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Review

The native distribution range of the European marine non-indigenous species

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Abstract

In this study, we have performed a large-scale assessment on the native distribution range of the marine non-indigenous species (NIS) found in at least one of the European Seas (Mediterranean, NE Atlantic Ocean, Black, Baltic Sea). As a basis, we have used the most updated pan-European NIS inventory, provided by the European Alien Species Information Network. All taxonomic groups have been considered for this analysis, taking into account established NIS in European Seas (824 taxa in total). The vast majority of the European marine NIS have their native distribution in the Western and Central Indo-Pacific, being mostly associated with introductions into the Mediterranean Sea through the Suez Canal. However, this overall pattern is heavily influenced by the fact that 76% of all NIS primary introductions in Europe have been reported first from the Mediterranean Sea. A more detailed analysis revealed various patterns of the dominating native distributions of the primarily introduced NIS in Europe, depending on the European marine subregions where they have been initially introduced and their associated pathways. There seems to be a general decrease in NIS introductions in Europe, especially when it comes to NIS with native distribution in the Temperate Northern Pacific, although this trend should be treated with caution. The information provided in the current study can be useful for tailored management of specific primary pathways per marine subregion, supporting prioritization efforts.

Key words: alien, pathways, trends, invasive, Mediterranean Sea, Black Sea, Baltic Sea, NE Atlantic, MSFD

Introduction

Marine non-indigenous species (NIS) represent a significant risk to the receiving environments. They may exhibit invasive behavior and induce alterations to ecosystems' structure and functions, impede the provision of ecosystem services, and even result in negative socioeconomic effects in coastal areas (Wallentinus and Nyberg 2007; Molnar et al. 2008; Katsanevakis et al. 2014). New introductions of NIS have been accelerated in recent decades by the rapid globalization and increasing trends of human activities (shipping, aquaculture, fisheries, tourism, etc.) (Boudouresque and Verlaque 2005; Katsanevakis et al. 2013a).

By 2013, at least 1,369 NIS have been reported from all European and contiguous seas (Katsanevakis et al. 2013b). Due to the threats they pose, European NIS are targeted in a series of legislative instruments, such as the European Union Marine Strategy Framework Directive (MSFD) (EC 2008) and the Biodiversity Strategy (EC 2014). At the same time, aiming to assist policy makers and environmental managers in their decisions on prevention or mitigation actions, NIS have been thoroughly addressed by the scientific community, through the provision of recommendations for monitoring (e.g. Lehtiniemi et al. 2015), the revision of species inventories and spatial and temporal patterns (Zenetos et al. 2012, 2017; Katsanevakis et al. 2013b; Galil et al. 2016; Ojaveer et al. 2016), pathways, gateways and their trends (Nunes et al. 2014; Galil et al. 2017), impacts (Katsanevakis et al. 2014, 2016), and biological traits of the most widespread species (Cardeccia et al. 2016). Specific focus has been given to the Mediterranean Sea, the most invaded marine region of the world, with at least 821 multicellular NIS (casuals included) reported by early 2017 (Zenetos et al. 2017).

Several studies have addressed the native distribution range (possible origin) of the European marine NIS, but most of them have examined this issue only at regional or country level. Some examples include the native distribution of NIS of the Baltic Sea (Leppäkoski et al. 2002), Belgium (Kerckhof et al. 2007), Germany (Gollasch and Nehring 2006), British Isles (Minchin et al. 2013), Israel (Galil 2007), Italy (Occhipinti-Ambrogi et al. 2011), and Greece (Zenetos et al. 2009). In addition, the CIESM atlases provide information on the native distribution of NIS belonging to four taxonomic groups in the Mediterranean Sea, namely Fish, Crustacea, Mollusca, Macrophytes, but with no detailed analysis (Galil et al. 2002; Golani et al. 2002; Zenetos et al. 2004; Verlaque et al. 2015). Surprisingly, there has not been any study so far providing a large-scale assessment of the native distribution of all NIS across all European Seas.

In this study, we investigate the native distribution of NIS recorded in at least one of the main European Seas: the Mediterranean, NE Atlantic Ocean, the Black and the Baltic Seas. All taxonomic groups of NIS have been considered for this analysis. In addition, primary pathways of introduction are examined in relation to each main native distribution area of NIS. Time trends of species introductions in relation with the prevailing native distribution areas are also investigated.

Methods

For the present analysis, we have used the pan-European inventory of NIS provided by the European Alien Species Information Network (EASIN – Katsanevakis et al. 2012) and updated up to March 2017 (EASIN Catalogue version 5.6), based also on the recent work by Zenetos et al. (2017). EASIN is a dynamic inventory that is continuously updated to follow the latest scientific findings about new NIS species in Europe and their status. The latest version of the EASIN database contains 1,411 NIS reported from European marine waters, including all taxonomic groups, from bacteria to mammals. Species with a native distribution in at least one European Sea but with alien range into other(s) have been also included in our analysis, hereafter referred to as NIS with "European origin". Only established NIS have been taken into consideration. To this end, we have excluded casual (i.e. NIS not established in Europe, found only once or twice), cryptogenic (i.e. species with no definite evidence of their native or introduced status) and questionable species (i.e. NIS with insufficient information or new entries not verified by experts or NIS with unresolved taxonomic status). Species that are predominantly freshwater but which might also appear in oligohaline environments (i.e. with salinity < 5 psu) were also excluded from the current study. Consequently, 824 established NIS have been considered in the present paper (Appendix 1). The Taxonomic classification (Kingdom, Phylum, Class, Order and Family) of each NIS followed WoRMS (2017).

The EASIN data encompass the four main European Seas: the Black Sea, the Mediterranean Sea, the NE Atlantic Ocean, and the Baltic Sea. To have full coverage of the four Seas surrounding Europe, EASIN contains NIS reported from the whole Mediterranean Sea, including also North African and Near East Mediterranean countries. EU overseas territories (including the Outermost Regions, e.g. the Macaronesia Sea) were not considered.

