

Research Article

Gateways to alien invasions in the European seas

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Abstract

The spatial pattern of initial introductions of marine alien species in the European Seas (including the entire Mediterranean) was investigated. Marked geographic patterns depending on the pathway of introduction were revealed, with specific countries acting as gateways to alien invasions. France and Italy were the countries mostly responsible for introductions by aquaculture, while Lessepsian species were first reported (as anticipated) in the countries of the Levantine Sea, especially Israel. Shipping was the most important pathway of introduction, with a widely dispersed geographic pattern of initial introductions, especially near large ports. Certain taxonomic groups were mostly introduced by specific pathways, and hence the taxonomic identity of the introduced alien species in each region was greatly dependent on the dominant maritime activities/interventions and the related pathways of introduction. Our data can be very useful for informing and supporting national policy and management decisions necessary to prevent future introductions of marine alien species.

Key words: biological invasions, Europe, pathways, aquaculture, Suez Canal, shipping

Introduction

The introduction of alien species is currently considered as one of the main threats to global biodiversity (Sala et al. 2000; MEA 2005). The rate at which alien species are introduced into new environments has reached an unprecedented rate and continues to increase (Vitousek et al. 1997; Hulme 2009; Katsanevakis et al. 2013a). By creating novel ecological contexts, introduced species can profoundly alter the structure and functioning of invaded ecosystems, with serious negative, but also often positive, impacts on ecosystem services and biodiversity (Sakai et al. 2001; Schlaepfer et al. 2005, 2012; Vilà et al. 2010; Simberloff et al. 2013). The marine environment is no exception, with alien species often representing a component of abrupt change with serious economic and ecological implications (Grosholz 2002; Occhipinti-Ambrogi and Savini 2003; Wallentinus and Nyberg 2007; Molnar et al. 2008).

The invasion process consists of three main steps: the introduction of an alien species outside its native range through a transport pathway; the establishment of a viable, self-sustaining population

in the new ecosystem; and the subsequent dispersal of the species outside its point of introduction (Vermeij 1996; Kolar and Lodge 2001; Sakai et al. 2001). The study of the first step is extremely important for the prevention of new introductions of alien species.

Assessing pathways of introduction, the diverse mechanisms through which alien species are introduced into new locations, is fundamental to the study of the introduction phase of the invasion process (Vermeij 1996). There are many not mutually exclusive pathways through which an organism can be introduced into a new region (Hulme et al. 2008). For marine species in European Seas, the main pathway of introduction is shipping, followed by introductions through the Suez Canal (marine corridor), aquaculture activities, aquarium trade, and inland corridors (Katsanevakis et al. 2013a). Shipping seems to be the most common pathway of introduction of marine species at a global scale (Molnar et al. 2008).

Shipping refers to both the transportation of holoplanktonic or meroplanktonic organisms, seeds, or resting stages (e.g. cysts or eggs) in ballast water, and the introduction of fouling species

attached to the ships' hulls. Over the last decades the rate of biological invasions mediated by shipping has increased at an alarming pace mostly due to an increase in the volume of world seaborne commercial traffic and trade (Seebens et al. 2013; Katsanevakis et al. 2013a). The opening of the Suez Canal in 1869 and its continuous enlargement has since then allowed for the progressive introduction of many species of Indo-Pacific origin into the Mediterranean Sea (called Lessepsian immigrants) (Por 1978; Galil 2006; Rilov and Galil 2009; Katsanevakis et al. 2013a). Aquaculture has led into numerous introductions of unwanted alien species into the wild, causing unpredictable and often irreversible ecological impacts (Naylor et al. 2001). It includes the introduction of both commodities and contaminants, respectively commercial species that were introduced with the aim to be cultured and species accidentally introduced together with imported target species. The aquarium trade is emerging as another important source for species likely to invade aquatic habitats (Padilla and Williams 2004; Katsanevakis et al. 2013a). It refers to both species released by aquarium hobbyists and species released or escaped from public aquaria. Inland canals refers to a complex European network of inland waterways, made up of >28000 km of navigable rivers and constructed canals (Panov et al. 2009), connecting some previously isolated catchments in southern (Caspian, Azov, Black, Mediterranean seas) and northern (Baltic, North, Wadden, White Seas) Europe. This pathway refers to species that are partly native in Europe, i.e. native in some regional Seas but alien to others.

Once alien species become established in the marine environment, it is usually impossible to eradicate them (Thresher and Kuris 2004 – but see Anderson 2005). Accounting for the means of species initial introduction is essential for preventing future movements of alien organisms, for predicting future trends of invasions, and for developing adequate management options. Furthermore, identification of key recipient regions of biological invasions is essential to understand the first stage of the invasion process, since it helps to identify geographical hotspots where actions should be focused in order to prevent, control or eradicate new introductions in the initial phases (Vermeij 1996). This acquires special relevance considering the new Regulation proposed by the European Commission to the Council and the Parliament on September 9th 2013 (<http://ec.europa.eu/environment/nature/invasivealien/>), with the aim to prevent

and manage the rapidly growing threat posed by invasive species.

In this study we sought to identify which countries act as the major gateways (recipient countries) to marine alien invasions in European Seas and investigated how major human activities affect new introductions. Such an analysis will improve our understanding of the observed spatial patterns of alien invasions in the European Seas and will assist prioritisation of management measures on both national and European levels for reversing the increasing trend of marine alien species introductions in Europe.

Methods

For the present analysis, we used the inventory of marine alien and cryptogenic species present in Europe archived by the European Alien Species Information Network and updated as of October 2013 (EASIN; <http://easin.jrc.ec.europa.eu/>; Katsanevakis et al. 2012, 2013b). This is a dynamic inventory that is continuously updated to follow the latest scientific findings about new alien species and their status. It currently includes 1383 marine species reported as alien or suspected to be alien in European marine waters (i.e., it also includes 118 cryptogenic and 80 questionable species). It encompassed all four European seas, including alien marine species reported from the entire Mediterranean Sea, which includes North African and Near East Mediterranean countries. EU overseas territories (including the Outermost Regions, e.g. the Macaronesian Sea) were not considered.

