O							J			J	J			J	EN	O O	
Austrominius (Elminius) modestus	O												J					O O	
Callinectes sapidus	O O																		
Caprella mutica													J			E	C		
Cercopagis pengoi	O J										J					C	J	J J	
Charybdis (Charybdis) japonica																			

Table 2 (continued). Impact Matrix: Negative (red) and positive (green) impacts of alien marine species in European waters on ecosystem services (sensu Liqueste et al. 2013a) and biodiversity. Species that have not been previously listed as high-impact species in DAISIE, NOBANIS, SEBI, or CABI are indicated in bold. 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.

Alien species	Impact on marine ecosystem services (<i>sensu</i> Liqueste et al. 2013)											Impact on biodiversity												
	Provisioning			Regulating and maintenance						Cultural		Little/Unknown	Single-species impact	Multiple-species impact	Impact on keystone species or species of high conservation value	Affects entire ecosystem processes / wider ecosystem functioning	Ecosystem engineer - creator of novel habitat							
	Food (fisheries, aquaculture etc)	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				
Crustacea																								
<i>Charybdis helleri</i>																								
<i>Chionoecetes opilio</i>	J																							
<i>Eriocheir sinensis</i>	O	O	O	O													O	O						
<i>Gammarus tigrinus</i>	O																							
<i>Hemigrapsus sanguineus</i>																	E							
<i>Hemimysis anomala</i>																								
<i>Homarus americanus</i>	OJ	J																						
<i>Marsupenaeus japonicus</i>	O																							
<i>Monocorophium sextonae</i> (Cr)																								
<i>Palaemon elegans</i>																								
<i>Palaemon macrodactylus</i>	O																							
<i>Paralithodes camtschaticus</i>	O	O																						
<i>Percnon gibbesi</i>																								
<i>Platorchestia platensis</i> (Cr)																								
<i>Portunus segnis</i>	O																							
<i>Rhithropanopeus harrisi</i>	OJ	O											J											
Insecta																								
<i>Telmatogeton japonicus</i>																								
Mollusca																								
<i>Anadara kagoshimensis</i>	C					J		J	J									O	O					
<i>Anadara transversa</i>	OC					J		J	J										O	O				
<i>Arcuatula senhousia</i>	J			J				J	J											O	O			
<i>Brachidontes pharaonis</i>		O		J		J		J	J									C	C		O	O		
Chama pacifica			O	J		J		J	J												O	O		
<i>Crassostrea gigas</i>	CO	O		J	J	J	J	J	J	J	J	J	J					ENC	ENC	C	M	C	O	O
<i>Crassostrea virginica</i>						J		J	J	J	J	J	J											
<i>Crepidula fornicata</i>	EO	O		O	J		J	J	J	C	EN			J				EN	ENO	OJ	OJ	O	O	
<i>Ensis directus</i>	OJ			J		J	J	J	J				O					CJ				O	O	
<i>Mercenaria mercenaria</i>	O													J										
<i>Mya arenaria</i>	O		O	J		J		J	J					J				C	COJ		NOC	NO	NO	
<i>Mytilus edulis</i>						J		J	J					J										
<i>Petricolaria pholadiformis</i>						J		J	J					J				J				O	O	
<i>Pinctada imbricata radiata</i>	O	O		J		J		J	J					J				J	J			O	O	
<i>Potamopyrgus antipodarum</i>						J		J	J									C						
<i>Rapana venosa</i>	OC	O	O	J		J		J	J			J	J					J		OC	OJ			
Spondylus spinosus	O		O	J		J		J	J									C	J			O	O	
<i>Teredo navalis</i> (Cr)												O												
<i>Urosalpinx cinerea</i>	O																	OJ						
<i>Venerupis philippinarum</i>	O			C		J		J	NC									OC	M		ECO	ECO	O	O
Ascidacea																								
<i>Botryllodes violaceus</i>																		NI						
<i>Didemnum vexillum</i>																								
<i>Diplosoma listerianum</i> (Cr)																								
<i>Microcosmus squamiger</i>	O																	JO	C					
<i>Molgula manhattensis</i> (Cr)																								
<i>Polyandrocarpa zorritensis</i>																								
<i>Styela clava</i>	O																	CJ						

Table 2 (continued). Impact Matrix: Negative (red) and positive (green) impacts of alien marine species in European waters on ecosystem services (sensu Lique et al. 2013a) and biodiversity. Species that have not been previously listed as high-impact species in DAISIE, NOBANIS, SEBI, or CABI are indicated in bold. 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.

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Bryozoa																			
<i>Bugula neritina</i>													J						
<i>Tricellaria inopinata</i>																	C		
<i>Victorella pavidia</i> (Cr)																	J	O	
Cnidaria																			
<i>Blackfordia virginica</i>																			
<i>Cordylophora caspia</i>		O	O														O	O	
<i>Gonionemus vertens</i>																			
<i>Oculina patagonica</i>		J		J					J		J	J	J				O		
<i>Phyllorhiza punctata</i>																			
<i>Rhopilema nomadica</i>		O	O										O				CI		
Ctenophora																			
<i>Beroe ovata</i>		J		J					J	O							CO		J
<i>Mnemiopsis leidyi</i>		CO		O					CO								CO	CO	C
Echinodermata																			
<i>Acanthaster planci</i>																			
Fish																			
<i>Liza haematocheila</i>		C	O														C		
<i>Fistularia commersonii</i>		J	O														J		
<i>Lagocephalus sceleratus</i>			O														J		
<i>Neogobius melanostomus</i>		C	CI														CI	O	
<i>Oncorhynchus mykiss</i>																			
<i>Oncorhynchus tshawytscha</i>																			
<i>Plotosus lineatus</i>		O																	
<i>Salvelinus fontinalis</i>																			
<i>Saurida undosquamis</i>		C	O						J		J	J	J				C		
<i>Siganus luridus</i>		J	O		J	J		J			J	J	J				ECI	E	E
<i>Siganus rivulatus</i>		J	O		J	J		J			J	J	J				ECI	E	E

species (in terms of both positive and negative impacts) (Table 2; Figure 2; Supplement 1). Following food provision, the ecosystem services that were negatively affected by most species were ocean nourishment, recreation and tourism, and lifecycle maintenance, while the ecosystem services that were positively impacted by most species were cognitive benefits, water purification, and climate regulation (Table 2; Figure 2; Supplement 1). There was a variety of mechanisms through which alien species impact ecosystem services, which are different for each service (Figure 3). No impact was documented for weather regulation, and low numbers of species have

been reported to affect air quality regulation and biological regulation. No impact on any ecosystem service was reported for 31 species, while impacts on only one ecosystem service were documented for 21 species; the rest impacted (either in a positive or in a negative way) more than one ecosystem service (Figure 4). The highest number of ecosystem services impacted by a species was ten, documented for three species: the macroalga *Sargassum muticum* and the tracheophytes *Spartina alterniflora* and *S. anglica*. Tracheophyta and macroalgae were the taxonomic groups with the highest average numbers of impacted ecosystem services (9.0 and 6.1 respectively).

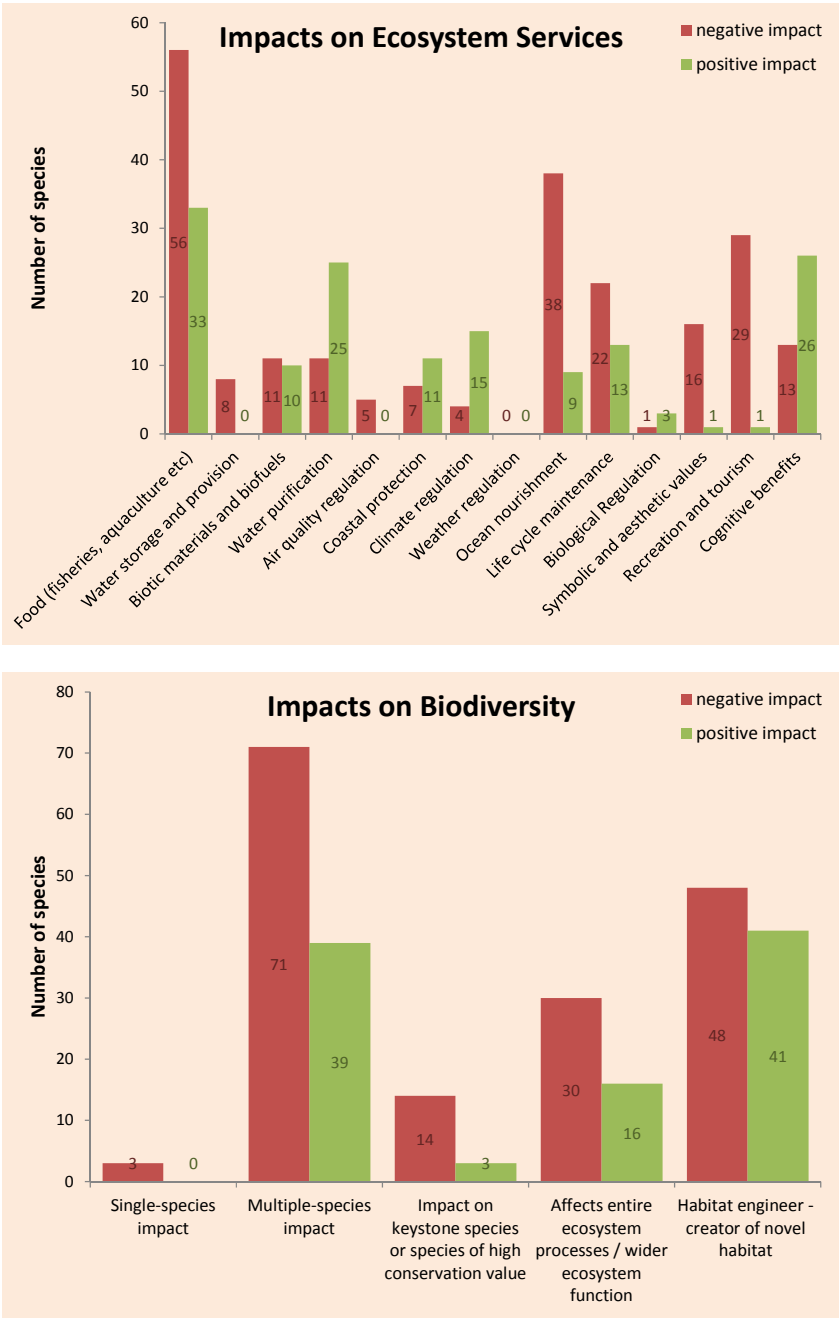


Figure 2. Overview of the number of taxa that have been reported to impact ecosystem services (Top) or biodiversity (Bottom).

The majority of the assessed alien species have been reported to affect more than one native species through a variety of mechanisms (Figure 5), more often, i.e. 65%, in a negative way, while 35% have been reported to have a positive impact on other species (Figure 2). In many cases, the aliens also impacted keystone species or species of high conservation value. Thirty-three of the

assessed species affected entire ecosystem processes or wider ecosystem functions, more often in a negative way (Figure 2; Table 2). Forty-nine of the assessed species have been reported to be ecosystem engineers (Wallentinus and Nyberg 2007; Berke 2010) that fundamentally modify, create or define habitats by altering their physical or chemical properties.

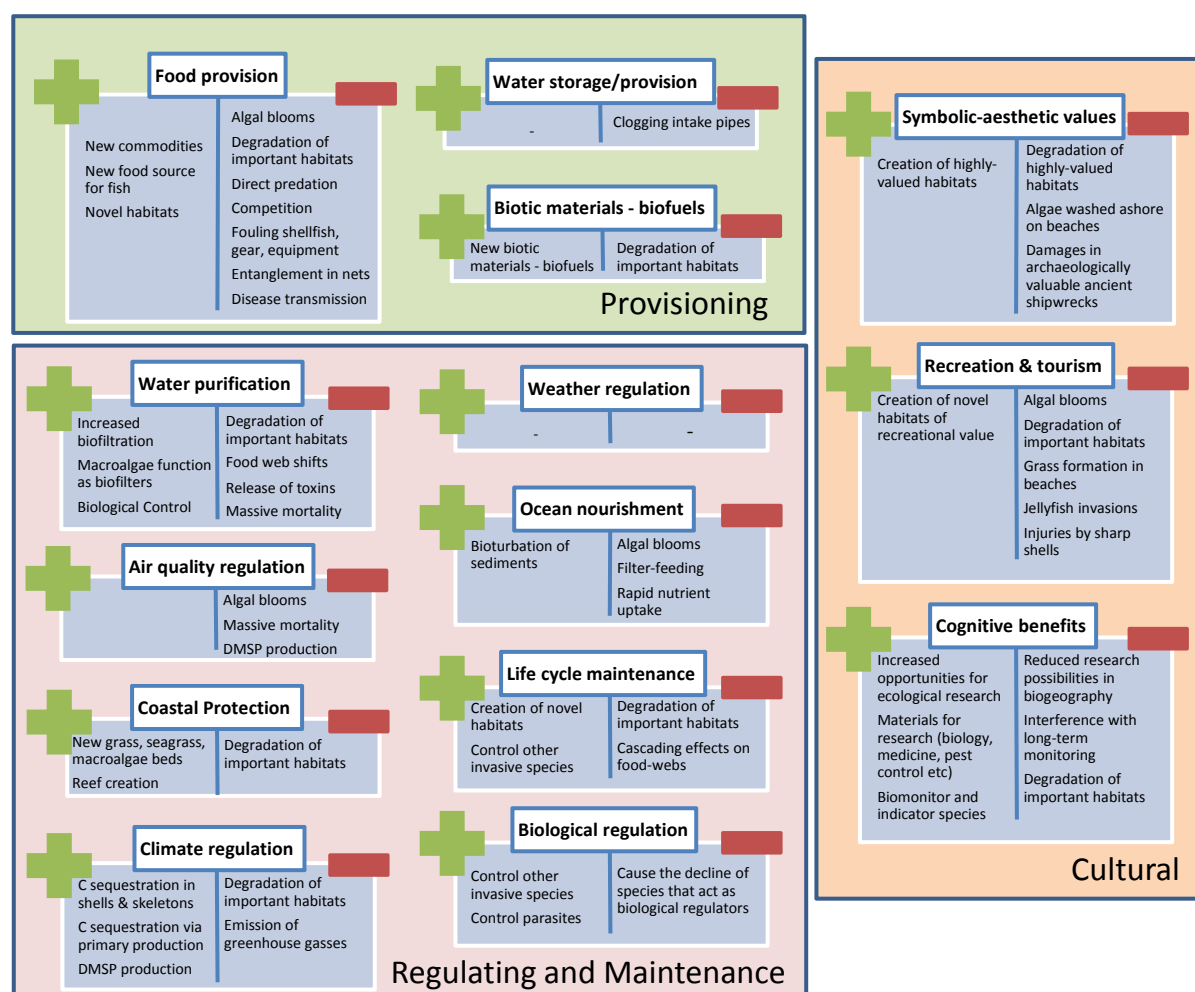


Figure 3. Main mechanisms through which alien species impact ecosystem services (sensu Lique et al. 2013a). Green cross: positive impacts; Red minus sign: negative impacts.

Reported impacts on ecosystem services and biodiversity are presented in detail below. A superscript (E) or (N) was added to indicate species for which inference of an effect was based on manipulative or natural experiments respectively. This was done to highlight, which specific impacts are supported by strong evidence. We do not provide extensive lists of references for all reported impacts but rather selected examples, with a focus on manipulative and natural experiments. A full list of references is provided in the supplementary material (Supplement 1).

Impact on ecosystem services

Food provision

Due to its economic relevance and the existence of market prices to provide a value, food provision was the most analysed marine ecosystem service. The most meaningful indicators of this service included abundance or biomass of commercial marine living resources, sea food quality, catches, landings, number of viable fisheries, and income and jobs from fisheries and aquaculture (Lique et al. 2013a). There are many mechanisms through which alien species impact food provision (Figure 3).

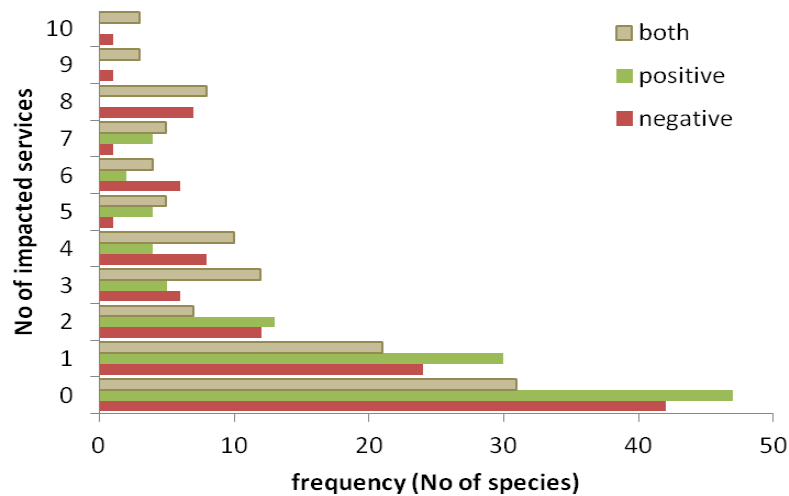


Figure 4. Frequency chart of the number of impacted ecosystem services by each species (i.e. how many species affect 0, 1, 2, 3, etc., ecosystem services).