We have assigned the known native distribution to each NIS of the EASIN dataset based on the scientific literature, AquaNIS Editorial Board (2015) and WoRMS Editorial Board (2017). Afterwards, the native distribution of each NIS was classified based on the global marine biogeographic realms proposed by Spalding et al. (2007), slightly modified for the aims of our study. To this end, we have split the realm "Temperate Northern Atlantic" into 3 distinct realms: a) the "***Temperate Northwest Atlantic***", including the provinces "Cold Temperate Northwest Atlantic" and the "Warm Temperate Northwest Atlantic"; b) the "***European Seas***", which include the provinces "Northern European Seas", "Mediterranean Sea", "Black Sea", and the ecoregion "South European Atlantic Shelf"; and c) the "***Saharan Upwelling***" (see also Figure 1). In case the native distribution of a species covers more than one marine realm, multiple realms were assigned to that species. For few NIS the native distribution is unknown (13 taxa; see Appendix 1).

Based on an extensive revision of the information found in EASIN and the scientific literature, we have analyzed the information on primary introduction pathways for each marine NIS in Europe, i.e. the pathway(s) related to the first arrival of a NIS in Europe. Pathways followed the classification scheme proposed by CBD (2014). A certainty score was given to each assigned pathway for every NIS, based on the scheme proposed by Katsanevakis et al. (2013a), and slightly modified as follows:

High certainty (score = 3): there is direct evidence of a pathway; this is the case e.g. for most intentional introductions (e.g. Release in Nature: fishery in the wild – including game fishing) and in many cases of Lessepsian immigrants (Corridor: interconnected waterways/basins/seas) when there is direct evidence

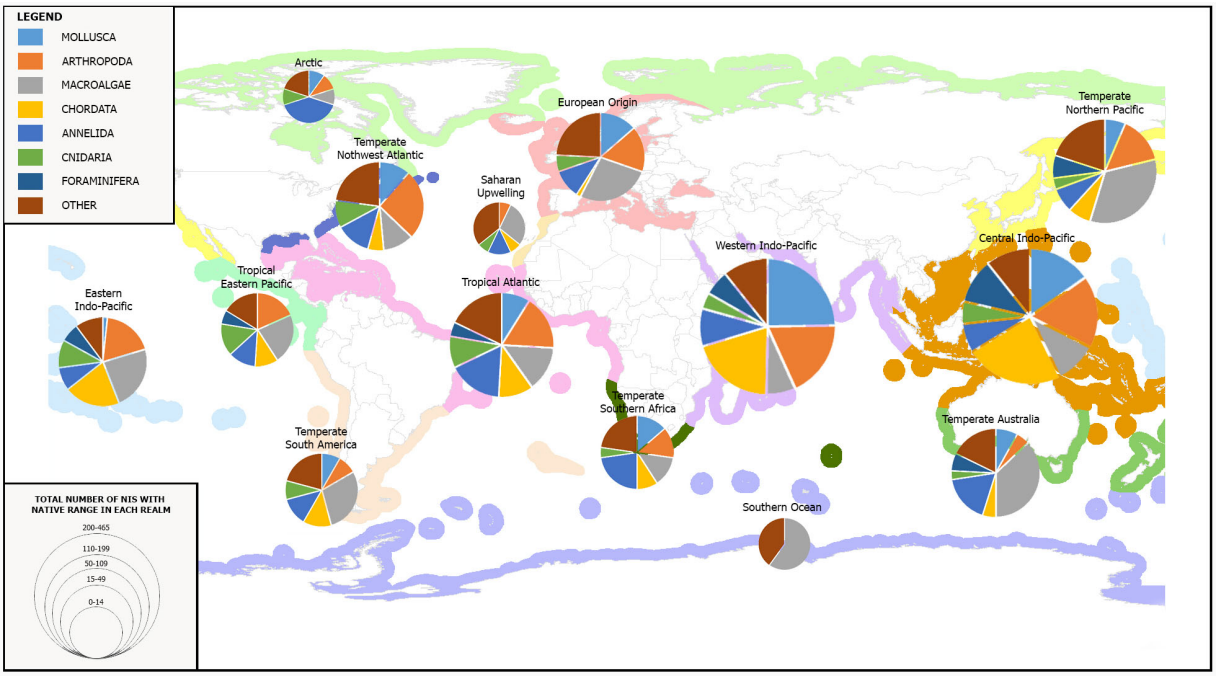

Figure 1. Native distribution range of NIS established in one or more European Seas, based on the classification of the global marine biogeographic realms by Spalding et al. (2007), slightly modified for the current study (see Materials and Methods). The size of each pie chart represents the total number of NIS whose native distribution covers a specific realm. Each NIS can have a native distribution extending to one or more realms. For each realm the proportion of the European NIS major taxonomic groups is given. NIS associated with "European Origin" are those with native distribution in at least one European Sea but with alien range into other(s).

of a gradual expansion along the Suez Canal and then in the localities around the exit of the Canal in the Mediterranean.

Medium certainty (score = 2): a likely pathway can be inferred; the NIS appears for the first time in a locality where a pathway is known to operate. This applies to many species introduced e.g. by shipping ballast (Transport – Stowaway: ship/boat ballast water) or as aquaculture contaminants (Transport – Contaminant: contaminant on animals – except parasites, species transported by host/vector). In many cases inference is based on known examples of introductions elsewhere for the same species, the biology and ecology of the species, the habitats and locales it occupies in both the native and introduced range, and its pattern of dispersal (if known), e.g. for a fouling species frequently recorded in/near ports, Transport – Stowaway: ship/boat hull fouling has been assumed to be the most probable pathway.

Low certainty (score = 1): the NIS cannot be convincingly ascribed to a single pathway; usually, two or more possible pathways can be inferred. Inference is based on the activities in the locality where the NIS was found and may include evidence on similarly behaving species reported elsewhere.

For 6 taxa (Appendix 1), no primary introduction pathway could be assigned or even inferred; for these NIS the pathway of introduction was assigned as "unknown". Secondary introductions and their pathways, i.e. further spread of a NIS from one infested European marine area to another one, were not considered.