Based on a thorough review of the scientific and grey literature, the country and year of initial introduction of marine alien species in Europe was identified for 1380 species. The country through which a species was first introduced in Europe is hereafter called the 'recipient country'. For 32 species, more than one recipient country was associated to their introduction into European Seas. This may happen when a species has been collected independently at the same year from different countries, e.g., *Desdemona ornata* Banse, 1957 from Italy (Lardicci and Castelli 1986) and Greece (Panagopoulos and Nicolaidou 1989-90); *Fibrocapsa japonica* Toriumi and Takano, 1973 from France (Billard 1992), The Netherlands (Vrieling et al. 1995), and Germany (Elbrächter 1994; Gollasch and Nehring 2006); and *Hemigrapsus sanguineus* De Haan, 1835 from France and The Netherlands (Breton et al. 2002). In some cases, recipient countries can be identified with certainty (e.g. most commodity species introduced through

aquaculture), while in other cases the country of first observation of the species in Europe was assumed to be the recipient country. The date of first observation of an alien species in Europe was used as the best available estimate of the year of its initial introduction, when the latter could not be determined with certainty. The information on the country and year of first introduction of each species is publicly available through the species search widgets of EASIN (<http://easin.jrc.ec.europa.eu/use-easin/species-search>) and is also provided in the Supplementary material (Table S1). For species for which information was available, the approximate location of initial introduction in the recipient country was also identified. In some cases, more than one location within a country may be associated to a species introduction event.

Species were linked to the five main pathway(s) of introduction in European waters, i.e. shipping, Suez Canal, aquaculture, aquarium trade and inland canals (for details see Katsanevakis et al. (2013a) and references therein). Species introduced by all other minor pathways were pooled together in a category named “Other” (including live food, bait trade, packaging material, game animals, etc.). Of the 1383 marine alien species, 1150 were linked to a single pathway of introduction, while the pathway was unknown for 90 species (Table S1). For the remaining 143 species, more than one pathway of introduction was associated to their initial introduction into European waters. Information on pathways is also publicly available through the species search widgets of EASIN (<http://easin.jrc.ec.europa.eu/use-easin/species-search>).

Introduction events have been also analysed by Phylum. The Phyla most common in the inventory of marine alien species in Europe were, in decreasing order, Mollusca, Arthropoda, Chordata, Annelida, Rhodophyta, Ochrophyta and Foraminifera (Katsanevakis et al. 2013b). All of the other Phyla were pooled in the ‘Other’ category. The taxonomic classification of each marine alien species was mainly based on the World Register of Marine Species (WoRMS; WoRMS Editorial Board 2013).

Taking into account the recipient country (and location within the country), the year of initial introduction, the pathway of introduction and the taxonomic classification of species, patterns and trends of introductions of marine alien species in Europe were analysed. Invasion patterns were studied for all the pathways considered, but were

examined in more detail for shipping, the Suez Canal, and aquaculture.

We investigated the possible correlation between the volume of maritime freight transport in European countries and the number of new alien species introduced through shipping per country. Data on the average gross weight of goods handled in all European countries (plus Turkey) from 1997 to 2011 was used, as retrieved from the European Commission’s EUROSTAT Statistics Database (http://appsso.eurostat.ec.europa.eu/nui/show.do?dataset=mar_go_aa&lang=en). As countries from Africa and Asia (N=9) are not included in these statistics, they were not included in this analysis.

We also checked for a correlation between the distance of each Mediterranean country from the Suez Canal and the number of new Lessepsian immigrants entering the Mediterranean Sea. The distance (in kilometres) from the northern terminus of the Suez Canal (Port Said, Egypt) to the midpoint of each Mediterranean country was estimated following the coastline in the Eastward direction. This direction was chosen because the most common invasion pattern of Lessepsian immigrants is to become established close to the Suez Canal and then to spread to the rest of the Mediterranean in a counter-clockwise direction (Katsanevakis et al. 2013a). For calculating the distances from Italy onwards (for France, Spain, Morocco, and Algeria), a line was drawn from Albania to Italy at the Strait of Otranto, in order to follow the patterns of marine currents. A similar approach was used to calculate the distance to Tunisia (and Algeria), by drawing a line from Sicily to this country. For the islands of Cyprus and Malta, the distance was again calculated in the Eastward direction until the mainland country closest to these islands (Lebanon for Cyprus and Sicily/Italy for Malta) and then drawing a straight line between these and the closest point for each of the islands.

To examine if there was a relationship between the average shellfish aquaculture production per country and the number of new marine alien species introduced through aquaculture, data on the average shellfish production from 1950 to 2011 was retrieved from the Food and Agriculture Organization’s Global Production Statistics (online query), from the Fishery Statistical Collections (<http://www.fao.org/fishery/statistics/global-production/en>). Only marine bivalve production was used because the majority of the alien species introduced through aquaculture in marine

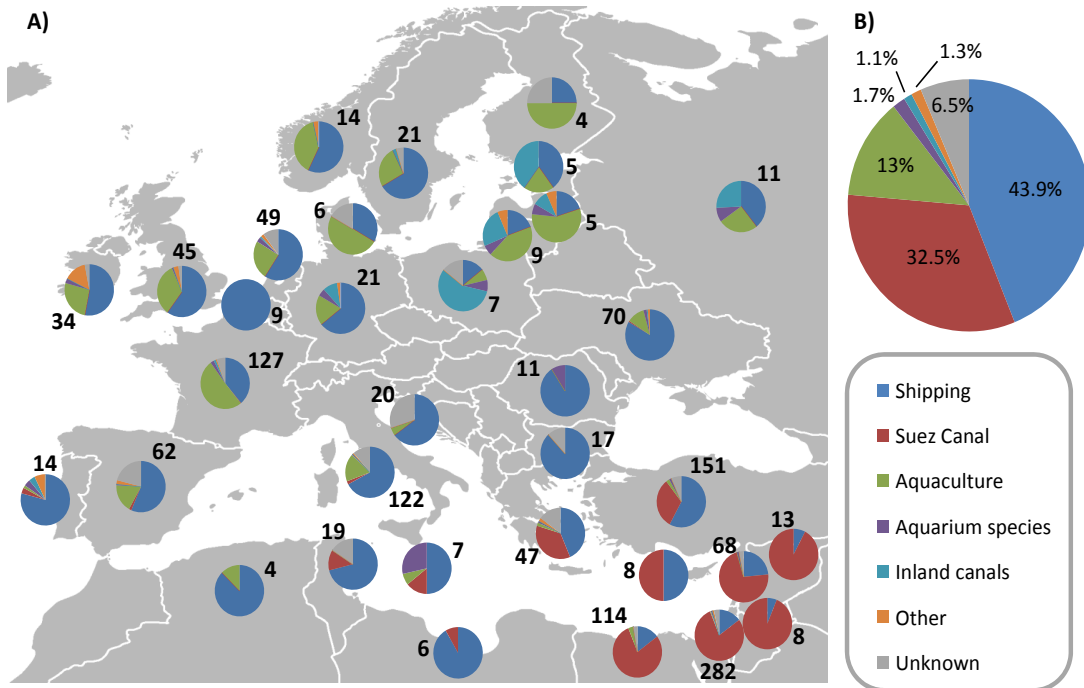


Figure 1. (A) Proportion of marine alien species introduced for the first time in European waters through different pathways of introduction, per recipient country (i.e. countries of initial introduction in Europe). For clarity, data is shown for countries with more than two recorded first introduction events (numbers shown next to the charts). Figure (B) shows the European total of first introduction events per pathway of introduction. Species that were linked to more than one pathway ($n = 143$) were given a value of $1/k$ for each of the k associated pathways so that the overall contribution of each species to the total number of new aliens was always 1.

waters are either commercial bivalve species or contaminants of introduced bivalves, i.e. species (mainly algae and small invertebrates) accidentally introduced together with imported target species. As such, only data for the FAO subgroups ‘Abalones, winkles, conchs’; ‘Clams, cockles, arkshells’; ‘Mussels’; ‘Oysters’; and ‘Scallops, pectens’ were retrieved. All the countries registering introductions through aquaculture were considered, except the ones for which data could not be found in the website (Egypt, Estonia, Finland, Latvia, Malta and Poland).