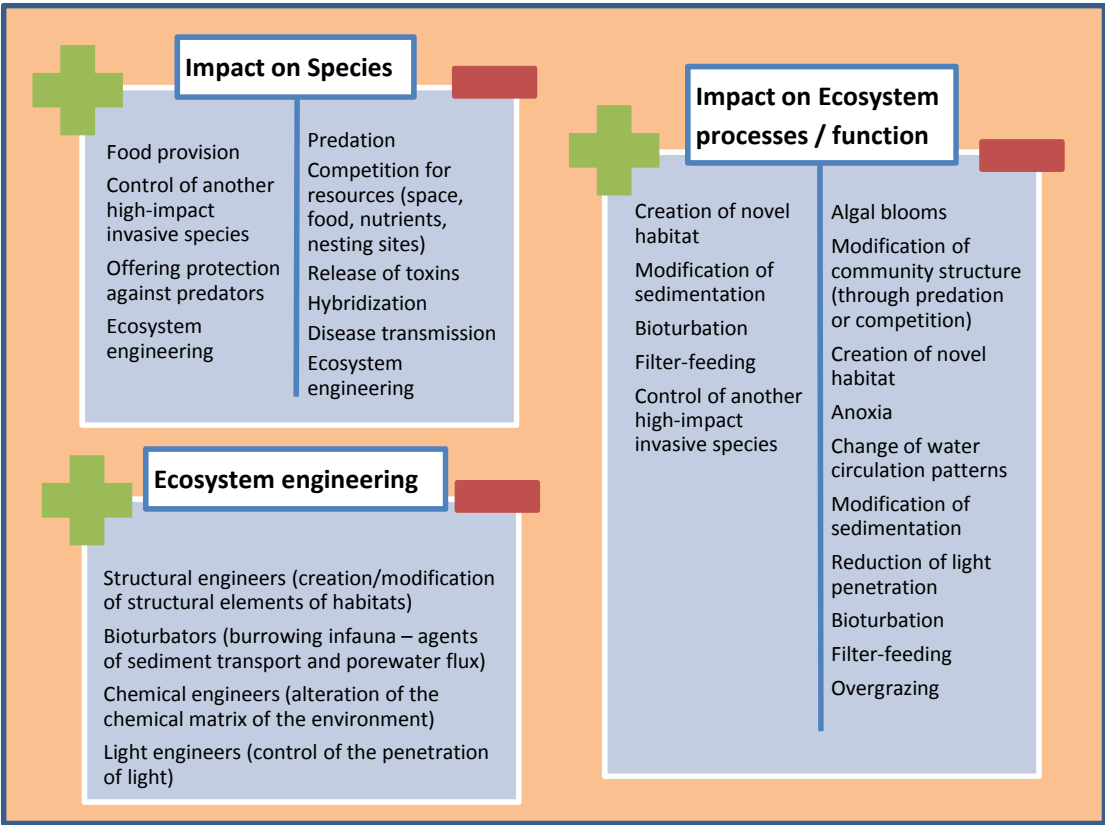


Figure 5. Main mechanisms through which alien species impact biodiversity. Green cross: positive impacts; Red minus sign: negative impacts.

Phytoplanktonic invasive species may bloom, causing severe damage to aquaculture or fisheries. *Alexandrium minutum* has caused persistent blooms in northern Europe since 1985, causing severe economic losses to aquaculture (Nehring 1998). *Karenia mikimotoi*, known as a fish-killer, has caused massive mortalities of fish and demersal animals in north-western Europe from 1968 onwards, including farmed finfish and shellfish (Raine et al. 2001 and references therein). *Gymnodinium catenatum* has become an abundant and well-established species in the Alborán Sea, and is associated with frequent toxic events. Over the past four decades, blooms of *G. catenatum* have caused Paralytic Shellfish Poisoning (PSP) episodes along the west coast of the Iberian Peninsula (Portugal and Spain), leading to the interruption of harvesting and commercialization of shellfish, with severe economic losses to the sector (Ribeiro et al. 2012). The ichthyotoxic (Skjelbred et al. 2011) flagellate *Pseudochattonella verruculosa*^(E) caused the death of 350 tonnes of farmed Norwegian salmon in 1998 and 1,100 tonnes in 2001 (Edvardsen et al. 2007), also causing mortalities of wild fish (garfish, herring, sandeel and mackerel) along the west coast of Denmark (Naustvoll 2010). *Phaeocystis pouchetii*^(E,N) has been reported to reduce growth in farmed salmon, and water from algal cultures was found to be toxic to cod larvae (Aanesen et al. 1998). During *Coscinodiscus wailesii* blooms, copious amounts of mucilage can be produced, which may cause extensive clogging of fishing nets, aquaculture cages and other equipment (Boalch and Harbour 1977; Boalch 1984).

Many alien species such as the macroalgae *Acrothamnion preissii*, *Caulerpa cylindracea*, *C. taxifolia*, *Codium fragile* subsp. *fragile*, *Gracilaria vermiculophylla*, *Lophocladia lallemandii*, *Sargassum muticum*, and *Womersleyella setacea*, the two *Spartina* grasses, and the coral *Oculina patagonica* may cause the degradation of important biotopes, which support stocks of commercial and non-commercial fish in many ways (e.g. by providing food, refuge and nursery grounds). Hence, these species may have an indirect negative impact on food provision as they impact essential habitats for fish stocks, such as sublittoral algae, seagrass and coralligenous communities. On the other hand, the novel habitats created by some of these ecosystem engineers may support (presumably different) stocks of commercial species, and it is often difficult to assess the overall balance of the effect on food provision, which may vary depending on several factors.

One of the most marked examples of impact on food provision is the invasion of the carnivorous ctenophore *Mnemiopsis leidyi* in the Black and Caspian Seas, which caused dramatic reductions in zooplankton, ichthyoplankton, and zooplanktivorous fish populations in the 1980s and early 1990s (Shiganova 1998; Shiganova et al. 2001b; Leppäkoski et al. 2009). This species, probably in combination with other stress factors (Bilio and Niermann 2004), affected stocks of many commercial fish, especially anchovy *Engraulis encrasicolus*, Mediterranean horse mackerel *Trachurus mediterraneus*, and Azov kilka *Clupeonella cultriventris* (Shiganova et al. 2001b). The annual financial loss of the fish catch attributed to the *Mnemiopsis* plague was calculated to be approximately 200 million USD in the Black Sea and 30–40 million USD in the Sea of Azov (GESAMP 1997). By contrast, one of the most marked examples of invasion events of gelatinous organisms with potentially positive impact was the establishment of the ctenophore *Beroe ovata* in the Black Sea. *B. ovata* is a predator of *M. leidyi* and has been reported to cause its decline in the Black Sea as well as a partial recovery of the planktonic food web structure (Shiganova et al. 2001a; Finenko et al. 2003).

Decline of commercial stocks due to direct predation or competition for resources (food or space) is the presumed mechanism of negative impact in the cases of the decapods *Homarus americanus* and *Paralithodes camtschaticus*, the fish *Fistularia commersonii*, *Neogobius melastomus*, *Saurida undosquamis*, *Liza haematocheila*, *Siganus luridus* and *S. rivulatus*, the bivalves *Crassostrea gigas* and *Pictada imbricata radiata*, and the gastropods *Urosalpinx cinerea* and *Rapana venosa*. Notably, *Rapana venosa* is responsible for the depletion of large stocks of commercial bivalves (esp. *Mytilus galloprovincialis* and *Ostrea edulis*) and the associated communities in the Black Sea since the 1950s (Zolotarev 1996; Salomidi et al. 2012). On the other hand, most of the same species are fished or farmed and have substantial positive impact on food provision, e.g. the above-mentioned *R. venosa* has supported very profitable fisheries in the Black Sea (Sahin et al. 2009 as *R. thomasi*).

The following alien species are edible and are important, some on a large-scale and others locally, for fisheries or aquaculture in their introduced range: the fish *Liza haematocheila*, *Saurida undosquamis*, *Siganus luridus*, *S. rivulatus*, the molluscs *Ensis directus*, *Mercenaria mercenaria*,

Mya arenaria, *Venerupis philippinarum*, and *Crepidula fornicata* the decapods *Chionoecetes opilio*, *Marsupenaeus japonicus*, *Palaemon macrodactylus*, *Paralithodes camtschaticus*, and *Portunus segnis*, and the brown alga *Undaria pinnatifida*. For example, *V. philippinarum* is one of the most important species in shellfish farming and its production accounts for >20% of the global shellfish market; Italy is the largest European producer with a production worth over 100 million euros (Otero et al. 2013).

Some macroalgae (e.g. *Codium fragile* subsp. *fragile*, *Gracilaria vermiculophylla*, *Grateloupia turuturu*, *Sargassum muticum*, *Undaria pinnatifida*) can have an economic negative impact on aquaculture and fisheries by fouling shellfish facilities, fishing gear and shellfish beds, smothering mussels and scallops, clogging scallop dredges, and interfering with harvesting. The cladoceran *Cercopagis pengoi* attaches to fishing gear and clogs nets and trawls, potentially causing problems and substantial economic losses for fishermen and fish farms. Other alien sessile species that may negatively affect aquaculture and fisheries by fouling gear, equipment or shellfish are the polychaetes *Ficopomatus enigmaticus*, *Hydroides dianthus* and *Hydroides elegans*, the barnacles *Amphibalanus improvisus* and *Austrominius modestus*, the gastropod *Crepidula fornicata*^(E), the ascidians *Microcosmus squamiger*, and *Styela clava*, and the hydrozoan *Cordylophora caspia* (e.g., Thieltges 2005a). These fouling species may compete for space with cultured bivalves causing a reduction of production, bring additional costs for sorting and cleaning fouled shells before marketing, and lead to extra costs for maintenance of fishing gear or aquaculture equipment.

The entanglement of some species (e.g. *Eriocheir sinensis*, *Gammarus tigrinus*, *Plotosus lineatus*) in fish and shrimp nets may increase handling times and damage the nets or the target species. Coastal trawling and purse-seine fishing are disrupted in Israel when massive swarms of the jellyfish *Rhopilema nomadica* appear, as the overwhelming presence of these venomous medusas in the nets causes net clogging and inability to sort the catch (Rilov and Galil 2009).

Disease transmission from alien species might be the cause of increased mortality in native populations of commercially important species or in holding facilities. For example, heavy mortalities of European lobsters in a South Wales holding facility in 2006 were due to gaffkaemia, a bacterial disease caused by the

Aerococcus viridans var. *homari*, which was transmitted to native lobsters by imported American lobsters (*Homarus americanus*) (Stebbing et al. 2012). *Rhithropanopeus harrisii* was identified as a carrier of the white spot syndrome, a viral infection causing a highly lethal and contagious disease in commercially harvested and aquacultured penaeid shrimp (Payen and Bonami 1979).

Many alien species (their planktonic larvae included) are thought to have a positive impact to fish populations by being a potential food source. This is the case for the polychaetes *Marenzelleria* spp., which are a food source for demersal fish such as plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) (Winkler and Debus 1997). The copepod *Acartia tonsa* constitutes significant prey for pelagic fish, and has also been used to produce live feed for aquacultured species (Sørensen et al. 2007), e.g. turbot reared in the Black Sea. The cladoceran *Cercopagis pengoi* is a very important food source for many fish, such as small herring, stickleback, smelt, and bleak (Ojaveer et al. 2004; Kotta et al. 2006).

Water storage and provision

The main type of negative impact of alien species on water provision is by clogging the intake pipes of industrial plants. This has been reported for the macroalgae *Lophocladia lallemandii* and *Sargassum muticum*, the polychaete *Ficopomatus enigmaticus*, the barnacle *Amphibalanus improvisus*, the decapods *Eriocheir sinensis* and *Rhithropanopeus harrisii*, the bivalve *Brachidontes pharaonis*, the hydrozoan *Cordylophora caspia*, and the jellyfish *Rhopilema nomadica*. No positive effect on water storage and provision has been attributed to any alien marine species.

Biotic materials and biofuels

Many alien species may have a negative impact on the provision of biotic materials by causing the degradation of important habitats that provide such materials, such as sublittoral algae, coralligenous communities, maerl beds, and seagrass meadows (Salomidi et al. 2012). Alien species that potentially cause the degradation of such habitats include the macroalgae *Acrothamnion preissii*, *Caulerpa cylindracea*, *C. taxifolia*, *Codium fragile* subsp. *fragile*, *Gracilaria vermiculophylla*, *Lophocladia lallemandii*, *Sargassum muticum*, and *Womersleyella setacea*, the fish *Siganus luridus* and *S. rivulatus*, the gastropod *Crepidula fornicata*, and the coral *Oculina patagonica*.

On the other hand, some alien species are the source of useful biotic materials. Both *Asparagopsis* species have been farmed as a source for compounds used in medicine and in cosmetics. *Gracilaria vermiculophylla* is farmed to produce agar. *Sargassum muticum* has a commercial value for extracting polyphenols, and when chemically treated its biomass can absorb heavy metals, as can char made from *Undaria pinnatifida*. The grasses *Spartina alterniflora* and *S. anglica* have been used as a food product for animals and can potentially be used as biofuels and as raw material for paper production. The crab *Eriocheir sinensis* has been used as live fish bait, for fishmeal production, as agricultural fertiliser, and for cosmetic products. *Mya arenaria* is also used in some localities to feed poultry, and *Crepidula fornicata* as a calcareous supplement for agriculture. The bivalves *Chama pacifica* and *Spondylus spinosus* are valuable species for seashell collectors, with a small trading market, and *Rapana venosa* shells are marketed as tourist souvenirs.

Water purification

Many alien species may have a negative impact on water purification by causing the degradation of important communities and their habitats that provide such a service, such as those of sublittoral algae, seagrasses, and mussel or oyster reefs. These species include the gastropod *Rapana venosa*, and the fish *Siganus luridus* and *S. rivulatus*. *R. venosa* is responsible (through predation) for the substantial reduction in the range and density of oyster and mussel settlements in the Black Sea (Zolotarev 1996; Salomidi et al. 2012), while *Siganus* spp. are responsible (because of overgrazing) for the gradual transformation of the eastern Mediterranean sublittoral ecosystem from one dominated by lush and diverse brown algal forests to one dominated by bare rock (Sala et al. 2011).

Alien suspension feeders such as bivalves, the gastropod *Crepidula fornicata*^(N), and the polychaetes *Ficopomatus enigmaticus*^(E), *Hydroides elegans*, *H. dianthus*, and *H. ezoensis* may substantially contribute to water purification by increased biofiltration, removal of suspended particulate matter and increased sedimentation (e.g. Davies et al. 1989; Pranovi et al. 2006). *C. fornicata*^(N) greatly improves water quality and causes a shift of phytoplankton blooms from toxic flagellates to diatoms (Ragueneau et al. 2002). Alien macrophytes can make a positive contribution to water purification by absorbing

pollutants and some (e.g. *Asparagopsis armata*^(E), *A. taxiformis*, *Gracilaria vermiculophylla*^(E), *Undaria pinnatifida*^(E)) are used in aquaculture as biofilters (e.g., Schuenhoff et al. 2006).

On the other hand, the population outbreak of *Mnemiopsis leidyi* in the Black Sea, and the resulting trophic cascade, has led to increased phytoplankton and bacterioplankton populations, triggering increases in zooflagellates and infusoria populations, and causing an overall decline in water quality. During blooms of phytoplanktonic species, extracellular toxins can be measured in the seawater, e.g. *Gymnodinium catenatum* in Portugal (Costa et al. 2010). Species that control harmful species that have a negative impact on water quality are considered as having a positive impact on water purification, e.g. *Acartia tonsa* can serve as a biological control of algal blooms and *Beroe ovata* controls *M. leidyi* outbreaks in the Black Sea.

Mortality of massive aggregations of alien species can be problematic for water quality. For example, *M. leidyi* has been reported to cause anoxia in near-bottom waters due to the massive deposition of dead individuals (Streftaris and Zenetos 2006). The copious mucilage, which may be produced during *Coscinodiscus wailesii* blooms, can aggregate, sink and cover the seabed, likely causing anoxic conditions.

Air quality regulation

Not many alien marine species have been reported to impact air quality regulation. Bloom-forming phytoplanktonic species such as *Karenia mikimotoi* and *Phaeocystis pouchetii* may negatively affect air quality due to the anoxia caused by the dying, sinking bloom and the smell of dead organisms. Also, the mass development of algae (e.g. *Lophocladia lallemandii*, *Womersleyella setacea*) can often result in anoxia. Along the Romanian beaches, stinking masses of dead *Mya arenaria* had to be removed regularly from the shoreline during the tourist season (Leppäkoski 1991). Species producing dimethylsul-phoniopropionate (DMSP) such as *Phaeocystis pouchetii*, *Codium fragile* subsp. *fragile*, *Spartina alterniflora*, and *S. anglica* have a negative impact on air quality (see also the section on Climate Regulation below).