In association with the native distribution range of each marine NIS in Europe, we have considered the locations of the primary introduction events at European scale, i.e. the European marine subregion where a NIS first appeared in Europe. This information was extracted from EASIN and was analyzed based on the geographical scale of the European marine subregions defined in Art. 4 of the MSFD: Black Sea, Aegean-Levantine Sea, Ionian Sea and the Central Mediterranean Sea, Adriatic Sea, Western Mediterranean Sea, Bay of Biscay and the Iberian Coast, Celtic Seas, Greater North Sea, and Baltic Sea. We have also used the ecoregions of Spalding et al. (2007) "South and West Iceland" and "Northern Norway and Finnmark" to include European marine areas outside the MSFD coverage (see also Figure 3). As above, the Macaronesia subregion was excluded from our analysis. Primary introduction

events of NIS in Europe were depicted per European marine subregion and analyzed with the related native distribution of the NIS, linked also with their primary introduction pathways. Regarding the latter, we have calculated the proportion (%) of each primary pathway contribution, associated per European marine subregion and each major native distribution of the related NIS. The relative contribution (%) of each pathway has been calculated based on the scoring system of the pathway certainty applied to each NIS (High = 3, Medium = 2, Low = 1); i.e. the total score points of a certain pathway to the sum points of all pathways, depicted as % value.

For addressing time trends of new NIS introductions, we have used the date of first observation of each NIS in Europe (linked with the primary introduction events based on the EASIN data), which is considered the best possible estimate of the year of first introduction. Specifically, for the time trends of new introductions casual NIS (355 taxa) were additionally considered in the analysis (Appendix 1). Time trends of new NIS were accounted for between 1951 and 2015, in 5-year intervals.

Results

Most NIS which established in one or more European Seas have their native distribution range in the Western Indo-Pacific (465 taxa) (see also Figure 1). The Central Indo-Pacific (243 taxa), the Temperate Northern Pacific (170 taxa), the Tropical Atlantic (112 taxa), and the Temperate Northwest Atlantic (70 taxa) constitute also important realms of European NIS native distribution. In addition, there are 66 taxa native to at least one of the European Seas but introduced to another (NIS of European origin). These taxa include: a) taxa that are native to the NE Atlantic Ocean but have been primarily introduced into the Mediterranean (23 taxa), the Black Sea (14 taxa), the Baltic Sea (2 taxa) and in South and West Iceland (2 taxa); b) taxa that are native to the Mediterranean but have been introduced into the NE Atlantic Ocean (8 taxa), the Black (5 taxa) and the Baltic Sea (1 taxon); c) taxa which are native to the Baltic but have been primarily introduced in the NE Atlantic Ocean (5 taxa) and in the Mediterranean Sea (1 taxon); d) finally, taxa native to the Black Sea that have been introduced in the Baltic (4 taxa) and in the Mediterranean Sea (1 taxon). Very few NIS have their native distribution in the Arctic (10 taxa) and Southern Ocean (5 taxa) (see also Figure 1). More details on the number of NIS with native distribution in each marine realm are provided in Appendix 2.

For each marine realm, the relative proportion of the main taxonomic groups of the European marine NIS differs (Figure 1). For instance, molluscs dominate in the pool of NIS with Western Indo-Pacific native distribution, while NIS related with the Central Indo-Pacific realm are dominated by fish (Chordata). On the other hand, NIS associated with the Temperate Northern Pacific realm belong mainly to Macroalgae (Bryopsidophyceae, Chlorophyceae, Ulvophyceae, Phaeophyceae, Rhodophyta), while those linked to the Tropical Atlantic correspond mainly to Arthropoda and Annelida. Dominating NIS with native distribution in the Temperate Northwest Atlantic and NIS of European origin are Arthropoda and Macroalgae respectively. In absolute numbers, for all main taxonomic groups the majority of European marine NIS have their native distribution mostly in the Western Indo-Pacific, with the exception of the Macroalgae which have their native range mainly in the Temperate Northern Pacific (Appendix 2).

The primary pathways of introduction of NIS in Europe were analyzed in relation to the six most important marine realms of European NIS' native distribution: Western Indo-Pacific, Central Indo-Pacific, Temperate Northern Pacific, Tropical Atlantic, Temperate Northwest Atlantic and European Seas (see also Figure 1). The analysis has shown different patterns of the most important pathways among the native distribution realms (Figure 2). NIS with native distribution in the Western and Central Indo-Pacific have been introduced into Europe mostly through "Corridor: interconnected waterways/basins/Seas", corresponding to the Suez Canal. On the other hand, NIS with native distribution in the Temperate Northern Pacific have been introduced mainly through shipping, including both "Transport-stowaway: ship/boat ballast water" (hereafter referred to as shipping-ballast) and "Transport-stowaway: ship/boat hull fouling" (hereafter referred to as shipping-fouling). "Transport-contaminant: contaminant on animals (except parasites, species transported by host/vector)" (hereafter referred to as aquaculture-contamination) is also important for NIS of Temperate Northern Pacific. Most NIS with native distribution in the Tropical Atlantic are associated either with shipping (both ballast and fouling). Similarly, NIS related to the Temperate Northwest Atlantic realm are mainly linked with shipping-ballast and to a lesser extent with shipping-fouling. Finally, NIS with European origin have been introduced from one European Sea to another mainly through shipping-ballast, but also due to shipping-fouling and aquaculture-contamination. NIS related to the pathway "Escape from confinement: pet/aquarium/terrarium species (including live food for such species)" were relatively low in numbers for all main marine realms of native distribution (Figure 2). The rest of the assigned primary pathways [Release in nature:

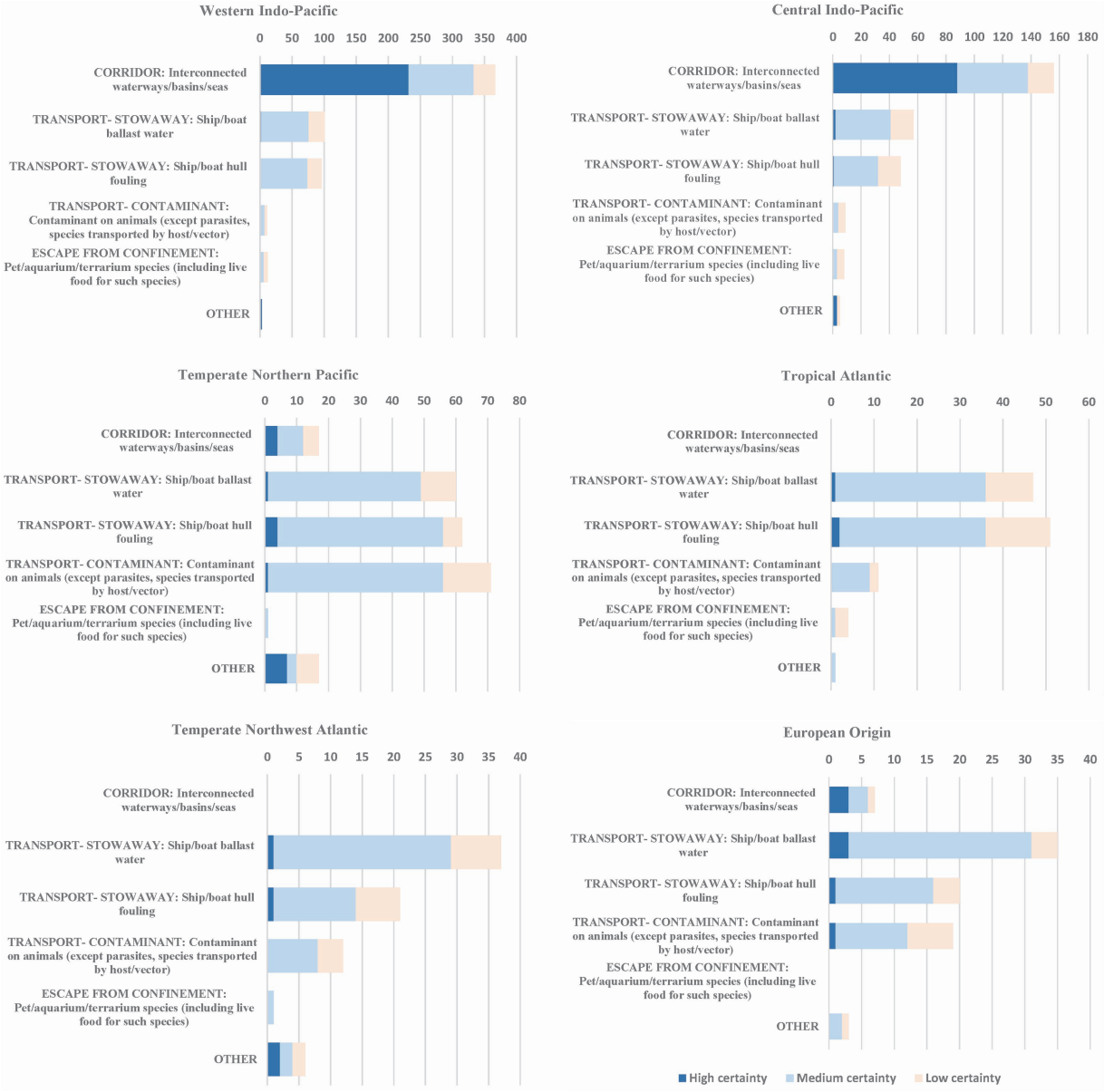

Figure 2. Number of established marine NIS introduced in Europe through primary introduction pathways, based on CBD (2014) scheme, associated with each of the six major realms of European NIS' native distribution. Several taxa are linked to more than one pathway. Distinction in certainty categories for each assigned pathway is also given.

fishery in the wild (including game fishing); Escape from confinement: aquaculture/mariculture; Escape from confinement: botanical garden/zoo/aquaria (excluding domestic aquaria); Escape from confinement: live food and live bait; Transport-contaminant: parasites on animals (including species transported by host and vector); Transport-stowaway: angling/ fishing equipment; Transport-stowaway: other means of transport; see also Appendix 1] had an insignificant contribution to marine NIS introductions into Europe and were grouped together as "Other" (Figure 2). It should be noted that the certainty level was relatively high only for the NIS related to "Corridor: interconnected waterways/basins/Seas", while for all the rest of the pathways the certainty level was mainly medium or low (Figure 2).