For all investigated relationships, the number of new alien species by recipient country was \ln -transformed [$\ln(x + 1)$] to stabilise variance and achieve random distribution of residuals.

Results

The main pathways by which alien species have been introduced in European Seas were shipping, the Suez Canal (Lessepsian immigrants), and aquaculture (Figure 1B). The predominant pathway

of introduction in most countries was shipping (Figure 1A). For 22 out of the 34 countries having more than two recorded first introduction events, over 40% of the alien species were introduced through this pathway. Lessepsian migration was the predominant pathway of first introductions in Egypt, Lebanon, Israel, Syria and the Palestine Authority (all in the eastern Mediterranean), representing more than 70% of each country’s first introduction events (Figure 1A).

Israel is the country with the highest number of recorded first introductions in European Seas, followed by Turkey, France, and Italy (Figure 1A). However, while species introductions for Turkey and Italy were mainly due to shipping activities (58 and 67%, respectively), in France shipping represented only 39% of the introduction events, with aquaculture responsible for 51% of the new introductions. In most of the North-East Atlantic countries, although shipping is still the major pathway of introduction, a high proportion of introductions (18–51%) have occurred due to aquaculture activities (Figure 1A). Eleven countries

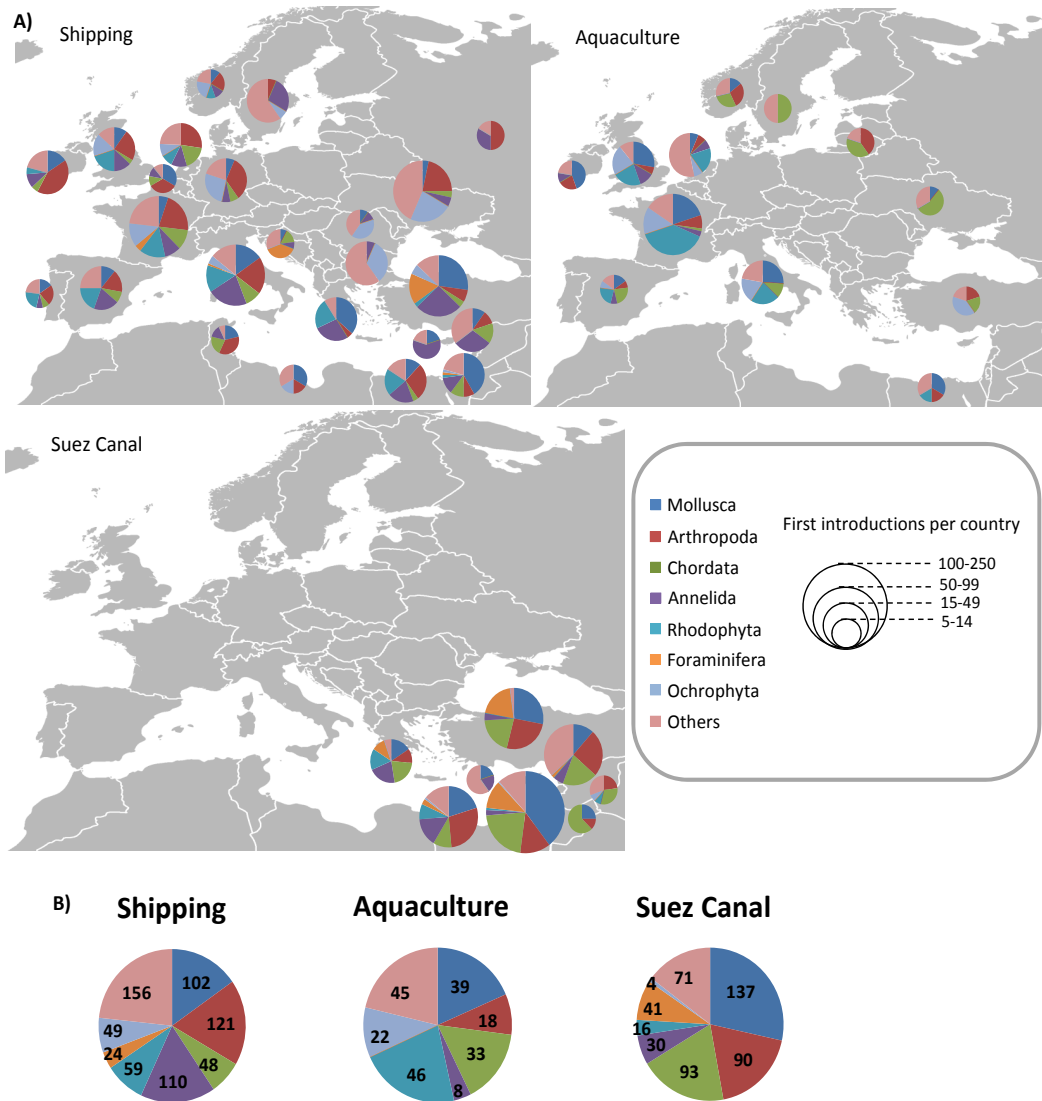


Figure 2. Major taxonomic groups of new marine alien species introduced into European waters through the three main pathways of introduction (Shipping, Aquaculture and the Suez Canal) (A) per country and (B) for overall European waters. Species linked to more than one of these pathways contribute to all corresponding pie charts. For Figure 2A the pie size represents the number of new species introduced per recipient country, arriving through a specific pathway. For clarity, for each pathway, data is only shown for recipient countries with five or more first introduction records.

report alien species arriving through inland canals, with the highest observed percentages in Poland (57%), Estonia (40%), Russia (26%), and Lithuania (25%). Nineteen out of the 34 countries have been recipient countries for species introduced through aquarium trade (Figure 1A).