Coastal protection

Important habitats for coastal protection include biogenic reefs (e.g. oyster and mussel reefs), kelp beds, and seagrass meadows (Boström et al.

2011; Salomidi et al. 2012; Liqueste et al. 2013b). Alien species that cause the degradation of such habitats (e.g. *Acrothamnion preissii*, *Gracilaria vermiculophylla*, *Lophocladia lallemandii*, *Womersleyella setacea*) can have a severe negative impact on coastal protection, although the same species may trap sediments (i.e., have a positive impact). The loss of, for example, eelgrass typically results in loss of positive feedbacks and a permanently turbid state of coarse sediment. *Caulerpa taxifolia* has been reported to outcompete the native seagrasses *Cymodocea nodosa* and *Posidonia oceanica* or affect their performance. However, it seems that the impact of this species on native seagrass beds has been overstated; dense and healthy seagrass beds are probably not affected by *C. taxifolia* (Jaubert et al. 1999). Furthermore, *C. taxifolia*^(E) beds (as well as *C. cylindracea* beds^(E)) in already degraded seagrass beds, stressed environments, or over bare soft substrata might have an overall positive effect on protection of sediments from erosion and provide coastal protection (Hendriks et al. 2010). Similar is the case of *Sargassum muticum*, which outcompetes seagrasses and native kelp, but on the other hand, its dense stands may contribute to coastal protection. *Rapana venosa* caused extensive damage to the oyster and mussel reefs of the Black Sea, and thus severely impacted the coastal protection service of these biogenic structures.

Spartina alterniflora and *S. anglica* are grasses that can accrete large volumes of tidal sediment leading to substantial increases in marsh elevation. This property made the species valuable for coastal protection, stabilisation of mudflats, and reclamation schemes in the early 20th century, and the species have been intentionally introduced by coastal engineers to coastal and estuarine mudflats throughout the world to control natural coastal erosion (Nehring and Adersen 2006). Like other phanerogames, *Halophila stipulacea* forms dense beds in soft substrata, contributing to sediment stability.

Another species with a potentially positive impact on coastal protection is *Crassostrea gigas*, which constructs extensive oyster reefs. *C. gigas* displaces mussel beds, which also offer coastal protection, but the overall balance of this change seems to be positive. Mature *C. gigas* reefs appear to be more persistent than mussel beds and may therefore stabilise the sediments on a longer time scale. As these mature reefs are anchored deep in the sediment, they consolidate the substrate firmly and thus prevent erosion of intertidal flats (Troost 2010).

Climate regulation

Once dissolved in the seawater, CO₂ reacts with the water and forms carbonic acid, the anion of which (carbonate) is used by shelled molluscs and corals to make calcium carbonate skeletons or shells and by algae to strengthen their cell walls against grazers. Hence, alien species that create such skeletons or shells have a potentially positive impact on carbon sequestration and thus on climate regulation. All the alien shelled molluscs that develop massive populations, increasing the overall mass of calcium carbonate, have a positive impact on climate regulation. For example, the gastropod *Crepidula fornicata*, may create dense populations that entirely cover the seabed; the bivalve *Mya arenaria*, can form dense aggregations of shell (death assemblages) that persist for decades; the oysters *Crassostrea gigas*, *Chama pacifica* and *Spondylus spinosus* can form massive oyster reefs; and the serpulid polychaete species *Ficopomatus enigmaticus* can form reef-like biogenic constructions in estuarine areas.

Mass occurrences of some alien species result in a decline of the carbon storage capacity of the ecosystem by causing the degradation of important habitats for carbon storage and sequestration, such as seagrass meadows and communities of sublittoral perennial algae. For example, the fish *Siganus luridus* and *S. rivulatus* cause the degradation of sublittoral brown algal forests, substantially reducing the carbon storage capacity of the shallow sublittoral zone in the eastern Mediterranean. Other species such as many macroalgae, the gastropod *Crepidula fornicata*, and the coral *Oculina patagonica* cause a shift from native habitats to novel habitats that offer the same service, and it is unknown what the overall balance is. We found no studies that set out to assess this balance. The grasses *Spartina* spp. and the seagrass *Halophila stipulacea* have a positive impact on carbon sequestration by storing carbon in their leaves and rhizomes.

Phaeocystis pouchetii, *Codium fragile* subsp. *fragile*, *Spartina alterniflora*, and *S. anglica* are species known for producing dimethylsulphonio-propionate (DMSP). DMSP can be enzymatically converted into dimethylsulphide (DMS), which is involved in the biological regulation of climate. DMS is a source of cloud-condensation nuclei (CCN), which regulate the reflectance (albedo) of clouds (Bates et al. 1987; Charlson et al. 1987; Carslaw et al. 2010). DMS emission seems to have a cooling tendency (as CO₂ pumping) through its effect on planetary albedo, and thus these DMSP

producers are considered to have a positive impact on climate regulation. However, the sensitivity of CCN to changes in DMS emissions seem to be rather weak (Woodhouse et al. 2010; Quinn and Bates 2011). Schoemann et al. (2005) estimated that the contribution of *Phaeocystis* blooms to the global DMS flux to the atmosphere is 5 to 10%. On the other hand, *S. alterniflora* communities have been shown to also produce high emissions of the greenhouse gas methane (Tong et al. 2012), which has a negative impact on climate.

Ocean nourishment

Large algal blooms consume nutrients, and thus alien species that build up such blooms, such as *Alexandrium minutum*, *Karenia mikimotoi*, *Gymnodinium catenatum*, *Phaeocystis pouchetii*, *Coscinodiscus wailesii*, *Fibrocapsa japonica*, and *Pseudochattonella verruculosa* may have a negative impact on ocean nourishment. However, the fate of the nutrients absorbed during the blooms and the extent of remineralisation varies substantially depending on the specific conditions (Schoemann et al. 2005). Due to their large surface-to-volume ratios, many of the filamentous macroalgae (but also thin flat ones) have rapid uptake rates of nutrients (Littler 1980; Littler and Littler 1980; Wallentinus 1984), which are then unavailable to other species. If short-lived they may, however, decompose quite quickly, and the nutrients will be circulated back to the system. On the other hand, the seagrass *Halophila stipulacea* makes a positive contribution to ocean nourishment as it absorbs its nutrients from the sediment, but the leaves have quite a fast turnover rate, meaning that the bound nutrients could be used within the food web.

Filter feeders, such as the bivalves *Anadara kagoshimensis*, *A. transversa*, *Arcuatula senhousia*, *Brachidontes pharaonis*, *Chama pacifica*, *Crassostrea gigas*, *Ensis directus*, *Pinctada imbricata radiata*, the gastropod *Crepidula fornicata*, the barnacle *Amphibalanus improvisus*, and the reef-forming polychaete *Ficopomatus enigmaticus*, filter suspended particles and subsequently deposit faeces as well as particles captured but not consumed onto the sediments. They can greatly increase the rate at which particles are transported from the water column to the sediments. Such increased sedimentation can represent a significant loss of energy and nutrients from the water column and decrease pelagic production (Strayer et al. 1999; Vanni 2002). Some of the N and P that was originally

incorporated in phytoplankton, but was not digested by the bivalves, can become buried in the accumulating sediments (Newell 2004). Furthermore, where biodeposits are incorporated into aerobic surficial sediments that overlay deeper anaerobic sediments, microbially mediated, coupled nitrification-denitrification can permanently remove N from the sediments as N₂ gas (Newell 2004). If they end up in anaerobic sediments, the anammox process may also result in N₂ gas. Hence, although in the short-term filter feeders might increase the nutrients in the seawater through excretion and by reducing the standing biomass of phytoplankton, the overall balance is negative. Additionally, many bivalves represent a large harvestable biomass, whose removal actually removes nutrients from the system. Thus, in general, invasive filter feeders have a negative impact on ocean nourishment, as defined by Lique et al. (2013a). However, it has to be stressed that in areas heavily loaded by nutrients, ocean nourishment is not a concern; filter feeders in such locations are generally considered of positive impact as they greatly improve water quality and thus assist highly valued species (e.g., seagrasses and macrophytes) to grow to greater depths due to increased light penetration and reduced epiphyte overgrowth.

Additionally, bioturbation of sediments through soft-bottom bivalve movements (*Anadara kagoshimensis*, *A. transversa*, *Ensis directus*, *Mya arenaria*, *Venerupis philippinarum*^(N)) increases sediment water and oxygen content and releases nutrients from the sediment to the water column (Vaughn and Hakenkamp 2001), thus positively impacting ocean nourishment. For example, *V. philippinarum*^(N) is known to significantly increase bioturbation rates, sediment mixing and re-suspension rates, which enhance solute exchange with the overlying water column and can promote phytoplankton blooms and macroalgal growth, positively affecting primary production (Bartoli et al. 2001; Queirós et al. 2011). The polychaetes *Marenzelleria* spp. also re-circulate organic matter and nutrients deposited in deeper sediment and accelerate remineralisation through their bioturbation activity, thus nourishing the seawater (Kotta et al. 2001; Norkko et al. 2012).

Lifecycle maintenance

Important habitats that act as nurseries, spawning areas, or migratory routes are communities of infralittoral algae, coralligenous communities, maerl beds, seagrass meadows, and biogenic structures

such as mussel and oyster beds or polychaete worm reefs (Salomidi et al. 2012). Therefore, any aliens that cause the degradation of such habitats may have a severe impact on the lifecycle maintenance of associated species. This is the case with many aliens such as the macroalgae *Acrothamnion preissii*^(E), *Caulerpa cylindracea*, *C. taxifolia*, *Codium fragile* subsp. *fragile*, *Gracilaria vermiculophylla*, *Lophocladia lallemandii*, *Sargassum muticum*, *Undaria pinnatifida*, and *Womersleyella setacea*^(E,N), the grasses *Spartina alterniflora* and *S. anglica*, the oyster *Crassostrea gigas*, the gastropods *Crepidula fornicata* and *Rapana venosa*, the coral *Oculina patagonica*, and the fish *Siganus luridus* and *S. rivulatus* (see also the text on 'Water purification' above). On the other hand, some of these species are also providers of the same service, and the overall balance is usually unknown. For example, *U. pinnatifida* seems to be beneficial in areas with high sediment load and lower salinities, where less native vegetation occurs, by providing a nursery ground for small fish and shelter for macrofauna (Fletcher and Farrell 1999). *S. muticum* has been reported to dominate the macroalgal assemblages of many sites and has caused the decline of many seaweeds and some seagrass beds. On the other hand, the morphology of the species, with its lateral branches lifted in an upright position due to the many small air bladders, contributes to the establishment of a three-dimensional habitat, which is important for the lifecycle maintenance of many species.

Only positive impacts on lifecycle maintenance have been reported for the brown alga *Undaria pinnatifida*, the seagrass *Halophila stipulacea*, the serpulid polychaete *Ficopomatus enigmaticus*, and the bivalves *Chama pacifica*, *Pinctada imbricata radiata*, and *Spondylus spinosus*. These three bivalves can create dense oyster beds, increasing the spatial complexity of benthic habitats, and acting as important feeding and nursery grounds for many fish and invertebrate species. *F. enigmaticus* creates reef-like aggregates, in which tubes grow vertically to the substrate in clumps and attach to each other, offering substrate, shelter, and food for many species such as fish and migratory birds.

The introduction and outbreak of *Mnemiopsis leidyi* in the Black Sea rendered the pelagic habitat unfavourable for the reproduction and thriving of many species of zooplankton and pelagic fish. The invasive species was able to consume most of the zooplankton stock within a few days (Finenko et al. 2006), causing cascading effects such as the collapse of planktivorous fish

and vanishing dolphin populations (Shiganova 1998). The negative impact of *M. leidyi* on lifecycle maintenance has been mitigated by the arrival and expansion of its predator *Beroe ovata* (Shiganova et al. 2001a; Finenko et al. 2003), which is therefore considered as having a positive impact on lifecycle maintenance.

Biological regulation

Some alien species may control other invasive species and thus have a positive impact on biological regulation. Due to its high abundance and grazing abilities, the copepod *Acartia tonsa* can serve as a potential biological control of algal blooms (Leppäkoski et al. 2002). The gastropod *Crepidula fornicata*^(E,N) causes a shift of phytoplankton blooms from toxic flagellates to diatoms, and can also serve as a sink for infectious trematode parasites and hence be beneficial for bivalve basibionts (Ragueneau et al. 2002; Thielges et al. 2006, 2009). *Beroe ovata* is an important regulator of the invasive ctenophore *Mnemiopsis leidyi* (Shiganova et al. 2001a; Finenko et al. 2003). On the other hand, the predatory cladoceran *Cercopagis pengoi* has caused the decline in the Baltic Sea of native small-sized cladocerans such as *Bosmina coregoni maritima*, *Evadne nordmanni*, and *Pleopsis polyphemoides* probably due to direct predation (Ojaveer et al. 2004; Kotta et al. 2006), and may enhance algal blooms due to decreased grazing pressure.

Many macroalgae have potential benefits for pest and disease control, however to our knowledge none of these species is industrially exploited in Europe for such purposes. For this reason, we have only included such applications in cognitive benefits, as materials for research and education.

Symbolic and aesthetic values

The impact of alien species on symbolic and aesthetic values is predominantly negative, as they can outcompete native species and cause the degradation of important and symbolic habitats. Such highly-valued habitats include coralligenous communities (especially gorgonian facies), biogenic structures such as mussel beds and coral reefs, seagrass meadows, and communities of infralittoral algae (Salomidi et al. 2012). Alien species that have negative impacts on these habitats include many macroalgae such as *Acrothamnion preissii*, *Caulerpa taxifolia*, *C. cylindracea*, *Codium fragile* subsp. *fragile*, *Gracilaria vermiculophylla*,

Lophocladia lallemandii, *Sargassum muticum*, and *Womersleyella setacea*, the fish *Siganus luridus* and *S. rivulatus*, the bivalve *Crassostrea gigas*, the gastropod *Rapana venosa*, and the coral *Oculina patagonica*. *C. gigas* is the only species for which both negative and positive impacts on symbolic and aesthetic values have been reported, as it contributes to the decline of the North Sea mussel beds (Kochmann et al. 2008) but also creates highly-valued oyster reefs (Troost 2010). Occasionally, large amounts of detached alien macroalgae are seen cast ashore on beaches, reducing the aesthetic quality of the shores (e.g. Hay and Villouta 1993: 475).

The cryptogenic wood-boring marine bivalve *Teredo navalis* has caused enormous damage to wooden constructions, e.g. in the North Sea and even in the southernmost Baltic, including archaeologically-valuable wooden shipwrecks (Förster 2003).

Recreation and tourism

Phytoplanktonic invasive species such as *Alexandrium minutum*, *Karenia mikimotoi*, *Gymnodinium catenatum*, *Phaeocystis pouchetii*, *Coscinodiscus wailesii*, *Fibrocapsa japonica*, and *Pseudochattonella verruculosa* may bloom, with negative impacts on coastal recreational activities.

Many invasive species may cause the degradation of habitats such as coralligenous communities, kelp, seagrass meadows, communities of sublittoral algae, and biogenic reefs that are important for recreational activities such as snorkelling, SCUBA diving, and recreational fishing (Salomidi et al. 2012). Such species include the macroalgae *Acrothamnion preissii*, *Caulerpa cylindracea*, *C. taxifolia*, *Codium fragile* subsp. *fragile*, *Gracilaria vermiculophylla*, *Lophocladia lallemandii*, *Sargassum muticum*, *Undaria pinnatifida*, and *Womersleyella setacea*, the bivalve *Crassostrea gigas*, the gastropod *Rapana venosa*, the coral *Oculina patagonica*, and the fish *Siganus luridus* and *S. rivulatus*. On the other hand, *Crassostrea gigas* creates biogenic reefs and thus provides a new habitat with positive impacts for recreational fishing or diving.

Spartina anglica is an invasive grass that may impede recreational activities. Along the Kattegat coast, some of its establishments occur on sandy beaches that are attractive to tourists, where the formation of large swards would change the aspect of the beach and create a belt with unattractive sedimentation (Nehring and Adersen 2006).

Since the mid-1980s, massive swarms of the planktivorous jellyfish *Rhopilema nomadica* have appeared along the Levant coast, stretching over more than 100 km (Rilov and Galil 2009). These swarms frequently draw nearer to the shore and adversely affect tourism because of the public's concern over the painful stings inflicted by the jellyfish (Yoffe and Baruchin 2004).

Ensis directus (a bivalve of shallow subtidal sands) might have an impact on the recreational value of some beaches as its sharp shells can cause deep cuts on bathers' feet. Such injuries can also occur when stepping on native species, but *E. directus* lives at much shallower depths than native species and consequently injuries are more likely. Mechanical removal of dead shells is required in some beaches.