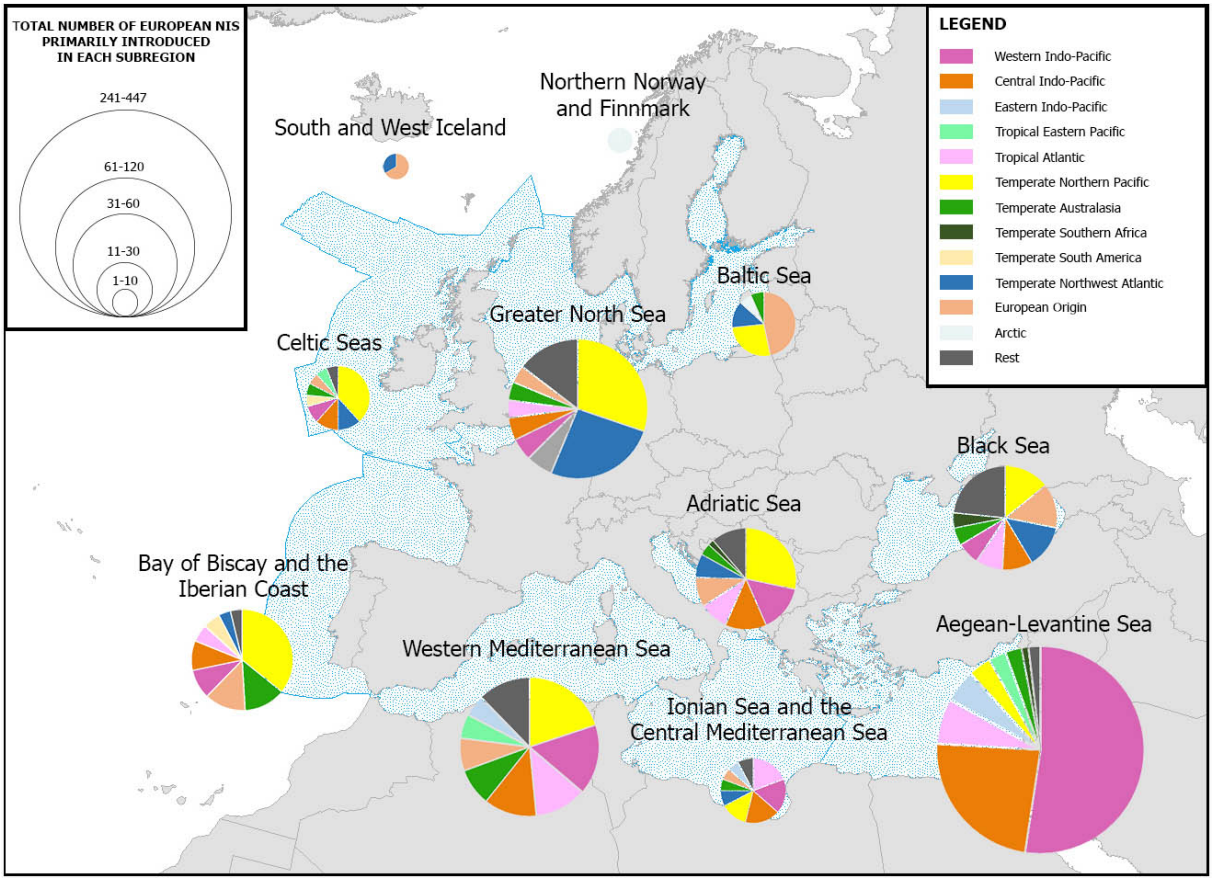

Figure 3. Proportion of the major native distribution ranges of established European marine NIS, associated with their first introduction events in Europe, depicted per marine sub-regions following the MSFD and Spalding et al. (2007) for non-EU seas classification systems. The size of each pie chart represents the total number of NIS primarily introduced in a subregion (the subregion of the initial arrival at European scale). NIS of European origin have been counted in the subregion of first introduction within their alien European range.

At European scale, most primary introduction events of currently established NIS occurred in the Aegean-Levantine Sea (447 taxa – 54% of all primary introductions in Europe), followed by primary introductions which took place in the Western Mediterranean Sea (112 taxa – 14%), the Greater North Sea (70 taxa – 9%) and the Black Sea (45 taxa – 5%). On the other hand, very few NIS have been recorded first in Europe from South and West Iceland (3 taxa – 0.3%) and Northern Norway and Finnmark (1 taxon – 0.1%) (Figure 3).

The native distribution of primarily introduced NIS in Europe varies, depending on the marine subregions where they were initially reported (Figure 3). Similarly, the associated primary pathways of introduction can vary substantially among NIS with different native distribution, depending also on the European subregions where they were initially introduced (Figures 4, 5). For instance, when it comes to the Mediterranean Sea, Europe's NIS first reported from the Aegean-Levantine Sea have their native distribution mostly in the Western and Central Indo-Pacific and related with introductions through the Suez Canal. European primary introductions that were first recorded in the Ionian Sea and the Central Mediterranean Sea have their native distribution mainly in the Tropical Atlantic (linked mostly with shipping), but also in the Western and Central Indo-Pacific (linked mostly with shipping and the Suez Canal). Europe's NIS primarily introduced in the Adriatic Sea are associated mostly to the Temperate Northern Pacific realm (mostly aquaculture-contamination and shipping-ballast), and Western and Central Indo-Pacific (both mainly shipping-ballast and the Suez Canal). First European introduction events that occurred in the Western Mediterranean Sea correspond