There was a marked geographical pattern related to introductions of marine alien species in European waters, depending on their pathways of introduction. While introductions by shipping

were quite widespread and distributed in high numbers throughout many different recipient countries, introductions by aquaculture were mainly observed in the western European countries and Italy, and Lessepsian immigrants were mainly first recorded, as expected, in one of the countries close to the Suez Canal. Further, introductions through inland canals were mainly concentrated in north-eastern European countries (Figures 1, 2 and 3).

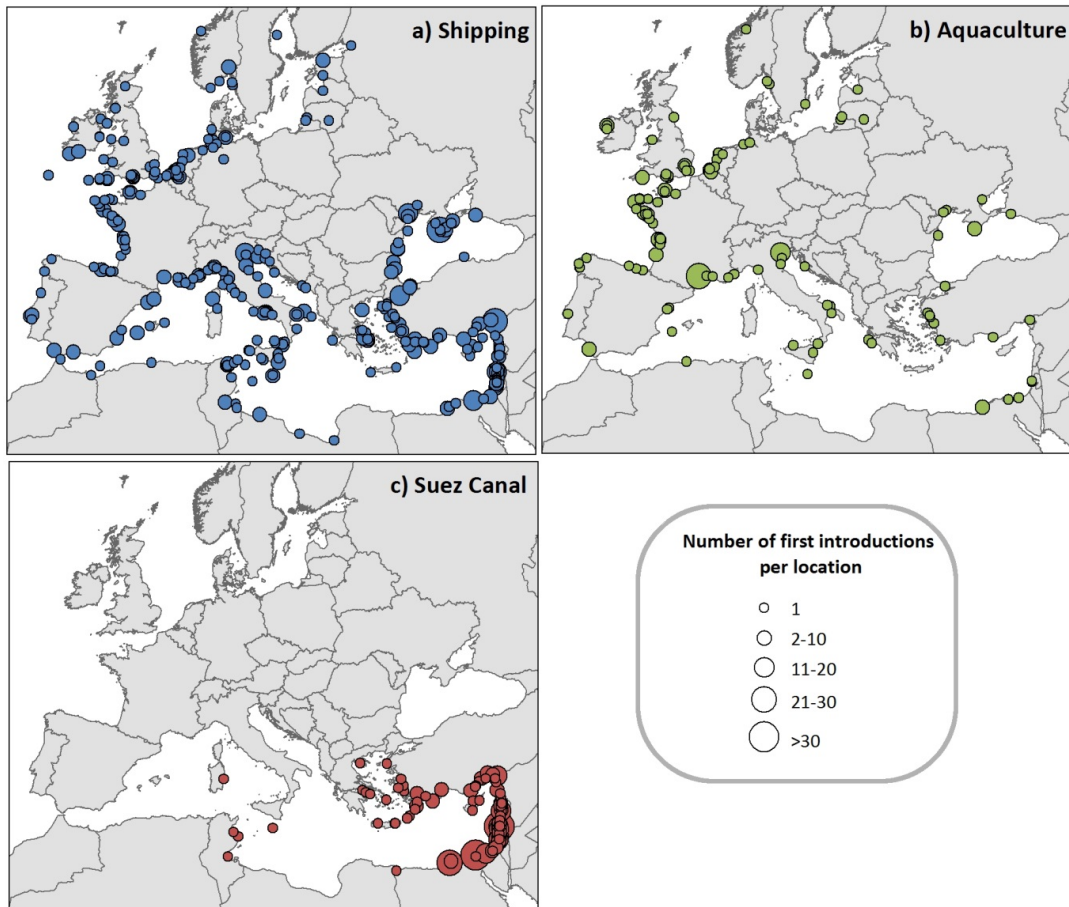


Figure 3. Maps illustrating locations of new alien species introductions in European waters, for the three main pathways of introduction: (A) Shipping (619 records); (B) Aquaculture (183 records); and (C) the Suez Canal (435 records). The circle size represents the number of new species introduced per location, arriving through a specific pathway.

For shipping-introduced species, Turkey registered the highest number of introductions through this pathway, with 26 first records having been found at the port of Iskenderun. Sevastopol, the second largest port in Ukraine, registered 24 first introduction events (Figure 3). France and Italy were the countries mostly responsible for aquaculture-mediated first introduction events, especially in the Thau (29 records) and Venice (12 records) Lagoons (Figure 3). Introductions through the Suez Canal were mainly reported in Haifa, Israel (72 records) and in Port Said (51 records) and Alexandria (23 records), Egypt (Figure 3).

The taxa most often detected in introductions by shipping were arthropods, followed by annelids, and molluscs (Figure 2B). Introductions through the Suez Canal were predominately molluscs,

chordates, and arthropods (Figure 2B). For the countries with the highest number of new Lessepsian immigrants (Israel, Egypt, Lebanon and Turkey), molluscs and arthropods were the most commonly introduced groups (Figure 2A). Rhodophytes were the main group introduced by aquaculture, followed by molluscs and chordates (Figure 2B). France, Spain, and Italy had the highest proportions of rhodophyte introductions (Figure 2A). Although species from most of the major phyla have been introduced through the three main pathways, annelids have mostly been introduced in European waters through shipping, foraminiferans through Lessepsian migrations, and rhodophytes through aquaculture (Figures 2B and 4).

Most of the five countries with the highest number of introductions of alien species through

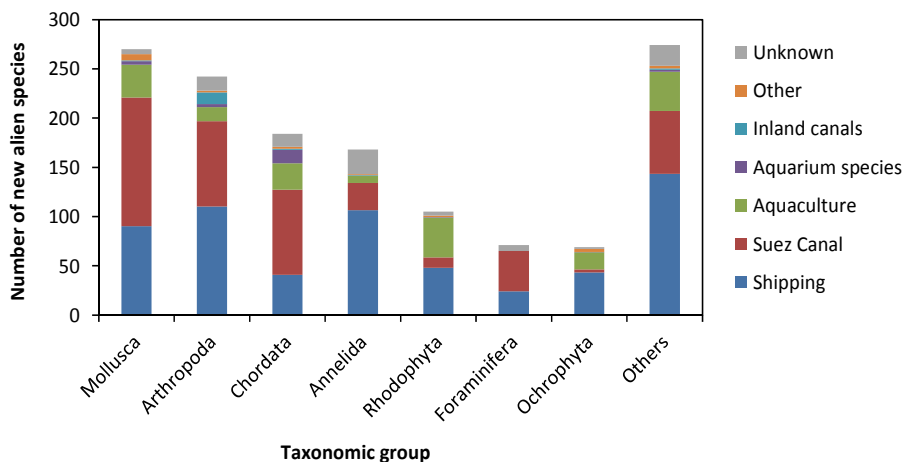


Figure 4. Pathways of introduction reported for the major phyla of marine alien species introduced in European waters. Species that were linked to more than one pathway ($n = 143$) were given a value of $1/k$ for each of the k associated pathways so that the overall contribution of each species to the total number of new aliens was always 1.