Cognitive benefits

Inevitably, alien species introductions and their establishment in a novel region and ecosystem open new opportunities for ecological research, as they can be used for studies of concepts such as adaptive strategies, niche construction, niche dimensions, keystone species, interspecific relationships, trophic cascades, rapid evolution, propagule pressure, ecosystem engineering, connectivity, and dispersal mechanisms. However, they also result in reduced research possibilities in biogeography (it is difficult to explain the causalities behind the present distribution of species) and population genetics (Leppäkoski 2002). Some alien invasions greatly interfere with research and monitoring activities. For example, in the Baltic Sea, a long-term international monitoring programme of benthic communities, that has been conducted since the 1910s, may be invalidated by the establishment of aliens such as the polychaetes *Marenzelleria* spp. that have become dominant in soft-bottom communities, utilising the space and energy resources in a different manner and rate, and restructuring food webs (Leppäkoski 2002).

Many alien species have been used as material for research. Experiments have been conducted on *Alexandrium minutum* to try to increase their biomass and lipid production in bioreactors, with the goal of producing biofuels. The huge cells of *Coscinodiscus wailesii* have been used in many basic experiments in ecology, morphology, and physiology. *Hydroides elegans* is an excellent model organism for experimental studies and is easily adapted for laboratory biofouling research because of its rapid generation time (~3 wks) and ease of propagation. Larvae of *Amphibalanus*

improvisus are regularly used in toxicity tests, especially in connection with antifouling substances. *Austrominius modestus* has also been used as a test organism for toxicity tests. Because of its size (10 cm), abundance, longevity (max. 28 years), and ease of identification, *Mya arenaria* is used as a biomonitor and indicator species in several Baltic countries. *Pinctada imbricata radiata* has been used as a bioindicator of heavy metal pollution, because of its tolerance to chemical contamination and its ability to accumulate metals to several orders of magnitude higher than the background medium. The use of the crustacean *Caprella mutica* to monitor trace metals, especially due to environmental perturbations (oil spill accidents, waste outfalls, etc.), has been suggested. The crab *Rhithropanopeus harrisi* has become a popular model organism in many developmental, physiological and ecotoxicity studies.

Basic ecological studies have been performed with the red alga *Bonnemaisonia hamifera* and the brown alga *Sargassum muticum* on how grazer-deterrent substances and mechanisms work. The red algae *Gracilaria vermiculophylla* and *Grateloupia turuturu* have been used for fundamental studies on how different light and nutrient regimes affect these species. For the brown alga *Undaria pinnatifida*, there are many studies within medicine, products for functional food, and basic physiological science, such as studies on a gene that might help to protect this alga against various abiotic stresses. A gene regulating biological processes has been sequenced for *Styopodium schimperi*, and enzymatic activities in the chloroplasts have been studied using the green alga *Codium fragile* subsp. *fragile*. *Asparagopsis armata* extracts were shown to have a cytotoxic activity against human cancer cells, and medical research has shown that methanol extracts from *Polysiphonia morrowii* have photo-protective effects against ultraviolet B radiation-induced keratinocyte damage. *Mercenaria mercenaria* is possibly important in pharmacology, as the visceral mass and especially the liver and the crystalline style, contain a substance capable of acting selectively on cancer cells. The bryozoan *Bugula neritina*, probably through its symbiotic bacteria, is the source of the bryostatins, a family of macrocyclic lactones with anticarcinogenic properties.

Substantial research has been conducted on the use of materials from macroalgae for pest and disease control. Extracts obtained from the red alga *Grateloupia turuturu*, as well as from *Asparagopsis armata* and *A. taxiformis*, exhibited

a strong activity against fish pathogenic bacteria, the latter two species also against the disease in humans caused by the protozoans of the genus *Leishmania*. Compounds in *Polysiphonia morrowii* showed antiviral activity for several fish diseases. Extracts or bacteria hosted by many macroalgae (e.g. *Gracilaria vermiculophylla*, *Grateloupia turuturu*, *Sargassum muticum*, *Undaria pinnatifida*) have been found to have great potential for the production of anti-fouling materials. The alkaloid of *C. cylindracea*, caulerpin, has various biological properties such as antioxidant, antifungal, antibacterial, antinociceptive, and anti-inflammatory and can also be used as an insecticide against mosquito larvae. The seagrass *Halophila stipulacea* has been shown to have compounds that are insecticidal against rice weevil.

The degradation of habitats such as coralligenous communities, maerl beds, seagrass meadows, and communities of sublittoral algae that support cognitive services (Salomidi et al. 2012) has been reported for many alien species such as the macroalgae *Acrothamnion preissii*, *Caulerpa cylindracea*, *C. taxifolia*, *Codium fragile* subsp. *fragile*, *Gracilaria vermiculophylla*, *Sargassum muticum*, and *Womersleyella setacea*, the coral *Oculina patagonica*, and the fish *Siganus luridus* and *S. rivulatus*.

Impact on biodiversity

For 29 of the assessed species, no impact on biodiversity was found to be documented in the scientific and grey literature. The rest (81 species) have been documented to affect biodiversity with negative or positive impacts of various extent and intensity, ranging from single-species interactions to effects on entire ecosystem processes and wider ecosystem function, through a variety of mechanisms (Figure 5). In most cases of interactions with native species, multiple-species impacts have been reported, while in only three cases the invasive species have been reported to impact only a single species. All of these three cases are crustaceans (the lobster *Homarus americanus*, the prawn *Marsupenaeus japonicus*, and the amphipod *Platorchestia platensis*) that have been reported to negatively impact native species of similar niches and of the same genus or family (the European lobster *Homarus gammarus*, the prawn *Melicerus kerathurus*, and the amphipod *Orchestia gammarellus*, respectively).

In all other cases, the invasive species have impacted (in a negative or positive way) more than one species or even entire communities.

There are various kinds of interactions with native species through competition for resources, predation, release of toxins, disease transmission, and ecosystem engineering. Hybridisation between some alien species and native congeners has been reported, e.g. between *Crassostrea gigas* and *C. angulata*, *Mytilus edulis* and *M. galloprovincialis*, *Venerupis philippinarum* and *V. decussata*, *Spartina alterniflora* and *S. maritima*, with implications for native populations. In the latter case, the hybrid subsequently underwent autogenic chromosome doubling to produce a new high-impact invasive fertile species, *Spartina anglica*.

Competition for resources (predominantly for space and secondarily for food or nutrients) is the most commonly reported mechanism by which native species are displaced. It has been reported for many macroalgae, such as *Acrothamnion preissii*^(E,N), *Asparagopsis armata*, *A. taxiformis*, *Bonnemaïsonia hamifera*^(E), *Caulerpa cylindracea*^(E,N), *C. taxifolia*^(E,N), *Codium fragile* subsp. *fragile*, *Gracilaria vermiculophylla*^(E), *Grateloupia turuturu*, *Lophocladia lallemandii*^(N), *Sargassum muticum*^(N), *Stypopodium schimperi*, *Undaria pinnatifida*, and *Womersleyella setacea*^(E,N), which may dominate algal assemblages by outcompeting native macroalgae and sessile invertebrates and often creating monospecific stands and homogenised microhabitats (e.g. Piazzì et al. 2005; Cebrian et al. 2012; Svensson et al. 2013). *Spartina* spp. alter natural coastal habitats, turning them into monoculture meadows and thereby displacing native flora and fauna. Sessile invertebrates such as the barnacles *Amphibalanus improvisus* and *Austrominius modestus*, the coral *Oculina patagonica*, the hydrozoan *Cordylophora caspia*, the bivalves *Brachidontes pharaonis*^(E), *Chama passifica*, *Crassostrea gigas*^(E,N), *Pinctada imbricata radiata*, and *Spondylus spinosus*, the gastropod *Crepidula fornicata*^(E,N), the ascidians *Botrylloides violaceus*^(N), *Microcosmus squamiger*, and *Styela clava*, and the bryozoan *Tricellaria inopinata* have been reported to dominate benthic communities, outcompeting other sessile species for space or food (e.g., Safriel and Sasson-Frosting 1988; Kochmann et al. 2008). Motile benthic invertebrates such as the crustaceans *Callinectes sapidus*, *Caprella mutica*^(E), *Eriocheir sinensis*, *Gammarus tigrinus*^(E), *Hemigrapsus sanguineus*^(E), *Palaemon elegans*, the polychaetes *Marenzelleria* spp.^(E) and the gastropod *Potamopyrgus antipodarum* compete with ecologically similar native species, which may be displaced under certain conditions

(e.g., Kotta and Ólafsson 2003; Neideman et al. 2003; Shucksmith et al. 2009; Landschoff et al. 2013). The fish *Neogobius melanostomus* successfully competes for space, nesting sites, and food resources with many other cohabiting benthic fishes. The lizardfish *Saurida undosquamis* has been reported to displace the hake *Merluccius merluccius* and the native lizardfish *Synodus saurus*. The Pacific mullet *Liza haematocheila* has been reported to compete for food with the native mullets *Mugil cephalus* and *M. auratus*. The copepod *Acartia tonsa* competes with native copepods, especially congeners, and may dominate zooplanktonic communities.

Eight alien species have been blamed for the decline of native populations due to direct predation. The Ponto-Caspian predatory cladoceran *Cercopagis pengoi* has caused the decline of native small-sized cladocerans in the Baltic Sea, such as *Bosmina coregoni maritima*, *Evadne nordmanni*, and *Pleopsis polyphemoides*, probably due to direct predation. The crab *Hemigrapsus sanguineus* has been observed to reach very high densities and have negative impacts on small recruits and juveniles of several native species of barnacles, littorine snails, brachyuran crabs, and mytilid bivalves. The large crab *Paralithodes camtschaticus* is an active predator on benthic fauna, especially in deep soft-bottom environments, and can have an enormous predatory impact on local species, especially during mass developments. The gastropod *Rapana venosa* feeds on bivalves and is responsible for the depletion of large stocks of commercial bivalves (esp. *Mytilus galloprovincialis*) and the associated communities in the Black Sea since the 1950s. The Atlantic oyster drill *Urosalpinx cinerea* preys on oysters, mussels and clams, and is a major pest to the commercial oyster industry. In the Black Sea, the carnivorous ctenophore *Mnemiopsis leidyi* has caused dramatic reductions in zooplankton, ichthyoplankton, and zooplanktivorous fish populations in the 1980s and early 1990s. The fishes *Fistularia commersonii* and *Lagocephalus sceleratus* predate on various fish and invertebrates, some of which are of commercial importance, and could potentially affect their stocks (Kalogirou 2013).

The release of toxins, which may be released into the seawater or transmitted through the food chain and accumulate in some species, thereby affecting their condition, behaviour and survival, has been documented for many phytoplanktonic aliens such as *Alexandrium minutum*, *Karenia mikimotoi*, *Gymnodinium catenatum*^(E), *Fibrocapsa*

japonica^(E), and *Pseudochattonella verruculosa*^(E) (e.g. Estrada et al. 2010; Skjelbred et al. 2011; de Boer et al. 2012). For *Bonnemaisonia hamifera*^(E) it has been shown that the grazer-deterrent 1,1,3,3-tetrabromo-2-heptanone, also works as an allelopathic compound, and it was proven that this can be transferred by direct contact, from this alien alga to a native host alga. The transferred compound remains active and with unaltered function; i.e., inhibiting recruitment of native competitors (Svensson et al. 2013). *C. taxifolia* produces caulerpenyne, a toxic secondary metabolite that protects this macroalga against epiphytes and herbivores, and thus it does not provide the same trophic support as seagrasses and native seaweeds. *Codium fragile* subsp. *fragile* has been shown to contain relatively high concentrations of dimethylsulfonio-propionate (DMSP) and the products of its cleavage, dimethylsulphide (DMS), and acrylic acid (AA), the latter two acting as chemical defences against sea urchins. *Lophocladia lallemandii*^(N) excretes lophocladines, alkaloids with cytotoxic effects, resulting in an increased antioxidant response by its host, the seagrass *Posidonia oceanica* (Suredda et al. 2008); these cytotoxic compounds may be the reason *L. lallemandii* is avoided by herbivorous fish, resulting in a negative impact on the higher levels of the food web.

Some alien species have been reported to transmit diseases to native populations. Gaffkaemia, caused by *Aerococcus viridans* var. *homari*, has been introduced in European waters by American lobsters (*Homarus americanus*) and has infected European lobsters (*H. gammarus*) both in holding facilities and in the wild (Stebbing et al. 2012). The white spot syndrome can be transmitted by *Rhithropanopeus harrisii* to native penaeid shrimp (Payen and Bonami 1979).

In some cases, invasive alien species have been reported to negatively impact keystone species or species of high conservation value. Such species include the protected Mediterranean endemic seagrass *Posidonia oceanica* and its associated communities, which are impacted by the macroalgae *Acrothamnion preissii*, *Caulerpa cylindracea*^(N), *C. taxifolia*^(N) (Dumay et al. 2002), *Lophocladia lallemandii*^(N) (Ballesteros et al. 2007), and *Womersleyella setacea*; the eelgrass *Zostera marina*, which is impacted by *Gracilaria vermiculophylla*^(E,N) (Martínez-Lüscher and Holmer 2010; Thomsen et al. 2013), and potentially by *Sargassum muticum*; the grass *Spartina maritima*, the eelgrass *Zostera noltii*, and the locally rare sea

lavender *Limonium humile* (impacted by *Spartina alterniflora* and *S. anglica*); mussel and oyster biogenic reefs (impacted by the oyster *Crassostrea gigas*, the macroalga *Codium fragile* subsp. *fragile*, and the gastropod *Rapana venosa*); gorgonians (impacted by *A. preissii*^(E) and *W. setacea*^(E); Linares et al. 2012; Cebrian et al. 2012); dolphins in the Black Sea and seals in the Caspian Sea (because of the collapse of pelagic fisheries due to *Mnemiopsis leidyi*); and the threatened *Cystoseira* forests in the Mediterranean Sea (impacted by *Siganus luridus*^(E) and *S. rivulatus*^(E); Sala et al. 2011). The only alien species which have been reported to have positive impacts on keystone species or species of high conservation value are (1) *Marenzelleria* spp.^(E), which by burying the seeds of *Z. marina* reduces seed predation and facilitates seed germination (Delefosse and Kristensen 2012); (2) *C. fragile* subsp. *fragile*^(E,N), which has been reported as being likely to speed up the process of recovery of mussel beds after their integrity has been disrupted by heat stress or human harvesting (Bulleri et al. 2006; based on experiments on breakwater structures); and (3) *C. cylindracea*^(E), which was reported to have both negative and positive impacts on the seagrasses *Cymodocea nodosa* and *Zostera noltii* (Ceccherelli and Campo 2002).

One potentially positive impact on other species is related to the alien being an abundant source of prey. For example, decapods such as the prawn *Crangon crangon* feed well on the alien diatom *Coscinodiscus wailesii*; *Spartina* spp. are a food source for many grazers such as geese, ducks and other water birds and wildlife; polychaetes such as *Ficopomatus enigmaticus*, *Hydroides* spp., and *Marenzelleria* spp. are excellent food for many species, including fish; the copepod *Acartia tonsa*, the cladoceran *Cercopagis pengoi*, and the amphipod *Caprella mutica* are significant prey for fish; the crab *Hemigrapsus sanguineus*, the shrimp *Palaemon elegans*, and the clams *Ensis directus* and *Mya arenaria* can serve as important food resources for many species of birds and fish; the chironomid insect *Telmatogeton japonicus* can be advantageous for native species as a food source, especially for birds; the introduction of the clam *Venerupis philippinarum* into European coastal waters has presented the Eurasian oystercatcher *Haematopus ostralegus* with a new food resource and reduced its predicted over-winter mortality rates; the mytilid *Brachidontes pharaonis* and the ascidian *Microcosmus squamiger* are preyed upon by the native whelk *Stramonita haemastoma*,

positively impacting its populations; and the fish *Neogobius melanostomus* is a very important food source for great cormorants (*Phalacrocorax carbo*).

A different type of positive impact has been reported for *Crepidula fornicata*^(E), which offers protection to mussels against starfish predation (Thieltges 2005b). *Amphibalanus improvisus*^(E) can promote the settlement success and further development of filamentous algae, probably by increasing nutrient availability in benthic systems through biodeposition (Kotta et al. 2006). *Beroe ovata* had a positive impact on many planktonic species by controlling their predator *Mnemiopsis leidyi*. In addition to that, alien ecosystem engineers probably have the most marked impacts on native species. The diversity and richness of native species is enhanced in many cases by alien ecosystem engineers (e.g. de Montaudouin and Sauriau 1999; Buschbaum et al. 2006; Markert et al. 2009; Thomsen 2010; Thomsen et al. 2013), especially by structural engineers (see the following section on ecosystem engineering).