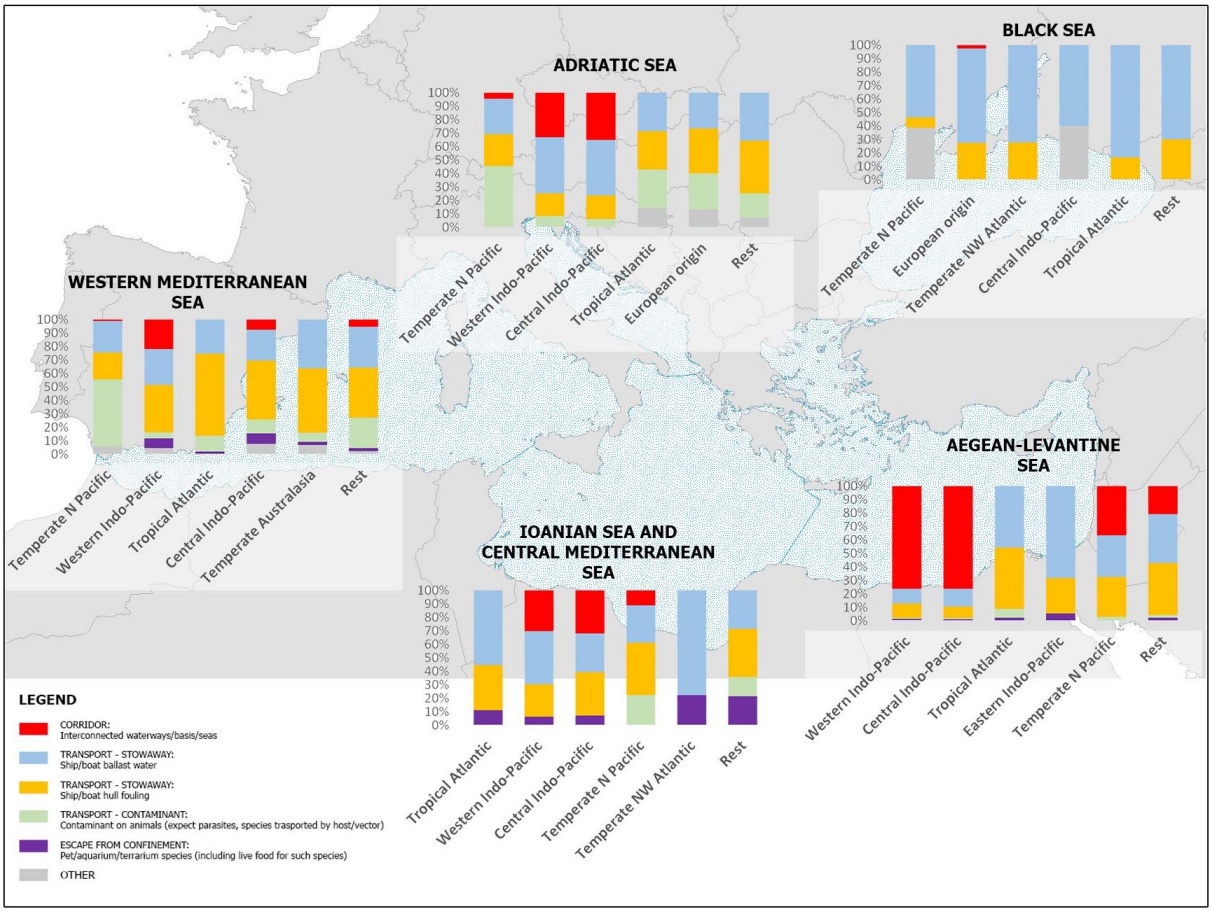

Figure 4. Proportion (%) of each primary pathway contribution to established NIS primary introductions in Europe, depicted per European marine subregion of the Mediterranean and Black Sea, associated with each major native distribution of the related NIS. The relative contribution of each pathway has been calculated based on the scoring system of the pathway certainty applied for each NIS (High = 3, Medium = 2, Low = 1).

to NIS related mainly with the Temperate Northern Pacific realm (linked mostly to aquaculture-contamination), Western Indo-Pacific and Tropical Atlantic (both mainly shipping-fouling).

Focusing on the NE Atlantic Ocean (Figure 5), NIS which were introduced first in the Bay of Biscay and the Iberian Coast have their native distribution mainly in the Temperate Northern Pacific (linked mainly to shipping and aquaculture-contamination), Temperate Australasia (mainly shipping-ballast and shipping-fouling) and other European Seas (mostly shipping-ballast). Primary introductions occurred in the Celtic Seas are associated with NIS having native distribution mainly in the Temperate Northern Pacific (linked mostly to aquaculture-contamination) and Temperate Northwest Atlantic (mostly shipping-ballast). Similarly, Greater North Sea primarily introduced NIS have their native distribution mostly in the Temperate Northern Pacific (linked mainly to shipping and aquaculture-contamination) and Temperate Northwest Atlantic (mainly shipping).

Most of the Europe's NIS which were primarily introduced first in the Baltic Sea are related with NIS with European origin (linked mostly to Corridor: interconnected waterways/basins/seas) and with NIS with native distribution in the Temperate Northern Pacific (linked mostly to the "Other" primary pathways group). European NIS first reported from the Black Sea are associated mainly to the Temperate Northern Pacific, other European Seas and Temperate Northwest Atlantic, linked in all cases mostly to shipping-ballast (Figure 4). The 3 taxa primarily found in the South and West Iceland have their native distribution in other European Seas and in the Temperate Northwest Atlantic, in all cases linked with shipping-ballast (not depicted in Figure 5).