shipping showed an increase in the rate of introductions over time. Israel, Ukraine, and especially Turkey show a marked increase in these introductions in the last 20 years (Figure 5A). The trend of new introductions of alien species through the Suez Canal was quite different depending on the recipient country. Egypt had the highest number of new introductions of Lessepsian immigrants registered until 1930 but, from 1931 onwards, the number decreased slightly, and Israel became the primary recipient country until 2010. Turkey and Lebanon registered very few introduction events until 1950 but, from 1951 onwards, the numbers started to increase (Figure 5B). For species introduced through aquaculture, France was the country with the highest number of introductions since the 1970s, when a substantial increase in introduction events occurred. In the last 20 years, however, a decrease has been observed (Figure 5C).

A positive correlation ($r = 0.73$, $N = 25$, $P < 0.001$) was found between the average maritime freight transport by country (as gross weight of goods handled in ports) between 1997 and 2011 and the number of new marine alien species introduced through shipping in each country (Figure 6). The coastline distance of each Mediterranean recipient country to the Suez Canal and the number of new Lessepsian immigrants arriving to their territorial waters were negatively correlated ($r = -0.76$, $N = 19$, $P < 0.001$; Figure 7). A positive correlation ($r = 0.77$, $N = 20$, $P < 0.001$) between

shellfish production by aquaculture and the number of new alien introductions through this pathway per country was found (Figure 8).

Discussion

The distribution patterns of marine alien species first introduction events in European Seas are largely defined by the distribution patterns of human activities/interventions. In this study we have found that there is a marked geographical pattern in the introductions of marine alien species depending on their (human-mediated) pathways of introduction. While introductions of marine aliens through shipping have been observed in several different countries, being quite widespread along the coastal European Seas, introductions by aquaculture have been mainly observed in a few Western European countries and introductions through the Suez Canal have been mainly reported in the Levantine countries. In fact, for all these three main pathways of introduction, strong correlations were found between their magnitude measure per country and the number of alien species introduced through each pathway. Although the number of newly introduced marine alien species in a country is also affected by factors other than human activities, analysing and measuring related human activities may be a very useful tool to help predicting each country's invasion risk. The number of new introductions in a country also

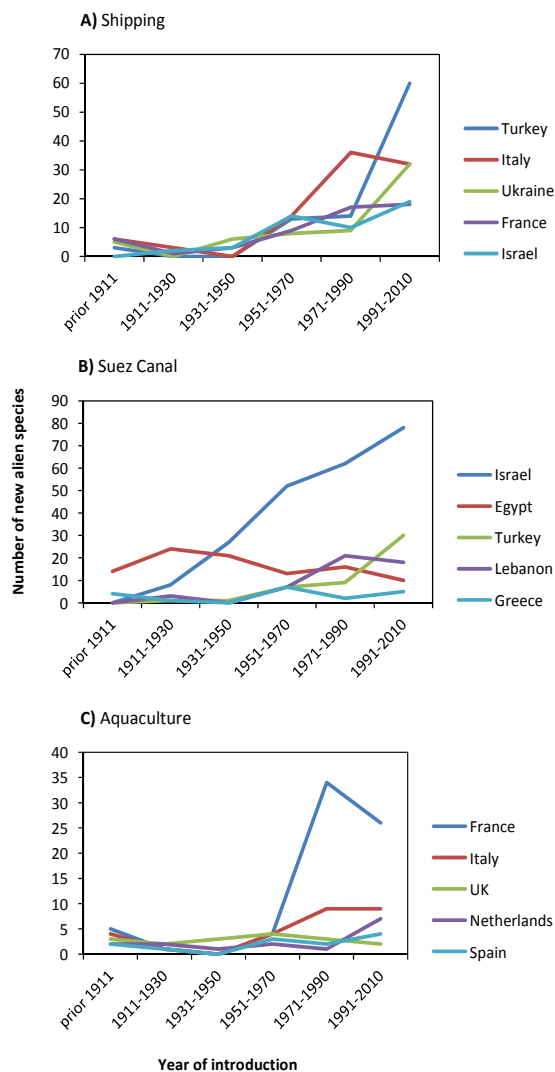


Figure 5. Marine alien species introductions into European waters, over 20 year intervals, for each of the three main pathways of introduction: (A) Shipping; (B) the Suez Canal; and (C) Aquaculture. Data is only shown for the five recipient countries with the highest numbers of recorded first introduction events per pathway. Species linked to more than one of these pathways contribute to all corresponding line charts.

depends on its coastline length, latitude, the number of different suitable habitats, and the number of different ecoregions within a country's marine territory (García-Berthou et al. 2005; Katsanevakis et al. 2013b).

We found considerable differences in the number of new marine alien species recorded per country, with Israel, Turkey and France acting as the main gateways to marine alien invasions in European Seas. These countries actually correspond to the top recipient countries for each of the three

main pathways of introduction, respectively the Suez Canal, shipping and aquaculture, reflecting the importance of pathways of introduction in this process. Introductions through the Suez Canal pathway also explain the high number of new alien species reported in most countries of the Levantine Basin, despite their relatively small coastline in comparison to other countries.

An important factor affecting the reported new introductions of marine alien species by country is the difference in monitoring and reporting effort. Low investment in related research and monitoring likely leads to an underestimation of new marine aliens reported by certain countries (Molnar et al. 2008; Katsanevakis et al. 2013b). Species that are not reported might be later detected in neighbouring countries with better reporting systems or may persist undetected for long time periods. Differences in the scientific interest of countries may also shape the reported number of new introduction events. For instance, Egypt only started to show increased scientific interest after 2010, even though data on introductions are available from earlier collection dates (e.g. for fish Halim and Rizkalla 2012).

Essentially all European coastal countries report species introductions arriving through shipping, as all of them have one or more ports with high levels of trade (Drake and Lodge 2004). We found that countries having a higher maritime transport of goods also report a higher number of marine alien species first introduction events. Similarly, both Ricciardi (2001) and Molnar et al. (2008) found a strong positive relationship between the magnitude of shipping activity (shipping cargo volume) and the number of nonindigenous harmful species reported. Turkey, Italy, and Ukraine are the main countries responsible for shipping-mediated introductions, the former two with introductions spread over most of their coastlines. Still, these countries seem to have hotspot locations responsible for a great majority of their marine introductions: Iskenderun (Turkey), Venice (Italy) and Sevastopol (Ukraine). The port of Iskenderun appears as the largest hotspot for shipping-mediated introductions of marine alien species probably due to being not only one of Turkey's largest ports on the Mediterranean Sea, subjected to intensive maritime transport, but also an important naval training base (Zenetos et al. 2010).