Many alien species may have a marked impact on ecosystem processes and the functioning of the broader ecosystem. Algal blooms can cause massive mortalities on the populations of many species, reduce the transfer of carbon and nutrients in food-webs, and change the physiochemical properties of water (e.g. by reducing available light for benthic autotrophs). Invasive macroalgae such as *Acrothamnion preissii*^(N), *Caulerpa cylindracea*^(N), *C. taxifolia*, *Codium fragile* subsp. *fragile*, *Gracilaria vermiculophylla*^(E,N), *Lophocladia lallemandii*, and *Womersleyella setacea*^(N), may entirely modify the community structure and trophic flows, may form mono-specific layers that often trap sediments and create an anoxic layer underneath, can modify the quality and intensity of physical, chemical and hydrodynamical factors, the number and quality of shelters, and substantially modify trophic webs (e.g. Piazzzi et al. 2007; Cacabelos et al. 2012). *Sargassum muticum*^(E,N) creates a novel three-dimensional habitat, modifies the trophic web, reduces photosynthetically active radiation on the under-storey layers, and has physical effects on its local environment, such as effects on sedimentation and light penetration, water movement, and oxygen levels (e.g. Strong et al. 2006). The grasses *Spartina* spp.^(E) can form extensive monocultural meadows, cause the elevation of mudbanks, change water circulation patterns, reduce tidal flows, increase the oxidising capacity of sediments, enhance total microbial mineralisation, and replace

open mudflat habitats associated with bottom-dwelling invertebrate communities with vegetative salt marsh species (e.g. Gribsholt and Kristensen 2002). Bioturbators such as the polychaetes *Marenzelleria* spp.^(E) and the burrowing bivalves *Mya arenaria*^(N) and *Venerupis philippinarum*^(E) re-circulate organic matter and nutrients deposited in deeper sediment layers, link benthic and pelagic subsystems, affect sediment and fluid transport processes, improve oxygen circulation and the aerobic transformation of organic matter, and affect nutrient fluxes (Kotta et al. 2001; Sgro et al. 2005; Hietanen et al. 2007; Quintana et al. 2013). Through severe predation or competition for resources, many species dramatically modify food webs and trophic flows within invaded ecosystems (e.g. *Acartia tonsa*, *Cercopagis pengoi*, *Rapana venosa*, *Mnemiopsis leidyi*, *Beroe ovata*). Filter feeders such as *Crassostrea gigas*, *Crepidula fornicata*, and *Mya arenaria* can substantially modify trophic structure, increase sedimentation, remove nutrients from the water column, and decrease pelagic production. The replacement of native species by *Gammarus tigrinus*^(E) can lead to a substantial decrease in the recycling rate of leaf litter (Piscart et al. 2011). *Paralithodes camtschaticus* can cause the degradation of sediment habitat quality due to hypoxic conditions and low levels of biological activity. *Arcuatula senhousia* alters sedimentary properties through the construction of byssal mats on the surface of soft sediments. *Oculina patagonica* can initiate an important change in community structure and end the monopolisation of algae in shallow assemblages; potentially it can greatly modify both the underwater seascape and the sources of primary production in the ecosystem. *Siganus* spp.^(E), through overgrazing, radically alter the community structure and the native food web of the rocky infralittoral zone, depriving the ecosystem of the valuable functions of algal forests (Sala et al. 2011).

In addition to the impacts of each single species on biodiversity, which were the focus of this review, alien species generally add to species pools, increasing γ -biodiversity. For example, ~1,000 alien marine species have been reported in the Mediterranean, of which more than half are established and spreading (Zenetos et al. 2012), while no basin-wide extinction related to invasive species has been recorded. On the other hand, as reported above, there are many examples of local extirpation and range shifts that are concurrent with alien invasions. Hence, α -diversity has locally decreased in some cases (see the

Siganus spp. example above) and increased in others (see the next section on ecosystem engineering) because of the habitat-specific increase in species richness. Biotic homogenisation as a result of invasive species has been suggested (Galil 2007; Ben Rais Lasram and Mouillot 2009), but this needs further investigation and is dependent on the spatial scale (Olden 2006).

Ecosystem engineering – creation of novel habitats

Ecosystem engineers are those organisms that “directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials. In so doing, they modify, maintain, and/or create habitat” (Jones et al. 1994). These novel habitats differ in composition and structure from past and present native habitats, and result in different species interactions and functions. In general, ecosystem engineers benefit the populations of some species, while they cause the local decline of others. Both positive and negative impacts are associated with most ecosystem engineers. Olenin and Leppäkoski (1999) were among the first to classify alien benthic species in brackish-water systems according to their habitat modifying ability and novel ecosystem services provided. Berke (2010) classified ecosystem engineers into four broad process-based categories that are not mutually exclusive: structural engineers, bioturbators, chemical engineers, and light engineers.

Structural engineers generally enhance diversity and richness, although not in every context (Berke 2010). This category consists of organisms that create or modify structural elements of the habitat, such as reef-builders, tube-builders, macroalgae, and seagrasses. Of the assessed species (Table 2), the alien structural engineers include: most macroalgae; the seagrass *Halophila stipulacea*; the grasses *Spartina* spp.; the reef-building polychaetes *Ficopomatus enigmaticus* and *Hydroides* spp.; the barnacles *Amphibalanus improvisus* and *Austrominius modestus*; the bivalves *Arcuatula senhousia*, *Anadara transversa*, *Brachidontes pharaonis*, *Chama pacifica*, *Crassostrea gigas*, *Mya arenaria*, *Petricolaria pholadiformis*, *Pinctada imbricata radiata*, and *Spondylus spinosus*; the gastropod *Crepidula fornicata*; the coral *Oculina patagonica*; and the hydrozoan *Cordylophora caspia*. With the exception of most macroalgae and the coral *O. patagonica* that might diminish structural complexity and species richness by outcompeting native assemblages, these species generally increase the spatial complexity of benthic

habitats, offer novel microhabitats, and provide nursery grounds, shelter for macro- and microfauna, and strongholds for a diverse community of algae and invertebrates.

Burrowing infauna have important roles in the geophysical environment and in community dynamics, being agents of sediment transport and porewater flux (Aller et al. 2001). Eight of the assessed alien species fall into this category of ecosystem engineers (other species might also exhibit burrowing activities, but there was no evidence of their having an important role as ecosystem engineers in European seas): *Marenzelleria* spp., *Eriocheir sinensis*, *Anadara kagoshimensis*, *Anadara transversa*, *Ensis directus*, *Mya arenaria*, *Venerupis philippinarum*. Due to their burrowing activity, these species can increase sediment water and oxygen content and enhance solute exchange with the overlying water column, thereby affecting nutrient cycling (Vaughn and Hakenkamp 2001; Bartoli et al. 2001; Queirós et al. 2011; Norkko et al. 2012). They also increase sediment erosion and re-suspension rates (Sgro et al. 2005), substantially modifying both benthic and pelagic habitats.

Chemical engineers alter the chemical matrix of their environment through physical or physiological activities; many of them are also structural engineers or bioturbators (Berke 2010). All the burrowing species mentioned above are also included in this category as their activity extends the oxygenated layer deeper into the sediment, thereby increasing local redox potential and contributing to sediment-water solute exchange (Aller et al. 2001). Other alien chemical engineers are: the grasses *Spartina alterniflora* and *S. anglica*^(E), as they increase the oxidising capacity of sediments and enhance total microbial mineralization in comparison to unvegetated areas (Gribsholt and Kristensen 2002); the bivalve *Arcuatula senhousia*, as it deposits large amounts of organic matter, altering the nutritional quality of the sediment, leading to the shallowing of the redox potential discontinuity layer, and making the environment within or under byssal mats unsuitable to adults or larvae of other species (Mistri et al. 2004); *Caulerpa cylindracea*^(N), as it can form compact multilayered mats up to 15 cm thick that trap sediment, beneath which an anoxic layer may develop (Piazzi et al. 2007; Klein and Verlaque 2008); *Crepidula fornicata*, as it traps suspended matter and produces considerable amounts of mucous pseudofaeces, transforming the primary sandy sediment into a muddy one with a high organic content that becomes rapidly

anoxic and unsuitable for other species; the phytoplanktonic species *Karenia mikimotoi* and *Phaeocystis pouchetii*, whose dying, sinking blooms cause anoxia; the diatom *Coscinodiscus wailesii*, whose copious mucilage can aggregate, sink and cover the seabed, likely causing anoxic conditions; *Mnemiopsis leidyi*, which can cause anoxia in near-bottom waters due to massive deposition of dead individuals (Streftaris and Zenetos 2006).

Light penetration is an important physical property of habitats, as it defines the depth at which photosynthesis can occur. Bloom-forming phytoplanktonic species, such as *Alexandrium minutum*, *Alexandrium monilatum*, *Karenia mikimotoi*, *Phaeocystis pouchetii*, *Coscinodiscus wailesii*, *Fibrocapsa japonica*, and *Pseudo-chatonella verruculosa*, reduce light penetration. *Mnemiopsis leidyi* causes the collapse of zooplankton, an increase in phytoplankton (which is free from grazing pressure), and thus a reduction in light penetration. All filter feeders (listed in the section on 'Ocean Nourishment') reduce turbidity and may substantially increase light penetration, leading to increased depths at which macrophytes grow and thus supporting greater biomasses per unit area by providing more three-dimensional habitat. Many of the alien macroalgae either build up thick mats or are so large that they reduce the amount of light reaching other primary producers. The filamentous or turf-forming *Acrothamnion preisii*, *Asparagopsis armata*, *Bonnemaisonia hamifera*, *Lophocladia lallemandii* and *Womersleyella setacea* often grow so densely on other primary producers that they significantly reduce the light that is available to them. Other species such as *Caulerpa cylindracea*, *C. taxifolia*, *Codium fragile* subsp. *fragile*, *Gracilaria vermiculophylla*, *Grateloupia turuturu*, *Sargassum muticum* and *Undaria pinnatifida* either form dense stands or are large enough to efficiently reduce the light that reaches understory species. The *Spartina* grasses, when occupying sediments, also cause a large reduction in the light available to sediment-dwelling primary producers.

Proposed inventory of high-impact alien marine species in Europe

Some alien marine species that are reported as being of high impact elsewhere, as documented in the CABI-ISC, do not seem to have become invasive in European seas. These species include the crustaceans *Charybdis japonica* and *C. helleri*, the bivalves *Crassostrea virginica* and *Mytilus*

edulis (considered alien to the Black Sea), the ascidians *Didemnum vexillum*, *Diplosoma listerianum*, and *Polyandrocarpa zorritensis*, the jellyfish *Phyllorhiza punctata*, the hydrozoan *Gonionemus vertens*, the bryozoan *Bugula neritina* (for which only some positive cognitive benefits were found), the starfish *Acanthaster planci* (its presence in Europe is questionable), and the alga *Ulva australis*. While, based on our current knowledge, they should not be considered as high-impact species in Europe (and thus were excluded from our proposed inventory), some of these species should remain on watch lists as they may become invasive in the future. Chinook salmon, *Oncorhynchus tshawytscha*, although included in the CABI-ISC database, is not considered to be invasive anywhere in the world (CABI 2013), and its establishment in Europe is uncertain.

Some predominantly freshwater species that are also found in marine environments have been included in our assessment. While they have a high impact in the freshwater environment, most of these species are not invasive in marine waters and thus were excluded from the proposed European inventory of alien species that have a high impact on the ecosystem services and biodiversity of the marine environment. These species include the mysid *Hemimysis anomala*, and the fishes *Oncorhynchus mykiss* and *Salvelinus fontinalis*.

For the diatom *Odontella sinensis* (DAISIE), the polychaetes *Pileolaria berkeleyana* (SEBI) and *Spirorbis marioni* (SEBI), the crustaceans *Monocorophium sextonae* (NOBANIS) and *Percnon gibbesi* (DAISIE; SEBI; CABI-ISC), the ascidian *Molgula manhattensis* (NOBANIS), and the hydrozoan *Blackfordia virginica* (SEBI), sufficient evidence of any impacts on ecosystem services and biodiversity was not available; therefore, these species were excluded from the proposed inventory. For example, for *P. gibbesi* the only impact mentioned by both DAISIE and CABI-ISC refers to its potential competition with the native species *Pachygrapsus marmoratus* (and to a lesser extent with *Eriphia verrucosa*). However, laboratory experiments indicate that *P. marmoratus* is unlikely to be excluded from its natural habitat by the alien species, and significant spatial resource partitioning on the part of *P. marmoratus* is unlikely to occur (Sciberras and Schembri 2008). Of the 101 high-impact marine species included in the lists of DAISIE, NOBANIS, CABI-ISC, and SEBI, we excluded 23 species for which we found no

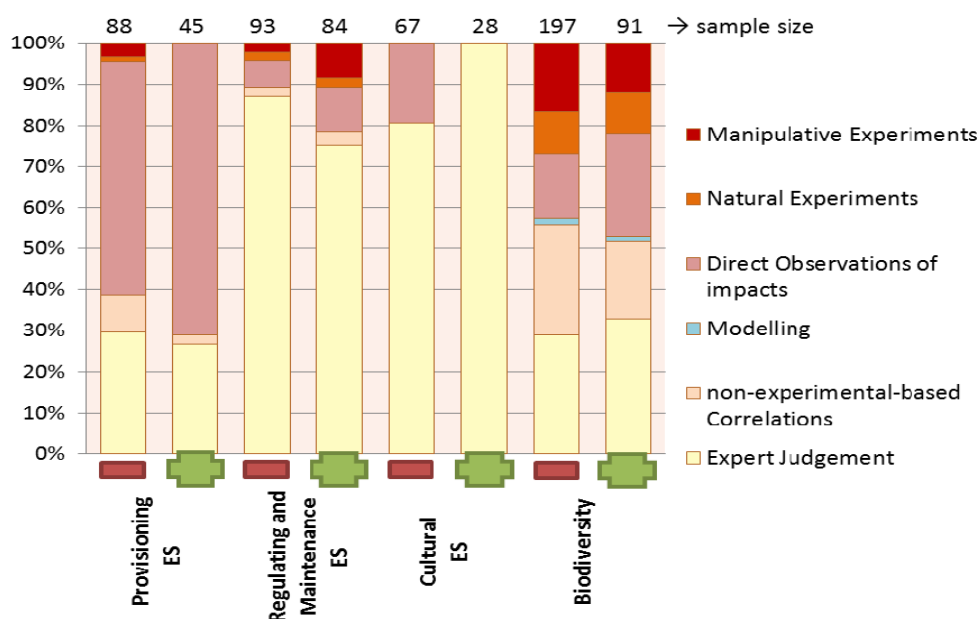


Figure 6. Type of evidence for the reported impacts on Ecosystem Services (ES) and Biodiversity. Positive (green cross) and negative impacts (red minus sign) are shown separately. The impact due to being ecosystem engineers (last column of Table 2) has not been included in this graph as essentially in all cases the main related type of evidence is ‘direct observation’.

evidence of high impact on ecosystem services or biodiversity. Hence, including the 9 species we added (which were not previously included in any of the above-mentioned lists), we came up with an inventory of 87 species that have a documented high impact on ecosystem services or biodiversity (Table 3).

Strength of evidence

Manipulative experiments provide the strongest possible evidence, yielding results that are more rigorous than those of virtually any other form of investigation. However, it is difficult and often impossible to carry out manipulative experiments in marine ecology. Furthermore, their results are not always realistic, because manipulation is by definition artificial, and hence a change that was achieved by deliberately separating correlated changes that might accompany it in nature, might not occur naturally (McArdle 1996). Natural experiments (‘pseudoexperiments’ or ‘designed observational studies’) have weaker inferential strength than manipulative experiments, as there is no true random selection of control and treatment sites, and correlations between the treatment effects and confounding environmental factors are generally difficult to avoid. Direct

observations of an impact, in the context of this work, also provide strong evidence of an impact, as it is the impact itself that is directly observed or measured and not the change of an indicator variable.

Models (e.g. trophic-web models) can make predictions or have structural features that can be tested or investigated in the field, allowing them to be falsified. However, the evidence provided by models is only as strong as the data that support them, and greatly depends on the underlying assumptions (McArdle 1996; Burnham and Anderson 2002).

Non-experimental-based correlations are poor evidence of causality. Such correlations can establish the possibility of an effect, but we can seldom distinguish these from other plausible hypotheses. Other abiotic and biotic factors could equally well correlate with the studied effect and provide other possible causal explanations. Although, expert judgement is valuable when formulating a set of alternative hypotheses that might explain an observed phenomenon, inference based solely on expert judgement is extremely weak. Without any supporting data and hypotheses testing, inference based only on expert judgement is just a subjective reflection of opinion and has

Table 3. Proposed inventory of alien and cryptogenic marine species with a reported high impact on ecosystem services or biodiversity. Species that have not been previously included in the lists of invasive species by DAISIE, NOBANIS, SEBI, and CABI-ISC are marked in bold. Cr: Cryptogenic. Species whose impact was only documented by Expert Judgement or non-experimental-based Correlations are marked in yellow (weak evidence); the rest are marked in orange. Species whose impact, at least for one ecosystem service or biodiversity component, is based on manipulative or natural experiments are marked with an asterisk (*).