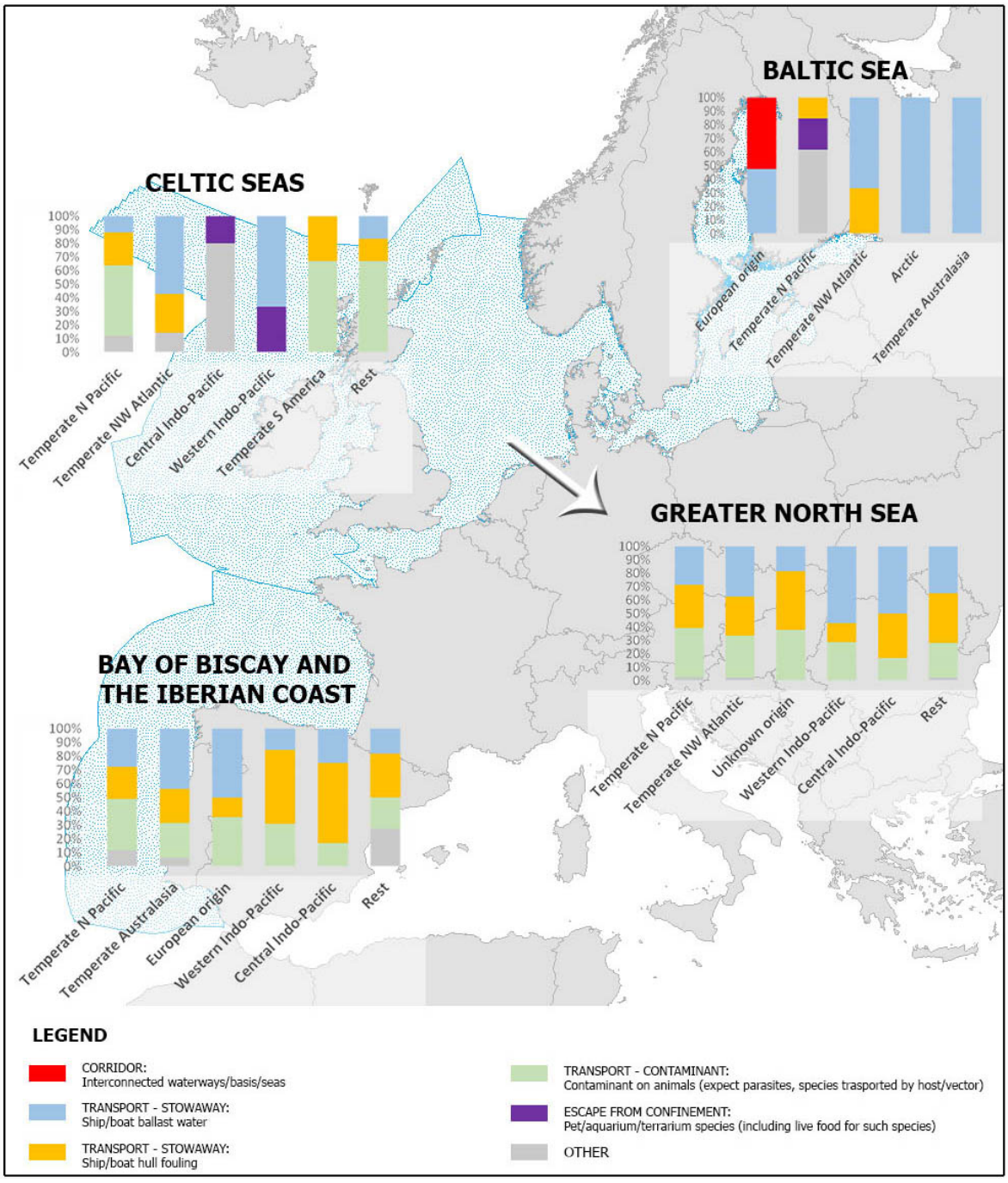

Figure 5. Proportion (%) of each primary pathway contribution to established NIS primary introductions in Europe, depicted per European marine subregion of the NE Atlantic Ocean and Baltic Sea, associated with each major native distribution of the related NIS. The relative contribution of each pathway has been calculated based on the scoring system of the pathway certainty applied for each NIS (High = 3, Medium = 2, Low = 1). For clarity, the related data for the South and West Iceland and Northern Norway and Finnmark are not shown.

Finally, the only NIS first reported from the Northern Norway and Finnmark has its native distribution in the Arctic and was possibly introduced through aquaculture-contamination (not depicted in Figure 5).

Up to 2005, temporal analysis revealed an overall increasing trend of new NIS introductions with native distribution in the Western and Central Indo-Pacific, Tropical Atlantic, Temperate Northwest Atlantic

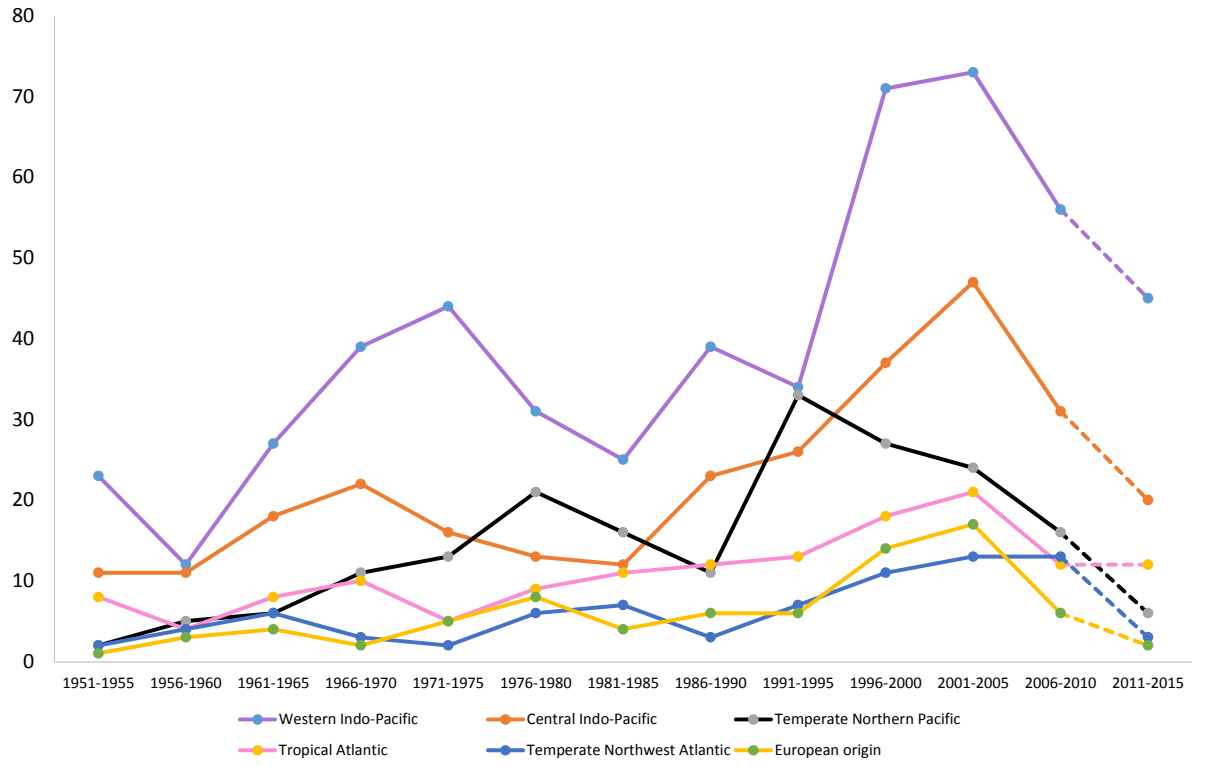

Figure 6. Temporal trends of new marine NIS introductions in Europe per 5-year intervals, whose native distribution corresponds to at least one of the six most important realms of European NIS' native distribution ranges. Casual NIS have also been taken into consideration. Due to the lag time between observation date of a new NIS and its subsequent reporting the last interval is depicted with dotted line.

and in other European Seas (Figure 6). After 2005, all of them present a decreasing trend, with the exception of NIS with native distribution falling in the Temperate Northwest Atlantic (stable up to 2010). NIS with native distribution in the Temperate Northern Pacific have a distinct trend, showing a general decrease of new species introductions already after 1995. Finally, NIS with native distribution falling in all main realms present a sharp decrease in new entries into Europe after 2010, with the exception of NIS with native distribution in the Tropical Atlantic (remained stable).

Discussion

In our study we have used the most recently updated pan-European inventory of NIS. Their number in Europe, including casuals, questionable and cryptogenic species, is currently 1,411, higher in comparison with the 1,369 taxa listed in the European inventory of 2013 (Katsanevakis et al. 2013b). Since then, several species have changed their status (e.g. from alien to cryptogenic and vice-versa or from casual to established). The latter is related to a substantial increase in the number of established NIS (824 taxa) compared to 2013 (738 taxa – Katsanevakis et al. 2013b).