As expected, Lessepsian species were first recorded in countries/locations in the vicinity of the Suez Canal, especially eastwards and northwards of the Canal along the Levantine coastal

Figure 6. Relationship between the number of new shipping-introduced marine alien species found in each recipient country and the average gross weight of goods handled in their ports between 1997 and 2011. For clarity, not all country names are shown.

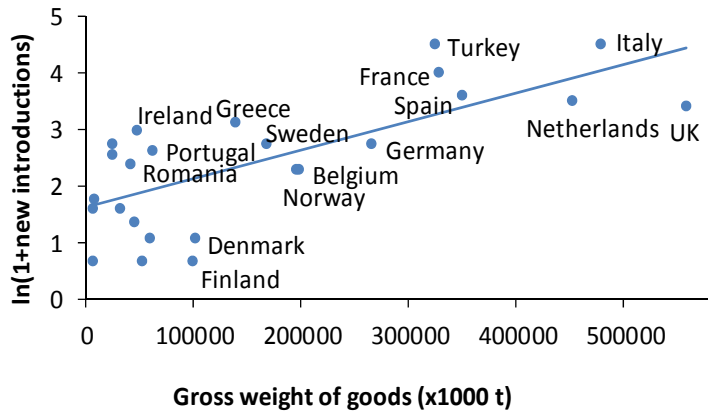


Figure 7. Relationship between the number of new Lessepsian species found in each recipient country and their 'coastline distance' from the Suez Canal (see 'methods' section for the definition of 'coastline distance').

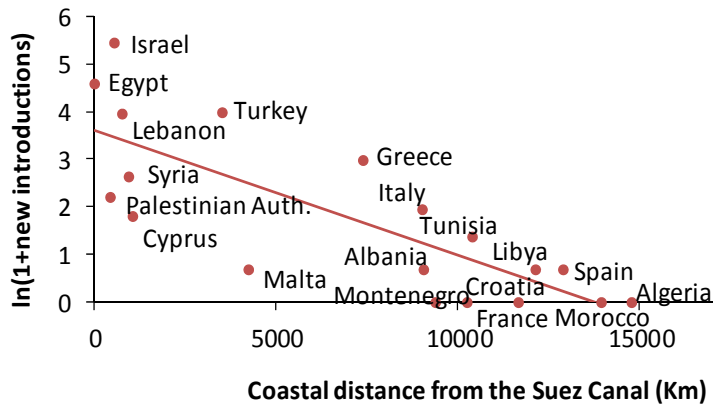
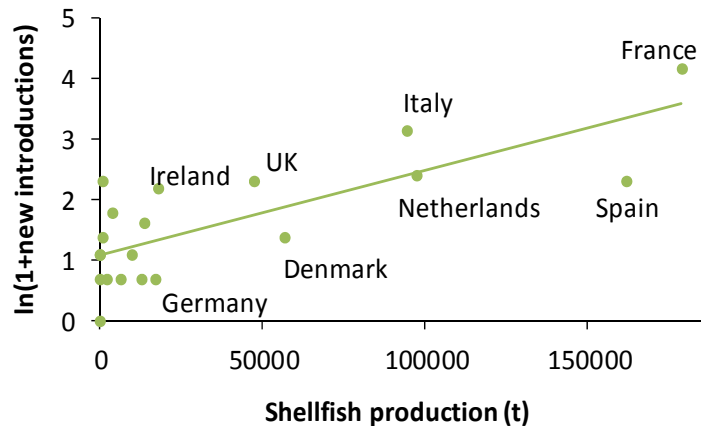


Figure 8. Relationship between the number of new aquaculture-introduced marine alien species found in each recipient country and the average production of shellfish (tonnes) for the period 1950-2011. For clarity, not all country names are shown.



area. However, there were a few species that were first recorded in locations far away from the Suez Canal, e.g. in Malta, Italy, North Tunisia, or along the Greek and Turkish coastlines of the northern Aegean. These seeming 'outsiders' can be justified by two main reasons:

(1) some species might indeed gradually spread through the Suez Canal, but then expand rapidly in the Mediterranean, while their initial introduction went unnoticed either because of reduced monitoring efforts or lack of relevant expertise. This seems to be the case for *Caulerpa*

racemosa var. *turbinata* J.Agardh, 1873, which was first reported from Tunisia by Hamel (1926), but is now known to be present in Israel, Syria, Lebanon, and Cyprus (Verlaque et al. in press), and for *Allolepidapedon fistulariae* Yamaguti, 1940, a parasite of the Lessepsian fish *Fistularia commersonii* Rüppell, 1838, first reported from Sardinia by Pais et al. (2007); (2) some fish species entered in the Mediterranean through the Suez Canal but instead of following the coastline, they travelled offshore across the basin, as is probably the case e.g. of the oceanodromous fish *Tylosurus crocodilus* Péron and Lesueur, 1821, first reported from northern Aegean by Sinis (2005).

Species introduced through aquaculture were mostly reported in France and Italy and mainly clustered in the Thau and Venice Lagoons. This is consistent with both these lagoons being sites of extensive mariculture activities and well-known hotspots for marine, alien, aquaculture-mediated, invasions in the Mediterranean Sea (Verlaque 2001; Occhipinti-Ambrogi and Savini 2003; Zenetos et al. 2012).

The taxonomic pattern of marine alien invasions in European Seas is also shaped by the distribution patterns of human activities. In contrast to Mollusca, which seem to enter European waters in high numbers through all the main pathways of introduction, Annelida have mostly been introduced through shipping, Rhodophyta through aquaculture, and Foraminifera through the Suez Canal. Consequently, Annelida are entering European waters through a diverse range of countries, while Rhodophyta are mostly invading through mid-latitude countries in Western Europe and Foraminifera through Eastern Mediterranean countries.