Dinophyta (Myzozoa)	Insecta	Mollusca
<i>Alexandrium minutum</i> (Cr)	<i>Telmatogeton japonicus</i>	<i>Anadara kagoshimensis</i>
<i>Alexandrium monilatum</i>	Crustacea	<i>Anadara transversa</i>
<i>Karenia mikimotoi</i> (Cr)	<i>Acartia (Acanthacartia) tonsa</i> (Cr)	<i>Arcuatula senhousia</i>
<i>Gymnodinium catenatum</i> (Cr) *	<i>Amphibalanus improvisus</i> (Cr) *	<i>Brachidontes pharaonis</i> *
Haptophyta	<i>Austrominius (Elminius) modestus</i>	<i>Chama pacifica</i>
<i>Phaeocystis pouchetii</i> (Cr) *	<i>Callinectes sapidus</i>	<i>Crassostrea gigas</i> *
Ochrophyta	<i>Caprella mutica</i> *	<i>Crepidula fornicata</i> *
<i>Coscinodiscus wailesii</i> (Cr)	<i>Cercopagis pengoi</i>	<i>Ensis directus</i>
<i>Fibrocapsa japonica</i> (Cr) *	<i>Chionoecetes opilio</i>	<i>Mercenaria mercenaria</i>
<i>Pseudochattonella verruculosa</i> (Cr)	<i>Eriocheir sinensis</i>	<i>Mya arenaria</i> *
Macroalgae	<i>Gammarus tigrinus</i> *	<i>Petricolaria pholadiformis</i>
<i>Acrothamnion preissii</i> *	<i>Hemigrapsus sanguineus</i> *	<i>Pinctada imbricata radiata</i>
<i>Asparagopsis armata</i> *	<i>Homarus americanus</i>	<i>Potamopyrgus antipodarum</i>
<i>Asparagopsis taxiformis</i> (Cr)	<i>Marsupenaeus japonicus</i>	<i>Rapana venosa</i>
<i>Bonnemaisionia hamifera</i> *	<i>Palaemon elegans</i>	<i>Spondylus spinosus</i>
<i>Caulerpa cylindracea</i> *	<i>Palaemon macrodactylus</i>	<i>Teredo navalis</i> (Cr)
<i>Caulerpa taxifolia</i> *	<i>Paralithodes camtschaticus</i> *	<i>Urosalpinx cinerea</i>
<i>Codium fragile</i> subsp. <i>Fragile</i> *	<i>Platorchestia platensis</i> (Cr)	<i>Venerupis philippinarum</i> *
<i>Gracilaria vermiculophylla</i> *	<i>Portunus segnis</i> ex <i>P. pelagicus</i>	Ascidiacea
<i>Grateloupia turuturu</i>	<i>Rhithropanopeus harrisi</i>	<i>Botrylloides violaceus</i> *
<i>Lophocladia lallemandii</i> *	Cnidaria	<i>Microcosmus squamiger</i>
<i>Polysiphonia morrowii</i>	<i>Cordylophora caspia</i>	<i>Styela clava</i>
<i>Sargassum muticum</i> *	<i>Oculina patagonica</i>	Fish
<i>Stypopodium schimperi</i>	<i>Rhopilema nomadica</i>	<i>Liza haematocheila</i>
<i>Undaria pinnatifida</i> *	Bryozoa	<i>Fistularia commersonii</i>
<i>Womersleyella setacea</i> *	<i>Tricellaria inopinata</i>	<i>Lagocephalus sceleratus</i>
Tracheophyta	<i>Victorella pavidia</i> (Cr)	<i>Plotosus lineatus</i>
<i>Halophila stipulacea</i>	Polychaeta	<i>Neogobius melanostomus</i>
<i>Spartina alterniflora</i> *	<i>Ficopomatus enigmaticus</i> *	<i>Saurida undosquamis</i>
<i>Spartina anglica</i> *	<i>Hydroides dianthus</i>	<i>Siganus luridus</i> *
Ctenophora	<i>Hydroides elegans</i>	<i>Siganus rivulatus</i> *
<i>Beroe ovata</i> (Cr)	<i>Hydroides ezoensis</i>	
<i>Mnemiopsis leidyi</i>	<i>Marenzelleria</i> spp. (<i>neglecta</i> & <i>viridis</i>) *	

very low inferential strength. Expert judgements may be influenced by value-laden opinions, lack of experience, and conflicts of interest, and are sensitive to a host of psychological idiosyncrasies and subjective biases, such as framing, overconfidence, anchoring, availability bias, confirmation bias and dominance (Gilovich et al. 2002; McBride et al. 2012). The “native good, alien bad” perception sometimes prejudices expert judgements when assessing the impact of alien species (Goodenough 2010).

Our assessment of the type of evidence of reported impacts yielded some interesting results (Figure 6): (1) only a low percentage of inferred impacts was based on manipulative experiments (8.1% of all cases), mainly for biodiversity impacts;

(2) inference based on natural experiments and modelling also represented only a small percentage of cases (4.9 and 0.6% of cases respectively); (3) macroalgae was the taxonomic group with the highest percentage of experimentally-based (manipulative or natural experiments) reported impacts; for this group a few other quantitative/meta-analytical reviews of impacts have been conducted (e.g., Thomsen et al. 2009, 2012); (4) evidence for the vast majority of reported impacts was weak as it was based on expert judgement or non-experimental-based correlations (50.7 and 12.1% respectively); (5) direct observations of impacts were the most common type of evidence for provisional ecosystem services (e.g. damage on fishing gear or catch; mortality events,

additional costs for fisheries and aquaculture because of fouling equipment) and were also quite common for biodiversity impacts (e.g. observed overgrowing of sessile species; measurements of predation rates using stomach content analyses); (6) the weakest evidence was provided for impacts on cultural, regulating and maintenance ecosystem services, as it was based mainly on expert judgement.

Although there is no doubt that invasive species have modified marine ecosystems, evidence for most of the reported impacts is weak (Figure 6). A similar result was reported by Ruiz et al. (1999) who reviewed the ecological impacts of alien species in Chesapeake Bay. They found quantitative data for only 6% of the examined species, of which many were restricted to correlations in space or time, confounding cause-effect relationships with other covariates. Given the complexity of marine ecosystems, it is often quite difficult to identify the interaction between native and alien species. Apart from invasive species, many other cumulative stressors impact marine ecosystems and their services, such as climate change and ocean acidification, extractive activities, marine pollution, and coastal development (Halpern et al. 2008). With expert judgements or non-experimental-based correlations between the presence/abundance of alien species and changes in ecosystem services or biodiversity, it is impossible to discriminate between the effect of an alien species and the cumulative effects of all the other stressors or natural variability. The dominance of aliens and the decline of natives within a community may be a consequence of, rather than the driving force behind, ecosystem disturbance (Chabrierie et al. 2008) because alien species are often better able to tolerate disturbance due to their generalist ecology and phenotypic plasticity (Smith 2009; Goodenough 2010).

There is an evident need for stronger inferences based on manipulative or well-designed natural experiments and on direct observations or measurements of impacts, to improve our knowledge base of marine biological invasions and better inform managers. On the other hand, conclusions based on expert judgement or non-experimental-based correlations can be useful where managers are required to act in the absence of better evidence. The risks and costs of inaction or of delayed response may outweigh the costs of making a wrong choice based on poor evidence (McArdle 1996). In the absence of stronger evidence, structured elicitation techniques (e.g. McBride et al. 2012) might be useful to reduce potential

sources of bias and error among experts, and improve impact assessments. Combining information from various sources, weighing the various types of evidence, and understanding the inherent difficulties and cost of obtaining better data should all be considered when deciding to invest on additional research or on management interventions.

Positive vs negative impacts

Among the species herein assessed as being high-impact species (Table 2), 17 had only negative and 7 only positive impacts; both negative and positive effects were reported for the majority (62 species) (Table 2). The “native good, alien bad” view is a misconception, and the role of most of the alien species in marine ecosystems is rather complex. Alien species often benefit some components of native biodiversity and can enhance or provide new ecosystem services. Furthermore, the impact of a native species that has become invasive can often be stronger than that of an alien invasive species. Thomsen et al. (2012), in a meta-analysis of seaweed impacts on seagrasses, found that alien invasive seaweeds had lower negative effects than native species. Alien invasive species often have negative effects on biodiversity within one trophic level but positive effects on the biodiversity of higher trophic levels. Such contrasting effects are manifested through community-wide antagonism (competition and consumption) versus facilitation (habitat and food provisioning) interactions (relative trophic position hypothesis; Thomsen et al. 2014). To develop effective management strategies and to move the discipline of invasion ecology forward, the impacts of alien species need to be seen under a holistic perspective and as a multifaceted process that takes account of societal perceptions and implications (Goodenough 2010; Simberloff et al. 2013).

Positive impacts of alien species are underestimated, as there is a persistent perception bias against alien species that is also reflected in an historical publication bias that favours descriptions of their negative effects (Gurevitch and Padilla 2004; Goodenough 2010; Schlaepfer et al. 2011, 2012; Simberloff et al. 2013; McLaughlan et al. 2013). However, the study of the positive effects of invasive species is receiving increasing attention (Thieltges et al. 2006; Schlaepfer et al. 2011; McLaughlan et al. 2013; Thomsen et al. 2010, 2014). In marine and coastal areas that have been greatly modified by climate change and human activities, alien species may be more likely than

native species to persist and provide ecosystem services. Alien ecosystem engineers are often key species, which create novel ecosystems that fulfil important roles that might otherwise be lost in degraded systems (Hobbs et al. 2009). In the future, some alien species might even contribute to the achievement of conservation goals (Schlaepfer et al. 2011).

The way forward

Currently, our knowledge of the effects of alien marine species on ecosystem services and biodiversity is mainly qualitative and largely based on weak evidence. The complexity of species interactions and the variety of both negative and positive impacts associated with an introduced species makes environmental management decisions quite difficult and often controversial. In addition, the lack of precise knowledge about the life history traits of alien species and their invasive strategies constitutes a big obstacle to understanding their functional roles in the prevailing ecosystems and their impacts on ecosystem services and biodiversity. Cost-benefit analyses of biological invasions and of alternative mitigation measures are a pillar of invasion economics, but they have to be fed with high-quality information on all the effects related to the introduction of a species.

The impacts of a species can differ among European marine areas. For example, around the mid 2000s, the comb jelly *Mnemiopsis leidyi* was reported as being present in several areas in northern European waters. However, although zooplankton biomasses were strongly reduced on, for example, the Swedish west coast during the first years following its introduction, not many of the other dramatic effects reported from its presence in the Black Sea have been reported. Furthermore, the numbers of *M. leidyi* in Sweden have decreased during the past years, although the species is still abundant in, for example, Belgium (L-J Hansson, pers. comm.). Hence, simple knowledge of the presence of alien species is insufficient to locally assess the magnitude of their impacts, which will generally vary across their distributional range. Furthermore, impacts may vary temporally, as there is a dynamic interaction between the population of alien species and the components of the recipient ecosystem. Significant time lags can occur between the introduction of a species and their subsequent impacts, or the magnitude of impacts over time can be reduced.

Quantification and mapping of impacts as well as a better understanding of how anthropogenic changes and human pressures facilitate many invasions will greatly assist managers and policy makers in their decisions on prevention or mitigation actions to be taken. Constraints to quantifying and mapping the impact of alien marine species include (1) the lack of coverage and resolution in the available natural and socio-economic data (e.g. habitat mapping, spatial distribution of native and alien species), (2) gaps in assessments of marine ecosystem services (Liquete et al. 2013a), which naturally precedes the assessment of any impact on them, and (3) the inherent complexity of the problem. Among the recommended next steps to be taken are the improvement of methods for the assessment of the impacts of alien species, the development of suitable indicators, better mapping of species distribution and abundance, and shifting from approaches that offer only weak evidence to experiments or measurements that offer both strong evidence of an impact as well as an estimate of the magnitude of the impact.

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References

- Aanesen RT, Eilertsen HC, Stabell OB (1998) Light induced toxic properties of the marine alga *Phaeocystis pouchetii* towards cod larvae. *Aquatic Toxicology* 40: 109–121, [http://dx.doi.org/10.1016/S0166-445X\(97\)00056-8](http://dx.doi.org/10.1016/S0166-445X(97)00056-8)
- Aller JY, Woodin SA, Aller RC (eds) (2001) Organism sediment interactions. University of South Carolina Press, Columbia, USA, 403 pp
- Ballesteros E, Cebrian E, Alcoverro T (2007) Mortality of shoots of *Posidonia oceanica* following meadow invasion by the red alga *Lophocladia lallemandii*. *Botanica Marina* 50: 8–13, <http://dx.doi.org/10.1515/BOT.2007.002>
- Bartoli M, Nizzoli D, Viaroli P, Turolla E, Castaldelli G, Fano EA, Rossi R (2001) Impact of *Tapes philippinarum* farming on nutrient dynamics and benthic respiration in the Sacca di Goro. *Hydrobiologia* 455: 203–212, <http://dx.doi.org/10.1023/A:1011910422400>