Europe is severely affected by marine NIS, since it is hosting the highest number of them worldwide (Katsanevakis et al. 2014). The vast majority of the European NIS have their native distribution in the Western and Central Indo-Pacific, being mostly associated with introductions of molluscs and fish taxa through the Suez Canal. In addition, a significant proportion of marine NIS has its native distribution in the Temperate Northern Pacific, corresponding mainly to macroalgae taxa introduced into Europe mostly through aquaculture-contamination. Other major groups of Europe's marine NIS have their native distribution in the Tropical Atlantic, the Northwestern Atlantic, but also within the European Seas, with shipping (both ballast and fouling) being the pathway most responsible for their introductions into/within Europe. On the other hand, very few NIS are associated to the Arctic and Southern Ocean, possibly due to climatic differences and the limited pathways presence in these marine realms.

It should be noted, however, that the above overall remarks on the Europe's NIS' native distribution are heavily influenced by the overwhelming number of Mediterranean NIS. Indeed, the Mediterranean Sea presents the highest number of marine NIS globally, linked not only to the presence of the Suez Canal and heavy shipping traffic, but also to the long history of marine monitoring (Galil et al. 2014; Zenetos et al. 2017). As a result, 76% of all Europe's NIS primary introductions were reported first from the Mediterranean Sea, with 54% first reported in the Aegean-Levantine Sea. On the other hand, far less primary introduction events took place in the Baltic Sea, where most species have been introduced through secondary human-mediated introductions and natural dispersal from infested neighboring European Seas (e.g. many NIS were introduced from infested areas of the NE Atlantic Ocean into the Baltic Sea – Ojaveer et al. 2016).

As expected, the patterns concerning the European marine NIS' native distribution differ among the European marine subregions, following the history and traits of the dominating primary pathways of introduction in each subregion. As a result, each European marine subregion exhibits its own particular features of native distributions of the primarily introduced NIS and combined pathways. For instance, most NIS introduced primarily in the Aegean-Levantine Sea have their native distribution in the Western and Central Indo-Pacific and linked with introductions through the Suez Canal (see also Zenetos et al. 2010, 2012; Galil et al. 2016), while NIS reported first from the Western Mediterranean Sea have their native distribution mainly in the Temperate Northern Pacific and linked to aquaculture-contamination, in most cases oyster farming (Verlaque et al. 2015). When it comes to the rest European Seas, the related patterns observed are similar to those of country-level studies in the NE Atlantic Ocean (Wolff 2005; Gollasch and Nehring 2006; Kerckhof et al. 2007; Minchin et al. 2013), the Black Sea (Zaitsev et al. 2002; Alexandrov et al. 2007), and the Baltic Sea (Leppäkoski et al. 2002; Gollasch and Nehring 2006).

The general decrease of new NIS primary introductions observed at European scale is in accordance with Galil et al. (2016), Zenetos (2017) and Zenetos et al. (2017), who noted an overall negative trend in species introductions into the Mediterranean Sea after 2010. However, this sharp decrease could be attributed to the time lag between observation date of a NIS and its subsequent reporting (see also Azzurro et al. 2016). Therefore, the observed general decrease in NIS introductions during the last years should be considered with caution. Nevertheless, there is a strong evidence that NIS with native distribution in the Temperate Northern Pacific are gradually slowing down, since there is a clear decreasing trend of their introductions since the early 1990's. This decrease should be attributed to the fewer introductions of NIS associated with aquaculture-contamination (see also Katsanevakis et al. 2013a) – mainly macroalgae introductions coming from Japan – presumably due to compulsory measures implemented at a national or European level (EU 2007; Savini et al. 2010).

It should be highlighted that our results are based exclusively on the primary introduction events of NIS in Europe, analyzed per each European marine subregion. NIS entries in each subregion resulted from secondary introductions from already infested neighboring subregions were not considered (e.g. Lessepsian NIS dispersing naturally from the Aegean-Levantine Sea towards the rest of the Mediterranean Sea or NIS entering the Baltic Sea from already infested areas of the Greater North Sea). Ideally, these secondary introductions should be taken into account when focusing on a specific subregional level, although there is a concern how these NIS introductions can be managed when they are spreading through natural dispersal across Europe. The monitoring bias is another issue which should not be neglected, especially when it comes to the reported locations and dates of first arrivals of marine NIS in Europe. Inevitably, more NIS primary introductions have been reported for well-known taxonomic groups (e.g. molluscs, fish, macroalgae) in areas that have a long history of marine monitoring (e.g. Greater North Sea vs North Africa coasts). Lastly, another limitation is the certainty level of the pathways of most European NIS, since for the majority of introductions the pathway certainty is not sufficient enough, with the exception of the Lessepsian immigrants. Consequently, more focused studies are needed when addressing the pathways of marine NIS.

Still, besides the above limitations, our study indicates what kind of primarily introduced NIS in Europe in terms of their native distribution are more common per European marine subregion. In addition, it indicates the relative importance of certain primary pathways in specific European subregions, combined with the related NIS' native distribution. The information concerning the pathways could be useful for NIS tailored management per marine subregion according to the MSFD, showing where priority should be given for tackling primary introductions. For instance, managing shipping introductions in the NE Atlantic Ocean coasts is crucial for tackling new primary NIS entries in that region. To this end, the

recent adoption by the International Maritime Organization (IMO) of the "International Convention for the Control and Management of Ships' Ballast Water and Sediments" (BWM Convention) and its imminent enforcement is encouraging. We would also encourage the endorsement of the guidance developed in the context of the Marine Environmental Protection Committee (MEPC 2011) regarding the shipping-fouling, a pathway that has an important role also on secondary introductions (Mineur et al. 2008; Murray et al. 2011; Foster et al. 2016). As a conclusion, in order to tackle NIS introductions in Europe, prevention efforts should be prioritized on a subregion level towards primarily introduced NIS with specific native distribution ranges and associated pathways.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Marine NIS in the European Seas and their traits (establishment success, region and year of first introduction in Europe, native distribution range, taxonomy, and primary pathways).

Appendix 2. Number of established marine NIS in European Seas of each main taxonomic group with native distribution range in each marine biogeographic realm based on Spalding et al. (2007) scheme, slightly modified for the current study.

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