The history of introductions differs for the different pathways. For all the top five countries registering shipping-mediated introductions, high numbers have been recorded only since the 1970s. This probably reflects the fact that over the last 40 years world seaborne trade has more than tripled (UNCTAD 2010), bringing about a marked increase in the appearance or spread of ship-mediated invasions. On the other hand, this could also be due to a different level of information available for introductions through this pathway, since the impact of Lessepsian immigrants was considered more important and was the focus of most alien species inventories. Similarly, the fact that Israel continuously registers a high number of invasions through the Suez Canal probably

reflects the existence of more exhaustive studies and report monitoring than in adjacent countries. France, the country registering the highest number of introductions through aquaculture since the 1970s, shows a decrease in marine invasions through aquaculture in the last 20 years. Since this has not been accompanied by a reduction in aquaculture production (FAO data), it probably reflects a more strict and effective implementation of management measures. In fact, in the last two decades, the accumulating scientific evidence of the ecological and economic impacts of alien species made administrators and policy makers recognise the need to apply rules to the aquaculture industry to prevent further introductions or translocations of already introduced species (Katsanevakis et al. 2013a). The FAO Code of Conduct for Responsible Fisheries (FAO 1995), the ICES Code of Practice on the Introduction and Transfer of Marine Organisms (ICES 2005), and the EU Regulation concerning the use of alien and locally absent species in aquaculture (EU 2007) are among the applied rules.

Marine alien invasions through shipping and the Suez Canal are not expected to halt or drastically reduce soon. Nevertheless, the establishment of prevention measures such as the ratification of the “International Convention for the Control and Management of Ships’ Ballast Water and Sediments” (BWM Convention) could definitely make a difference. With the constant enlargement of the Suez Canal and the removal of the previous barriers for the introduction of Red Sea species into the Mediterranean, many more species are expected to enter (Katsanevakis et al. 2013a). Aquaculture is perhaps the easiest pathway to control, given its fixed locations and regular procedures (Savini et al. 2010), so that stringent control measures should be implemented and continuously put into force to reduce or prevent the introduction of marine aliens. This actually is the only pathway for which a declining trend of new introductions has been observed, presumably because of the management measures taken so far, especially by EU countries (Katsanevakis et al. 2013a).

Considering the constant expansion of human activities related to aquatic environments, the introduction of marine alien species in European Seas has been occurring at an alarming pace and is likely to increase in the future. Given the frequent negative ecological and economic impacts resultant from these invasions, the control and survey of marine alien species is an urgent need. By pinpointing

the main gateways of introduction of marine alien species in European Seas, we hope this study will provide valuable information and draw the attention of institutional authorities, managers and politicians into where active measures can and should be taken in order to prevent new alien introductions in the European Seas.

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References

- Anderson LWJ (2005) California's reaction to *Caulerpa taxifolia*: a model for invasive species rapid response. *Biological Invasions* 7: 1003–1016, <http://dx.doi.org/10.1007/s10530-004-3123-z>
- Billard C (1992) *Fibrocapsa japonica* (Raphidophyceae), algue planctonique nouvelle pour les côtes de France. *Cryptogamie Algologie* 13: 225–231
- Breton G, Faasse M, Noël P, Vincent T (2002) A new alien crab in Europe: *Hemigrapsus sanguineus* (Decapoda: Brachyura: Grapsidae). *Journal of Crustacean Biology* 22: 184–189
- Drake JM, Lodge DM (2004) Global hotspots of biological invasions: evaluating options for ballast-water management. *Proceedings of the Royal Society, Series B* 271: 575–580, <http://dx.doi.org/10.1098/rspb.2003.2629>
- Elbrächter M (1994) Phytoplankton und toxische Algen. In: Lozán JL, Rachor E, Reise K, West-ernhagen Hv, Lenz W (eds), Warnsignale aus dem Wattenmeer. Blackwell, Berlin, Germany, pp 81–86
- EU (2007) Council Regulation Concerning Use of Alien and Locally Absent Species in Aquaculture. Regulation 708/2007, OJ L 168
- FAO (1995) Code of Conduct for Responsible Fisheries. FAO, Rome, Italy
- Galil BS (2006) The Suez Canal - The marine caravan - The Suez Canal and the Erythrean invasion. In: Gollasch S, Galil BS, Cohen AN (eds), Monographiae Biologicae: Bridging divides: Maritime canals as invasion corridors. Springer, Heidelberg, pp 207–300
- García-Berthou E, Alcaraz C, Pou-Rovira Q, Zamora L, Coenders G, Feo C (2005) Introduction pathways and establishment rates of invasive aquatic species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 453–463, <http://dx.doi.org/10.1139/f05-017>
- Gollasch S, Nehring S (2006) National checklist for aquatic alien species in Germany. *Aquatic Invasions* 1: 245–269, <http://dx.doi.org/10.3391/ai.2006.1.4.8>
- 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)
- Halim Y, Rizkalla S (2011) Aliens in Egyptian Mediterranean waters. A check-list of Erythrean fish with new records. *Mediterranean Marine Science* 12: 479–490, <http://dx.doi.org/10.12681/mms.46>
- Hamel G (1926) Quelques algues rares ou nouvelles pour la flore méditerranéenne. *Bulletin du Muséum National de Sciences Naturelles, Paris* 32(6): 420
- 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>
- Hulme PE, Bacher S, Kenis M, Klotz S, Kuhn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pysek P, Roques A, Sol D, Solarz W, Vila M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology* 45: 403–414, <http://dx.doi.org/10.1111/j.1365-2664.2007.01442.x>
- ICES (2005) Code of Practice on the Introductions and Transfers of Marine Organisms. ICES, Copenhagen, Denmark
- Katsanevakis S, Bogucarskis K, Gatto F, Vandekerkhove 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 (2013a) 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>
- Katsanevakis S, Gatto F, Zenetos A, Cardoso AC (2013b) How many marine aliens in Europe? *Management of Biological Invasions* 4: 37–42, <http://dx.doi.org/10.3391/mbi.2013.4.1.05>
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* 16: 199–204, [http://dx.doi.org/10.1016/S0169-5347\(01\)02101-2](http://dx.doi.org/10.1016/S0169-5347(01)02101-2)
- Lardicci C, Castelli A (1986) *Desdemona ornata* Banse, 1957 (Polychaeta: Sabellidae, Fabriciidae) new record in the Mediterranean Sea. *Oebalia* 13: 195–200
- MEA (Millennium Ecosystem Assessment) (2005) Ecosystems and Human Wellbeing: Biodiversity Synthesis. World Resources Institute, Washington DC, USA
- Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and Environment* 6(9): 485–492, <http://dx.doi.org/10.1890/070064>
- Naylor RL, Williams SL, Strong DR (2001) Aquaculture: A gateway for exotic species. *Science* 294: 1655–1656, <http://dx.doi.org/10.1126/science.1064875>
- Occhipinti-Ambrogi A, Savini D (2003) Biological invasions as a component of global change in stressed marine ecosystems. *Marine Pollution Bulletin* 46: 542–551, [http://dx.doi.org/10.1016/S0025-326X\(02\)00363-6](http://dx.doi.org/10.1016/S0025-326X(02)00363-6)
- Pais A, Merella P, Follesa MC, Garippa G (2007) Westward range expansion of the Lessepsian migrant *Fistularia commersonii* (Fistulariidae) in the Mediterranean Sea, with notes on its parasites. *Journal of Fish Biology* 70: 269–277, <http://dx.doi.org/10.1111/j.1095-8649.2006.01302.x>
- Padilla DK, Williams SL (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and the Environment* 2(3): 131–138, [http://dx.doi.org/10.1890/1540-9295\(2004\)002\[0131:BBWAAO\]2.0.CO;2](http://dx.doi.org/10.1890/1540-9295(2004)002[0131:BBWAAO]2.0.CO;2)
- Panagopoulos D, Nicolaidou A (1989–90) A population of *Desdemona ornata* Banse, 1957 (Polychaeta, Sabellidae) settled in a fully marine habitat of the Mediterranean. *Oebalia* 16: 35–39
- Panov VE, Alexandrov B, Arbačiauskas K, Binimelis R, Copp GH, Grabowski M, Lucy F, Leuven RSEW, Nehring S, Paunović M, Semenchenko V, Son MO (2009) Assessing the risks of aquatic species invasions via European inland waterways: from concepts to environmental indicators. *Integrated Environmental Assessment and Management* 5: 110–126, http://dx.doi.org/10.1897/IEAM_2008-034.1
- Por FD (1978) Lessepsian Migration – the influx of Red Sea biota into the Mediterranean by way of the Suez Canal. *Ecological Studies* 23, Springer-Verlag, Berlin-Heidelberg-New York, 228 pp
- Ricciardi A (2001) Facilitative interactions among aquatic invaders: is an “invasional meltdown” occurring in the Great Lakes? *Canadian Journal of Fisheries and Aquatic Sciences* 58: 2513–2525, <http://dx.doi.org/10.1139/r01-178>