- Bates TS, Charlson RJ, Gammon RH (1987) Evidence for the climatic role of marine biogenic sulphur. *Nature* 329: 319–321, <http://dx.doi.org/10.1038/329319a0>
- Ben Rais Lasram F, Mouillot D (2009) Increasing southern invasion enhances congruence between endemic and exotic Mediterranean fish fauna. *Biological Invasions* 11: 697–711, <http://dx.doi.org/10.1007/s10530-008-9284-4>
- Berke SK (2010) Functional groups of ecosystem engineers: a proposed classification with comments on current issues. *Integrative and Comparative Biology* 50(2): 147–157, <http://dx.doi.org/10.1093/icb/icq077>
- Bilio M, Niermann U (2004) Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. *Marine Ecology Progress Series* 269: 173–183, <http://dx.doi.org/10.3354/meps269173>
- Boalch GT (1984) Algal blooms and their effects on fishing in the English Channel. *Hydrobiologia* 116/117: 449–452, <http://dx.doi.org/10.1007/BF00027720>
- Boalch GT, Harbour DS (1977) Unusual diatom off the coast of south-west England and its effect on fishing. *Nature* 269: 687–688, <http://dx.doi.org/10.1038/269687a0>
- Boström C, Pittman S, Kneib R, Simenstad C (2011) Seascape ecology of coastal biogenic habitats: advances, gaps and challenges. *Marine Ecology Progress Series* 427: 191–217, <http://dx.doi.org/10.3354/meps09051>
- Bulleri F, Airolidi L, Branca GM, Abbiati M (2006) Positive effects of the introduced green alga, *Codium fragile* ssp. *tomentosoides*, on recruitment and survival of mussels. *Marine Biology* 148: 1213–1220, <http://dx.doi.org/10.1007/s00227-005-0181-4>
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York, 488 pp
- Buschbaum C, Chapman AS, Saier B (2006) How an introduced seaweed can affect epibiota diversity in different coastal systems. *Marine Biology* 148: 743–754, <http://dx.doi.org/10.1007/s00227-005-0128-9>
- CABI (2013) Invasive Species Compendium. CAB International, Wallingford, UK. <http://www.cabi.org/isc> (Accessed between January and June 2013)
- Cacabelos E, Engelen AH, Meijja A, Arenas F (2012) Comparison of the assemblage functioning of estuary systems dominated by the seagrass *Nanozostera noltii* versus the invasive drift seaweed *Gracilaria vermiculophylla*. *Journal of Sea Research* 72(1): 99–105, <http://dx.doi.org/10.1016/j.seares.2012.02.003>
- Carslaw KS, Boucher O, Spracklen DV, Mann GW, Rae JGL, Woodward S, Kulmala M (2010) A review of natural aerosol interactions and feedbacks within the Earth system. *Atmospheric Chemistry and Physics* 10: 1701–1737, <http://dx.doi.org/10.5194/acp-10-1701-2010>
- CBD (Convention on Biological Diversity) (2000) Interim Guiding Principles. Conference of the Parties Decision V/8 Alien species that threaten ecosystems, habitats or species. <http://www.cbd.int/decision/cop/default.shtml?id=7150> (Accessed 31 May 2013)
- Cebrian E, Linares C, Marschal C, Garrabou J (2012) Exploring the effects of invasive algae on the persistence of gorgonian populations. *Biological Invasions* 14: 2647–2656, <http://dx.doi.org/10.1007/s10530-012-0261-6>
- Ceccherelli G, Campo D (2002) Different effects of *Caulerpa racemosa* on two co-occurring seagrasses in the Mediterranean. *Botanica Marina* 45: 71–76, <http://dx.doi.org/10.1515/BOT.2002.009>
- Chaberrie O, Verheyen K, Saguez R, Decocq G (2008) Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest. *Diversity and Distributions* 14: 204–212, <http://dx.doi.org/10.1111/j.1472-4642.2007.00453.x>
- Charlson RJ, Lovelock JE, Andreae MO, Warren SG (1987) Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature* 326: 655–661, <http://dx.doi.org/10.1038/326655a0>
- Costa PR, Botelho MJ, Lefebvre KA (2010) Characterization of paralytic shellfish toxins in seawater and sardines (*Sardina pilchardus*) during blooms of *Gymnodinium catenatum*. *Hydrobiologia* 655: 89–97, <http://dx.doi.org/10.1007/s10750-010-0406-5>
- Costanza R, D'Arge R, De Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260, <http://dx.doi.org/10.1038/387253a0>
- Davies BR, Stuart V, de Villiers M (1989) The filtration activity of a serpulid polychaete population (*Ficopomatus enigmaticus* (Fauvel)) and its effects on water quality in a coastal marina. *Estuarine, Coastal and Shelf Science* 29: 613–620, [http://dx.doi.org/10.1016/0272-7714\(89\)90014-0](http://dx.doi.org/10.1016/0272-7714(89)90014-0)
- de Boer MK, Boerée C, Sjollem SB, de Vries T, Rijnsdorp AD, Buma AGJ (2012) The toxic effect of the marine raphidophyte *Fibrocapsa japonica* on larvae of the common flatfish sole (*Solea solea*). *Harmful Algae* 17: 92–101, <http://dx.doi.org/10.1016/j.hal.2012.03.005>
- de Montaudouin, Sauriau PG (1999) The proliferating Gastropoda *Crepidula fornicata* may stimulate macrozoobenthic diversity. *Journal of the Marine Biological Association of the UK* 79: 1069–1077, <http://dx.doi.org/10.1017/S0025315499001319>
- Delefosse M, Kritensen E (2012) Burial of *Zostera marina* seeds in sediment inhabited by three polychaetes: Laboratory and field studies. *Journal of Sea Research* 71: 41–49, <http://dx.doi.org/10.1016/j.seares.2012.04.006>
- Dumay O, Fernandez C, Pergent G (2002) Primary production and vegetative cycle in *Posidonia oceanica* when in competition with the green algae *Caulerpa taxifolia* and *Caulerpa racemosa*. *Journal of the Marine Biological Association of the UK* 82: 379–387, <http://dx.doi.org/10.1017/S0025315402005611>
- Edvardsen B, Eikrem W, Shalchian-Tabrizi K, Riisberg I, Johnson G, Naustvall L, Thronsen J (2007) *Verrucophora farcimen* gen. et sp. nov. (Dictyochophyceae, Heterokonta) - a bloom-forming ichthyotoxic flagellate from the Skagerrak, Norway. *Journal of Phycology* 43: 1054–1070, <http://dx.doi.org/10.1111/j.1529-8817.2007.00390.x>
- Estrada N, Rodríguez-Jaramillo C, Contreras G, Ascencio F (2010) Effects of induced paralysis on hemocytes and tissues of the giant lions-paw scallop by paralyzing shellfish poison. *Marine Biology* 157(6): 1401–1415, <http://dx.doi.org/10.1007/s00227-010-1418-4>
- EU (2008) Directive of the European Parliament and the Council Establishing a Framework for Community Action in the Field of Marine Environmental Policy (Marine Strategy Framework Directive). European Commission. Directive 2008/56/EC, OJ L 164
- EU (2011) Our life insurance, our natural capital: an EU biodiversity strategy to 2020. COM/2011/244, European Commission, Brussels, 16 pp
- Finenko GA, Romanova ZA, Abolmasova GI, Annisky BE, Svetlichny LS, Hubareva ES, Bat L, Kideys AE (2003) Population dynamics, ingestion, growth and reproduction rates of the invader *Beroe ovata* and its impact on plankton community in Sevastopol Bay, the Black Sea. *Journal of Plankton Research* 25: 539–549, <http://dx.doi.org/10.1093/plankt/25.5.539>
- Finenko GA, Kideys AE, Anninsky BE, Shiganova TA, Roohi A, Tabari MR, Rostami H, Bagheri S (2006) Invasive ctenophore *Mnemiopsis leidyi* in the Caspian Sea: feeding, respiration, reproduction and predatory impact on the zooplankton community. *Marine Ecology Progress Series* 314: 171–185, <http://dx.doi.org/10.3354/meps314171>

- Fletcher RL, Farrell P (1999) Introduced brown algae in the North East Atlantic with particular respect to *Undaria pinnatifida* (Harvey) Suringar. *Helgoländer Meeresuntersuchungen* 52: 259–275, <http://dx.doi.org/10.1007/BF02908901>
- Förster T (2003) New methods in monitoring shipwreck-sites. *MOSS Newsletter* 2003/2: 16–17
- Galil BS (2007) Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. *Marine Pollution Bulletin* 55: 314–322, <http://dx.doi.org/10.1016/j.marpolbul.2006.11.008>
- Galil BS, Marchini A, Occhipinti-Ambrogi A, Minchin D, Narščius A, Ojaveer H, Olenin S (2014) International arrivals: widespread bioinvasions in European Seas. *Ethology Ecology and Evolution* 26(2-3): 152–171, <http://dx.doi.org/10.1080/03949370.2014.897651>
- GESAMP (IMO/FAO/UNESCO-IOC/WMO/IAEA/UN/UNEP) (1997) Joint group of experts on the scientific aspects of marine environmental protection). Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* invasion in the Black Sea. *Reports and Studies* 58, 84 pp
- Gilovich T, Griffin D, Kahneman D (2002) Heuristics and Biases: The Psychology of Intuitive Judgement. Cambridge University Press, Cambridge, 874 pp, <http://dx.doi.org/10.1017/CBO9780511808098>
- Goodenough AE (2010) Are the ecological impacts of alien species misrepresented? A review of the “native good, alien bad” philosophy. *Community Ecology* 11(1): 13–21, <http://dx.doi.org/10.1556/ComEc.11.2010.1.3>
- Gribsholt B, Kristensen E (2002) Effects of bioturbation and plant roots on salt marsh biogeochemistry: a mesocosm study. *Marine Ecology Progress Series* 241: 71–87, <http://dx.doi.org/10.3354/meps241071>
- Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology & Evolution* 17: 22–27, [http://dx.doi.org/10.1016/S0169-5347\(01\)02358-8](http://dx.doi.org/10.1016/S0169-5347(01)02358-8)
- Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* 19: 470–474, <http://dx.doi.org/10.1016/j.tree.2004.07.005>
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. *Science* 319 (5865): 948–952, <http://dx.doi.org/10.1126/science.1149345>
- Hay CH, Villouta E (1993) Seasonality of the adventive Asian kelp *Undaria pinnatifida* in New Zealand. *Botanica Marina* 36(6): 461–476
- Hendriks IE, Bouma TJ, Morris EP, Duarte CM (2010) Effects of seagrasses and algae of the *Caulerpa* family on hydrodynamics and particle-trapping rates. *Marine Biology* 157: 473–481, <http://dx.doi.org/10.1007/s00227-009-1333-8>
- Hietanen S, Laine AO, Lukkari K (2007) The complex effects of the invasive polychaetes *Marenzelleria* spp. on benthic nutrient dynamics. *Journal of Experimental Marine Biology and Ecology* 352: 89–102, <http://dx.doi.org/10.1016/j.jembe.2007.07.018>
- Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution* 24: 599–605, <http://dx.doi.org/10.1016/j.tree.2009.05.012>
- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18, <http://dx.doi.org/10.1111/j.1365-2664.2008.01600.x>
- Jaubert JM, Chisholm JRM, Ducrot D, Ripley HT, Roy L, Passeron-Seitre G (1999) No deleterious alterations in *Posidonia oceanica* beds in the Bay of Menton (France) 8 years after *Caulerpa taxifolia* colonization. *Journal of Phycology* 35: 1113–1119, <http://dx.doi.org/10.1046/j.1529-8817.1999.3561113.x>
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69: 373–386, <http://dx.doi.org/10.2307/3545850>
- Kalogirou S (2013) Ecological characteristics of the invasive pufferfish *Lagocephalus sceleratus* (Gmelin, 1789) in Rhodes, Eastern Mediterranean Sea. A case study. *Mediterranean Marine Science* 14: 251–260, <http://dx.doi.org/10.12681/mms.364>
- Katsanevakis S, Bogucarskis K, Gatto F, Vandekerckhove J, Deriu I, Cardoso AC (2012) Building the European Alien Species Information Network (EASIN): a novel approach for the exploration of distributed alien species data. *BioInvasions Records* 1: 235–245, <http://dx.doi.org/10.3391/bir.2012.1.4.01>
- Katsanevakis S, Zenetos A, Belchior C, Cardoso AC (2013) Invading European Seas: assessing pathways of introduction of marine aliens. *Ocean and Coastal Management* 76: 64–74, <http://dx.doi.org/10.1016/j.ocecoaman.2013.02.024>
- Klein J, Verlaque M (2008) The *Caulerpa racemosa* invasion: a critical review. *Marine Pollution Bulletin* 56: 205–225, <http://dx.doi.org/10.1016/j.marpolbul.2007.09.043>
- Kochmann J, Buschbaum C, Volkenborn N, Reise K (2008) Shift from native mussels to alien oysters: Differential effects of ecosystem engineers. *Journal of Experimental Marine Biology and Ecology* 364: 1–10, <http://dx.doi.org/10.1016/j.jembe.2008.05.015>
- Kotta J, Orav H, Sandberg-Kilpi E (2001) Ecological consequence of the introduction of the polychaete *Marenzelleria viridis* into a shallow water biotope of the northern Baltic Sea. *Journal of Sea Research* 46: 273–280, [http://dx.doi.org/10.1016/S1385-1101\(01\)00088-0](http://dx.doi.org/10.1016/S1385-1101(01)00088-0)
- Kotta J, Olafsson E (2003) Competition for food between the introduced polychaete *Marenzelleria viridis* (Verrill) and the native amphipod *Monoporeia affinis* Lindström in the Baltic Sea. *Journal of Sea Research* 50: 27–35, [http://dx.doi.org/10.1016/S1385-1101\(03\)00041-8](http://dx.doi.org/10.1016/S1385-1101(03)00041-8)
- Kotta J, Kotta I, Simm M, Lankov A, Lauringson V, Põllumäe A, Ojaveer H (2006) Ecological consequences of biological invasions: three invertebrate case studies in the north-eastern Baltic Sea. *Helgoland Marine Research* 60: 106–112, <http://dx.doi.org/10.1007/s10152-006-0027-6>
- Landschoff J, Lackschewitz D, Kesy K, Reise K (2013) Globalization pressure and habitat change: Pacific rocky shore crabs invade armored shorelines in the Atlantic Wadden Sea. *Aquatic Invasions* 8: 77–87, <http://dx.doi.org/10.3391/ai.2013.8.1.09>
- Leppäkoski E (1991) Introduced species - resource or threat in brackish-water seas? Examples from the Baltic and the Black Sea. *Marine Pollution Bulletin* 23: 219–223, [http://dx.doi.org/10.1016/0025-326X\(91\)90678-L](http://dx.doi.org/10.1016/0025-326X(91)90678-L)
- Leppäkoski E (2002) Harmful non-native species in the Baltic Sea - an ignored problem. In: Schernewski G, Schiewer U (eds) Baltic coastal ecosystems: structure, function and coastal zone management. Central and Eastern European Development Studies, Springer-Verlag, Berlin Heidelberg, pp 253–275, http://dx.doi.org/10.1007/978-3-662-04769-9_20
- Leppäkoski E, Gollasch S, Olenin S (2002) The Baltic Sea - a field laboratory for invasion biology. In: Leppäkoski E, Gollasch S, Olenin S (eds), Invasive Aquatic species of Europe: distribution impacts and management. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 253–259
- Leppäkoski E, Shiganova T, Alexandrov B (2009) European enclosed and semi-enclosed seas. In: Rilov G, Crooks JA (eds), Biological invasions in marine ecosystems: ecological, management, and geographic perspectives. Springer (Ecological Studies Vol. 204), pp 529–547, http://dx.doi.org/10.1007/978-3-540-79236-9_30
- Linares C, Cebrian E, Coma R (2012) Effects of turf algae on recruitment and juvenile survival of gorgonian corals. *Marine Ecology Progress Series* 452: 81–88, <http://dx.doi.org/10.3354/meps09586>

- Liquete C, Piroddi C, Drakou EG, Gurney L, Katsanevakis S, Charef A, Egoh B (2013a) Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. *PLoS ONE* 8(7): e67737, <http://dx.doi.org/10.1371/journal.pone.0067737>
- Liquete C, Zulian G, Delgado I, Stips A, Maes J (2013b) Assessment of coastal protection as an ecosystem service in Europe. *Ecological Indicators* 30: 205–217
- Littler MM (1980) Morphological form and photosynthetic performances of marine macroalgae: tests of a functional/form hypothesis. *Botanica Marina* 22: 161–165
- Littler MM, Littler DS (1980) The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form. *American Naturalist* 116: 25–44, <http://dx.doi.org/10.1086/283610>
- Markert A, Wehrmann A, Kroncke I (2009) Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biological Invasions* 12: 15–32, <http://dx.doi.org/10.1007/s10530-009-9425-4>
- Martínez-Lüscher J, Holmer M (2010) Potential effects of the invasive species *Gracilaria vermiculophylla* on *Zostera marina* metabolism and survival. *Marine Environmental Research* 69(5): 345–349, <http://dx.doi.org/10.1016/j.marenvres.2009.12.009>
- Martínez ML, Intralawan A, Vázquez G, Pérez-Maqueo O, Sutton P, Landgrave R (2007) The coasts of our world: Ecological, economic and social importance. *Ecological Economics* 63: 254–272, <http://dx.doi.org/10.1016/j.ecolecon.2006.10.022>
- McArdle BH (1996) Levels of evidence in studies of competition, predation, and disease. *New Zealand Journal of Ecology* 20(1): 7–15
- McBride MF, Garnett ST, Szabo JK, Burbidge AH, Butchart SHM, Christidis L, Dutson G, Ford HA, Loyn RH, Watson DM, Burgman MA (2012) Structured elicitation of expert judgments for threatened species assessment: a case study on a continental scale using email. *Methods in Ecology and Evolution* 3(5): 906–920, <http://dx.doi.org/10.1111/j.2041-210X.2012.00221.x>
- McLaughlan C, Gallardo B, Aldridge DC (2013) How complete is our knowledge of the ecosystem services impacts of Europe's top 10 invasive species? *Acta Oecologica* 54: 119–130, <http://dx.doi.org/10.1016/j.actao.2013.03.005>
- MEA (Millennium Ecosystem Assessment) (2005) Ecosystems and Human Wellbeing: Biodiversity Synthesis. World Resources Institute, Washington, DC, 86 pp
- Mistri M, Rossi R, Fano EA (2004) The spread of an alien bivalve (*Musculista senhousia*) in the Sacca di Goro Lagoon (Adriatic Sea, Italy). *Journal of Molluscan Studies* 70: 257–261, <http://dx.doi.org/10.1093/mollus/70.3.257>
- Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* 6(9): 458–492, <http://dx.doi.org/10.1890/070064>
- Naustvoll LJ (2010) NOBANIS – Invasive Alien Species Fact Sheet – *Pseudochattonella farcimen*. Online Database of the North European and Baltic Network on Invasive Alien Species – NOBANIS. <http://www.nobanis.org> (Accessed 25 February 2013)
- Neideman R, Wenngren J, Ólafsson E (2003) Competition between the introduced polychaete *Marenzelleria* sp. and the native amphipod *Monoporeia affinis* in Baltic soft bottoms. *Marine Ecology Progress Series* 264: 49–55, <http://dx.doi.org/10.3354/meps264049>
- Nehring S (1998) Non-indigenous phytoplankton species in the North Sea: supposed region of origin and possible transport vector. *Archiv of Fishery and Marine Research* 46(3): 181–194
- Nehring S, Adersen H (2006) NOBANIS – Invasive Alien Species Fact Sheet – *Spartina anglica*. Online Database of the North European and Baltic Network on Invasive Alien Species – NOBANIS. <http://www.nobanis.org> (Accessed 1 December 2012)
- Newell RIE (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *Journal of Shellfish Research* 23: 51–61
- Norkko J, Reeds DC, Timmermann K, Norkko A, Gustafsson BG, Bonsdorff E, Slomp CP, Carstensen J, Conley DJ (2012) A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biology* 18: 422–443, <http://dx.doi.org/10.1111/j.1365-2486.2011.02513.x>
- Ojaveer H, Simm M, Lankov A (2004) Population dynamics and ecological impact of the non-indigenous *Cercopagis pengoi* in the Gulf of Riga (Baltic Sea). *Hydrobiologia* 522: 261–269, <http://dx.doi.org/10.1023/B:HYDR.0000029927.91756.41>
- Olden JD (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography* 33: 2027–2039, <http://dx.doi.org/10.1111/j.1365-2699.2006.01572.x>
- Olenin S, Leppäkoski E (1999) Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. *Hydrobiologia* 393: 233–243, <http://dx.doi.org/10.1023/A:1003511003766>
- Otero M, Cebrian E, Francour P, Galil B, Savini D (2013) Monitoring marine invasive species in Mediterranean Marine Protected Areas (MPAs): a strategy and practical guide for managers. Medpan North project, IUCN, Malaga, Spain, 136 pp
- Payen GG, Bonami JR (1979) Mise en évidence de particules d'allure virale associées aux noyaux des cellules mésodermiques de la zone germinative testiculaire du crabe *Rhithropanopeus harrisi* (Gould) (Brachyura, Xanthidae). *Revue des Travaux de l'Institut des Pêches Maritimes* 43: 361–365
- Perrings C (2002) Biological invasions in aquatic systems: The economic problem. *Bulletin of Marine Science* 70: 541–552
- Piazzi L, Balata D, Ceccherelli G, Cinelli F (2005) Interactive effect of sedimentation and *Caulerpa racemosa* var. *cylindracea* invasion on macroalgal assemblages in the Mediterranean Sea. *Estuarine, Coastal and Shelf Science* 64: 467–474, <http://dx.doi.org/10.1016/j.ecss.2005.03.010>
- Piazzi L, Balata D, Foresi L, Cristaudo C, Cinelli F (2007) Sediment as a constituent of Mediterranean benthic communities dominated by *Caulerpa racemosa* var. *cylindracea*. *Scientia Marina* 71(1): 129–135, <http://dx.doi.org/10.3989/scimar.2007.71n1129>
- Piscart C, Mermillod-Blondin F, Maazouzi C, Merigoux S, Marmonier P (2011) Potential impact of invasive amphipods on leaf litter recycling in aquatic ecosystems. *Biological Invasions* 13: 2861–2868, <http://dx.doi.org/10.1007/s10530-011-9969-y>
- Pranovi F, Franceschini G, Casale M, Zucchetta M, Torricelli P, Giovanardi O (2006) An ecological imbalance induced by a non-native species: the Manila clam in the Venice Lagoon. *Biological Invasions* 8: 595–609, <http://dx.doi.org/10.1007/s10530-005-1602-5>
- Queirós AM, Hiddink JG, Johnson G, Cabral HN, Kaiser MJ (2011) Context dependence of marine ecosystem engineer invasion impacts on benthic ecosystem functioning. *Biological Invasions* 13: 1059–1075, <http://dx.doi.org/10.1007/s10530-011-9948-3>
- Quinn PK, Bates TS (2011) The case against climate regulation via oceanic phytoplankton sulphur emissions. *Nature* 480: 51–56, <http://dx.doi.org/10.1038/nature10580>
- Quintana CO, Kristensen E, Valdemarsen T (2013) Impact of the invasive polychaete *Marenzelleria viridis* on the biogeochemistry of sandy marine sediments. *Biogeochemistry* 115: 95–109, <http://dx.doi.org/10.1007/s10533-012-9820-2>