- Rilov G, Galil B (2009) Marine bioinvasions in the Mediterranean Sea – history, distribution and ecology. In: Rilov G, Crooks JA (eds), *Biological Invasions in Marine Ecosystems*. Springer, Berlin, pp 549–576, http://dx.doi.org/10.1007/978-3-540-79236-9_31
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molesky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand N, McCauley DE, O’Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–332, <http://dx.doi.org/10.1146/annurev.ecolsys.32.081501.114037>
- Sala OE, Chapin III FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, LeRoy Poff N, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global Biodiversity Scenarios for the Year 2100. *Science* 287: 1770–1774, <http://dx.doi.org/10.1126/science.287.5459.1770>
- Savini D, Occhipinti–Ambrogi A, Marchini A, Tricarico E, Gherardi F, Olenin S, Gollasch S (2010) The top 27 animal alien species introduced into Europe for aquaculture and related activities. *Journal of Applied Ichthyology* 26(2): 1–7, <http://dx.doi.org/10.1111/j.1439-0426.2010.01503.x>
- Schlaepfer MA, Sherman PW, Blosser B, Runge MC (2005) Introduced species as evolutionary traps. *Ecology Letters* 8: 241–246, <http://dx.doi.org/10.1111/j.1461-0248.2005.00730.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>
- Seebens H, Gastner MT, Blasius B (2013) The risk of marine bioinvasion caused by global shipping. *Ecology Letters* 16(6): 782–790, <http://dx.doi.org/10.1111/ele.12111>
- Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-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(1): 58–66, <http://dx.doi.org/10.1016/j.tree.2012.07.013>
- Sinis AI (2005) First record of *Tylosurus crocodilus* (Péron & Lesueur 1821) (Pisces: Belontiidae) in the Mediterranean (North Aegean Sea, Greece). 12th Hellenic Ichthyologists Symposium Proceedings. Drama, Greece, October 2005, pp 304–307 (in Greek with English abstract)
- Thresher RE, Kuris AM (2004) Options for managing invasive marine species. *Biological Invasions* 6: 295–300, <http://dx.doi.org/10.1023/B:BINV.0000034598.28718.2e>
- UNCTAD (2010) Review of Maritime Transport. United Nations Conference on Trade and Development. UNCTAD/RMT/2010. United Nations Publication, Geneva, Switzerland
- Verlaque M (2001) Checklist of the macroalgae of Thau Lagoon (Hérault, France), a hot spot of marine species introduction in Europe. *Oceanologica Acta* 24(1): 29–49, [http://dx.doi.org/10.1016/S0399-1784\(00\)01127-0](http://dx.doi.org/10.1016/S0399-1784(00)01127-0)
- Verlaque M, Ruitton S, Mineur F, Boudouresque CF (in press) Macrophytes. CIESM Atlas of exotic species in the Mediterranean. CIESM Publishers, Monaco
- Vermeij GJ (1996) An agenda for invasion biology. *Biological Conservation* 78: 3–9, [http://dx.doi.org/10.1016/0006-3207\(96\)00013-4](http://dx.doi.org/10.1016/0006-3207(96)00013-4)
- Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, DAISIE partners (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>
- Vitousek PM, D’Antonio CM, Loope LL, Rejmánek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* 21: 1–16
- Vrieliel EG, Koeman RPT, Nagasaki K, Ishida Y, Peperzak L, Gieskes WWC, Veenhuis M (1995) *Chattonella* and *Fibrocapsa* (Raphidophyceae): first observation of, potentially harmful, red tide organisms in Dutch coastal waters. *Netherlands Journal of Sea Research* 33: 183–191, [http://dx.doi.org/10.1016/0077-7579\(95\)90005-5](http://dx.doi.org/10.1016/0077-7579(95)90005-5)
- 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>
- WoRMS Editorial Board (2013) World Register of Marine Species. Available from <http://www.marinespecies.org> at VLIZ (Accessed 11 December 2013)
- Zenetos A, Ovalis P, Eviker D (2010) On some Indo-Pacific boring endolithic Bivalvia species introduced into the Mediterranean Sea with their host – spread of *Sphenia rueppelli* A. Adams, 1850. *Mediterranean Marine Science* 11(1): 201–207, <http://dx.doi.org/10.12681/mms.104>
- Zenetos A, Gofas S, Morri C, Rosso A, Violanti D, Gracia Raso JE, Cinar ME, Almogi-Labin A, Ates AS, Azzurro E, Ballesteros E, Biachi CN, Bilecenoglu M, Gambi MC, Giangrande A, Gravili C, Hyams-Kaphzan O, Karachle PK, Katsanevakis S, Lipej L, Mastrototaro F, Mineur F, Pancucci-Papadopoulou MA, Ramos Espla A, Salas C, San Martin 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>

Supplementary material

The following supplementary material is available for this article:

Table 1S. Marine species included in the EASIN database (as of October 2013), the year and country of first introduction in Europe of each species, and the corresponding most probable pathway(s) of introduction.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2014/Supplements/AI_2014_Nunes_etal_Supplement.xls