- Ragueneau O, Chauvaud L, Leynaert A, Thouzeau G, Paulet Y-M, Bonnet S, Lorrain A, Grall J, Corvaisier R, Le Hir M, Jean F, Clavier J (2002) Direct evidence of a biologically active coastal silicate pump: Ecological implications. *Limnology and Oceanography* 47:1849–1854, <http://dx.doi.org/10.4319/lo.2002.47.6.1849>
- Raine R, O'Boyle S, O'Higgins T, White M, Patching J, Cahill B, McMahon T (2001) A satellite and field portrait of a *Karenia mikimotoi* (Hulbert) bloom off the south coast of Ireland, August 1998. *Hydrobiologia* 465: 187–193, <http://dx.doi.org/10.1023/A:1014524420705>
- Ribeiro S, Amorim A, Andersen TJ, Abrantes F, Ellegaard M (2012) Reconstructing the history of an invasion: the toxic phytoplankton species *Gymnodinium catenatum* in the Northeast Atlantic. *Biological Invasions* 14: 969–985, <http://dx.doi.org/10.1007/s10530-011-0132-6>
- Rilov G, Galil BS (2009) Marine bioinvasions in the Mediterranean Sea – history, distribution and ecology. In: Rilov G, Crooks JA (eds), Biological invasions in marine ecosystems: ecological, management, and geographic perspectives. Springer, Berlin, Heidelberg. *Ecological Studies* 204: 549–575
- Ruiz GM, Fofonoff P, Hines AH (1999) Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. *Limnology and Oceanography* 44(3): 950–972, http://dx.doi.org/10.4319/lo.1999.44.3_part_2.0950
- Safriel UN, Sasson-Frosting Z (1988) Can colonizing mussel outcompete indigenous mussel? *Journal of Experimental Marine Biology and Ecology* 117: 211–226, [http://dx.doi.org/10.1016/0022-0981\(88\)90058-5](http://dx.doi.org/10.1016/0022-0981(88)90058-5)
- Sahin C, Emiral H, Okumus I, Gozler AM, Kalayci F, Hacimurtteazoglu N (2009) The benthic exotic species of the Black Sea: Blood Cockle (*Anadara inaequalis*, Bruguiere, 1789: Bivalve) and Rapa Whelk (*Rapana thomasiana*, Crosse, 1861: Mollusc). *Journal of Animal and Veterinary Advances* 8(2): 240–245
- Sala E, Kizilkaya Z, Yildirim D, Ballesteros E (2011) Alien marine fishes deplete algal biomass in the eastern Mediterranean. *PLoS ONE* 6(2): e17356, <http://dx.doi.org/10.1371/journal.pone.0017356>
- Salomidi M, Katsanevakis S, Borja Á, Braeckman U, Damalas D, Galparsoro I, Mifsud R, Mirto S, Pascual M, Pipitone C, Rabaut M, Todorova V, Vassilopoulou V, Vega Fernández T (2012) Assessment of goods and services, vulnerability, and conservation status of European seabed biotopes: a stepping stone towards ecosystem-based marine spatial management. *Mediterranean Marine Science* 13(1): 49–88, <http://dx.doi.org/10.12681/mms.23>
- Schlaepfer MA, Sax DF, Olden JD (2011) The potential conservation value of non-native species. *Conservation Biology* 25: 428–437, <http://dx.doi.org/10.1111/j.1523-1739.2010.01646.x>
- Schlaepfer MA, Sax DF, Olden JD (2012) Toward a more balanced view of non-native species. *Conservation Biology* 26:1156–1158, <http://dx.doi.org/10.1111/j.1523-1739.2012.01948.x>
- Schoemann V, Becquevort S, Stefels J, Rousseau V, Lancelot C (2005) *Phaeocystis* blooms in the global ocean and their controlling mechanisms: a review. *Journal of Sea Research* 53: 43–66, <http://dx.doi.org/10.1016/j.seares.2004.01.008>
- Schuenhoff A, Mata L, Santos R (2006) The tetrasporophyte of *Asparagopsis armata* as a novel seaweed biofilter. *Aquaculture* 252(1): 3–11, <http://dx.doi.org/10.1016/j.aquaculture.2005.11.044>
- Sciberras M, Schembri PJ (2008) Biology and interspecific interactions of the alien crab *Percnon gibbesi* in the Maltese Islands. *Marine Biology Research* 4:321–332, <http://dx.doi.org/10.1080/17451000801964923>
- Sgro L, Mistri M, Widdows J (2005) Impact of the infaunal manila clam, *Ruditapes philippinarum*, on sediment stability. *Hydrobiologia* 550: 175–182, <http://dx.doi.org/10.1007/s10750-005-4375-z>
- Shiganova TA (1998) Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. *Fisheries Oceanography* 7(3/4): 305–310, <http://dx.doi.org/10.1046/j.1365-2419.1998.00080.x>
- Shiganova TA, Bulgakova YV, Volovik SP, Mirzoyan ZA, Dudkin SI (2001a) The new invader *Beroe ovata* Mayer 1912 and its effect on the ecosystem in the northeastern Black Sea. *Hydrobiologia* 451: 187–197, <http://dx.doi.org/10.1023/A:1011823903518>
- Shiganova TA, Mirzoyan ZA, Studenikina EA, Volovik SP, Siokou-Frangou I, Zervoudaki S, Christou ED, Skirta AY, Dumont HJ (2001b) Population development of the invader ctenophore *Mnemiopsis leidyi*, in the Black Sea and in other seas of the Mediterranean basin. *Marine Biology* 139: 431–445, <http://dx.doi.org/10.1007/s002270100554>
- Shucksmith R, Cook EJ, Hughes DJ, Burrows MT (2009) Competition between the non-native amphipod *Caprella mutica* and two native species of caprellids *Pseudoprotella phasma* and *Caprella linearis*. *Journal of the Marine Biological Association of the United Kingdom* 89: 1125–1132, <http://dx.doi.org/10.1017/S0025315409000435>
- Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, Garcia-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution* 28: 58–66, <http://dx.doi.org/10.1016/j.tree.2012.07.013>
- Skjeltbred B, Horsberg TE, Tollefsen KE, Andersen T, Edvardsen B (2011) Toxicity of the ichthyotoxic marine flagellate *Pseudochattonella* (Dictyochophyceae, Heterokonta) assessed by six bioassays. *Harmful Algae* 10(2): 144–154, <http://dx.doi.org/10.1016/j.hal.2010.08.007>
- Smith LD (2009) The role of phenotypic plasticity in marine biological invasions. In: Rilov G, Crooks JA (eds), Biological invasions in marine ecosystems: ecological, management, and geographic perspectives. Springer, Berlin, Heidelberg. *Ecological Studies* 204, pp 177–202
- Sørensen TF, Drillet G, Engell-Sørensen K, Hansen BW, Ramløv H (2007) Production and biochemical composition of eggs from neritic calanoid copepods reared in large outdoor tanks (Limfjord, Denmark). *Aquaculture* 263: 84–96, <http://dx.doi.org/10.1016/j.aquaculture.2006.12.001>
- Stebbing PD, Pond MJ, Peeler E, Small HJ, Greenwood SJ, Verner-Jeffreys D (2012) Limited prevalence of gaffkaemia (*Aerococcus viridans* var. *homari*) isolated from wild-caught European lobsters *Homarus gammarus* in England and Wales. *Diseases of Aquatic Organisms* 100: 159–167, <http://dx.doi.org/10.3354/dao02491>
- Strayer DL, Caraco NF, Cole JJ, Findlay S, Pace ML (1999) Transformation of freshwater ecosystems by bivalves—a case study of zebra mussels in the Hudson River. *BioScience* 49: 19–27, <http://dx.doi.org/10.2307/1313490>
- Streftaris N, Zenetos A (2006) Alien Marine Species in the Mediterranean - the 100 'Worst Invasives' and their Impact. *Mediterranean Marine Science* 7(1): 87–118, <http://dx.doi.org/10.12681/mms.180>
- Strong JA, Dring MJ, Maggs CA (2006) Colonisation and modification of soft substratum habitats by the invasive macroalga *Sargassum muticum*. *Marine Ecology Progress Series* 321: 87–97, <http://dx.doi.org/10.3354/meps321087>
- Sureda A, Box A, Terrados J, Deudero S, Pons A (2008) Antioxidant response of the seagrass *Posidonia oceanica* when epiphytized by the invasive macroalgae *Lophocladia lallemandii*. *Marine Environmental Research* 66(3): 359–363, <http://dx.doi.org/10.1016/j.marenvres.2008.05.009>
- Svensson JR, Nylund GM, Cervin G, Toth GB, Pavia H (2013) Novel chemical weapon of an exotic macroalga inhibits

- recruitment of native competitors in the invaded range. *Journal of Ecology* 101(1): 140–148, <http://dx.doi.org/10.1111/1365-2745.12028>
- Thieltges DW (2005a) Impact of an invader: epizootic American slipper limpet *Crepidula fornicata* reduces survival and growth in European mussels. *Marine Ecology Progress Series* 286: 13–19, <http://dx.doi.org/10.3354/meps286013>
- Thieltges DW (2005b) Benefit from an invader: American slipper limpet *Crepidula fornicata* reduces star fish predation on basibiont European mussels. *Hydrobiologia* 541: 241–244, <http://dx.doi.org/10.1007/s10750-004-4671-z>
- Thieltges DW, Reise K, Prinz K, Jensen KT (2009) Invaders interfere with native parasite–host interactions. *Biological Invasions* 11: 1421–1429, <http://dx.doi.org/10.1007/s10530-008-9350-y>
- Thieltges DW, Strasser M, Reise K (2006) How bad are invaders in coastal waters? The case of the American slipper limpet *Crepidula fornicata* in western Europe. *Biological Invasions* 8: 1673–1680, <http://dx.doi.org/10.1007/s10530-005-5279-6>
- Thomsen MS (2010) Experimental evidence for positive effects of invasive seaweed on native invertebrates via habitat-formation in a seagrass bed. *Aquatic Invasions* 5(4): 341–346, <http://dx.doi.org/10.3391/ai.2010.5.4.02>
- Thomsen MS, Wernberg T, Tuya F, Silliman BR (2009) Evidence for impacts of non-indigenous macroalgae: a meta-analysis of experimental field studies. *Journal of Phycology* 45: 812–819, <http://dx.doi.org/10.1111/j.1529-8817.2009.00709.x>
- Thomsen MS, Wernberg T, Engelen AH, Tuya F, Vanderklift MA, Holmer M, McGlathery KJ, Arenas F, Kotta J, Silliman BR (2012) A meta-analysis of seaweed impacts on seagrasses: generalities and knowledge gaps. *PLoS ONE* 7: e28595, <http://dx.doi.org/10.1371/journal.pone.0028595>
- Thomsen MS, Staehr PA, Nejrup LB, Schiel DR (2013) Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occurring foundation species and associated invertebrates. *Aquatic Invasions* 8: 133–145, <http://dx.doi.org/10.3391/ai.2013.8.2.02>
- Thomsen MS, Byers JE, Schiel DR, Bruno JF, Olden JD, Wernberg T, Silliman BR (2014) Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. *Marine Ecology Progress Series* 495: 39–47, <http://dx.doi.org/10.3354/meps10566>
- Tong C, Wang W-Q, Huang J-F, Gauci V, Zhang L-H, Zeng C-S (2012) Invasive alien plants increase CH₄ emissions from a subtropical tidal estuarine wetland. *Biochemistry* 111: 677–693
- Troost K (2010) Causes and effects of a highly successful marine invasion: Case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. *Journal of Sea Research* 64: 145–165, <http://dx.doi.org/10.1016/j.seares.2010.02.004>
- Vanni MJ (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* 33: 341–370, <http://dx.doi.org/10.1146/annurev.ecolsys.33.010802.150519>
- Vaughn CC, Hakenkamp CC (2001) The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology* 46: 1431–1446, <http://dx.doi.org/10.1046/j.1365-2427.2001.00771.x>
- Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* 8(3): 135–144, <http://dx.doi.org/10.1890/080083>
- Wallentinus I (1984) Comparisons of nutrient uptake rates for Baltic macroalgae with different thallus morphologies. *Marine Biology* 80: 215–225, <http://dx.doi.org/10.1007/BF02180189>
- Wallentinus I, Nyberg CD (2007) Introduced marine organisms as habitat modifiers. *Marine Pollution Bulletin* 55: 323–332, <http://dx.doi.org/10.1016/j.marpolbul.2006.11.010>
- Winkler HM, Debus L (1997) Is the polychaete *Marenzelleria viridis* an important food item for fish? Proceedings of the 13th Symposium of the Baltic Marine Biologists 13, pp 147–151
- Woodhouse MT, Carslaw KS, Mann GW, Vallina SM, Vogt M, Halloran PR, Boucher O (2010) Low sensitivity of cloud condensation nuclei to changes in the sea-air flux of dimethyl-sulphide. *Atmospheric Chemistry and Physics* 10: 7545–7559, <http://dx.doi.org/10.5194/acp-10-7545-2010>
- Yoffe B, Baruchin AM (2004) Mediterranean jellyfish (*Rhopilema nomadica*) sting. *Burns* 30: 503–504, <http://dx.doi.org/10.1016/j.burns.2004.01.013>
- Zenetos A, Gofas S, Morri C, Rosso A, Violanti D, García Raso JE, Çinar ME, Almogi Labin A, Ates AS, Azzuro E, Ballesteros E, Bianchi CN, Bilecenoglu M, Gambi MC, Giangrande A, Gravili C, Hyams-Kaphzan O, Karachle V, Katsanevakis S, Lipej L, Mastroiuto F, Mineur F, Pancucci-Papadopoulou MA, Ramos Esplá A, Salas C, San Martín G, Sfriso A, Streftaris N, Verlaque M (2012) Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science* 13: 328–352, <http://dx.doi.org/10.12681/mms.327>
- Zolotarev V (1996) The Black Sea ecosystem changes related to the introduction of new mollusc species. *PSZNI: Marine Ecology* 17: 227–236, <http://dx.doi.org/10.1111/j.1439-0485.1996.tb00504.x>

Supplementary material

The following supplementary material is available for this article:

Supplement 1. Species-specific review of the impacts of invasive alien species on ecosystem services and biodiversity in the European Seas, and other related information.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2014/Supplements/AI_2014_Katsanevakis_etal_Supplement.pdf