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Non-indigenous aquatic fauna in transitional waters from the Spanish Mediterranean coast: A comprehensive assessment

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ABSTRACT

Understanding drivers of spatial variation in non-indigenous species (NIS) is a key goal in invasion biology, but comprehensive assessments providing high-resolution data are extremely scarce. Anthropogenic modifications to transitional waters facilitate the invasion of NIS where they cause both ecological and economic important damage. By screening validated data sources, we conducted a comprehensive assessment of non-indigenous aquatic fauna in Spanish Mediterranean transitional waters (30 sites), as well as assessed introduction pathways, native regions, NIS assemblage patterns and temporal introduction rate. One hundred and twenty-nine NIS were inventoried, with 72 % established and more than half listed before 1980. Two intentional (release, escape) and two unintentional (contaminant, stowaway) introduction pathways were dominant. Recorded NIS originated mostly from North America and Asia. A clear nested pattern in NIS assemblages was observed across sites, suggesting secondary spread from the most invaded waters placed in the northern regions. Our updated inventory should be pivotal for designing prevention protocols and informing specific management plans on non-indigenous fauna in transitional waters.

1. Introduction

Biological invasions are identified as a main driver of the ongoing global biodiversity crisis as well as considered a major threat to human livelihoods, with increasing ecological, social and economic impacts (Blackburn et al., 2011; Early et al., 2016; Simberloff et al., 2013). Owing to the rising globalization, non-indigenous species (hereafter, NIS) can more frequently reach regions outside their native distribution range through intentional or accidental human-aided transportation, thus enabling the establishment of self-sustaining populations and their spread to other natural habitats (Cuthbert et al., 2021). When established, NIS may become harmful for the recipient environment by competing with and predating on native biota, transmitting diseases, disrupting ecological process and even strongly damaging human activities (Blackburn et al., 2014; Pyšek et al., 2020), thus being named invasive NIS. Recently, an increasing body of literature has quantified the impacts of invasive NIS from both ecological and economic perspective, with highly adverse effects being found on both spheres (Flood et al., 2020; Kourantidou et al., 2021). For instance, invasive NIS are involved in the extinction of 33 % of recently extirpated animal taxa around the world, and this threat is now listed as the second most frequent extinction driver (Blackburn et al., 2019). Invasive NIS also impact several human activities from different socioeconomic sectors, such as agriculture, fisheries and tourism, leading to large economic losses. In marine environments, invasive NIS are known to negatively affect food provision, tourism and recreation, though they may also have positive impacts on some ecosystem services such as water purification or climate regulation (Katsanevakis et al., 2014b; Tsirintanis et al., 2022). In this context, costs of invasive NIS management have grown by two orders of magnitude since 1960 and they have totaled over US $95.3 billion worldwide, whereas global damage costs of biological invasions have been recently estimated to reach US $1130 billion (Cuthbert et al., 2022).

Biological invasions are among the main threats affecting inland, marine and transitional aquatic ecosystems (Gallardo et al., 2016), with well-reported impacts not only on natural resources but also on

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economic and social aspects (Martínez-Vázquez et al., 2021; Preisler et al., 2009). Updating data on occurrence, temporal trend and spatial distribution of NIS is a prerequisite for delivering timely reliable information to environmental managers (Lucy et al., 2016; Zenetos et al., 2017). For instance, comprehensive data on NIS spread are increasingly required to assess the ecological status of transitional waters within aquatic ecosystem conservation schedules, such as the European Water Framework Directive (WFD) or the European Marine Strategy Framework Directive (MSFD) (Cabral et al., 2020; Chainho et al., 2015; Zenetos et al., 2022c). In this context, updating inventories on NIS through a given region and providing detailed information on their introduction pathways and their new distribution ranges as well as the temporal introduction trend (e.g., Anastácio et al., 2019; Muñoz-Mas and García-Berthou, 2020; Reise et al., 2006) can be pivotal for a knowledge-based policy and an effective implementation of early warning and rapid response (EWRR) protocols (EEA, 2010). Furthermore, the design of NIS prevention protocols requires an accurate identification of major gateways (i.e., main recipient sites) acting as initial introduction places within a given region, from which NIS can progressively disperse to other still non-invaded nearby areas (Ojaveer et al., 2018). Then, increased survey efforts to detect new introductions should be particularly focused on these gateways for an effective optimization of human and logistic resources when EWRR measures are implemented (Nunes et al., 2015). For that purpose, assessing the NIS assemblage structure across different sites within a region may provide essential information about gateways, as well as to test whether NIS assemblages from invader-poorer sites are subsets (nested pattern) of those assemblages from invader-richer sites (Traveset et al., 2014). However, this question remains not sufficiently explored in the literature on biological invasions and only a few studies have applied nestedness analysis to uncover distribution patterns of non-indigenous plant species across different sites (Thuiller et al., 2012; Traveset et al., 2014).

The Mediterranean Sea is a well-recognized hotspot of marine and estuarine NIS (Ferrario et al., 2018; Zenetos et al., 2018), and their marine ecoregions are considered among the most globally impacted ones by biological invasions (Bailey et al., 2020; Costello et al., 2010). The opening of the Suez Canal, an intense commercial shipping activity and widespread aquaculture practices have been highlighted as major drivers of this remarkably high number of NIS (Katsanevakis et al., 2014a), with over 1000 marine NIS reported to be introduced in the Mediterranean Sea and -at least- half of them being already completely established (Zenetos et al., 2022a, 2022b). Transitional waters (including brackish and estuarine waters) are particularly vulnerable to biological invasions as they are permanently exposed to several introduction vectors (Chainho et al., 2015; Cuesta et al., 2016; Orlando-Bonaca et al., 2021), but also because human-mediated disturbances increase the invasibility of these environments (González-Ortegón and Moreno-Andrés, 2021). In this context, NIS richness generally increases from open marine waters towards the shoreline and attains highest values in transitional waters (Nehring, 2006; Reise et al., 2006). As defined by the WFD, transitional waters are surface waterbodies in the vicinity of river mouths which are partly saline as a result of their proximity to coastal waters but they are substantially influenced by freshwater flows (European Commission, 2000). Due to their geographical location and mixohaline conditions, these transitional environments can be colonized by purely estuarine NIS, but also by both marine and freshwater NIS (Nehring, 2006). Then, adjacent river basins may exert a strong influence on NIS community composition at recipient transitional waters by facilitating the arrival of typically freshwater NIS, which can establish self-sustaining populations in river mouths and transitional environments. Within the Mediterranean basin, Iberian inland waters present a notably high richness of aquatic NIS as compared to other European regions (Hussner, 2012), and NIS account for about 40 % of the total Iberian richness for some biotic groups, such as freshwater fish (Clavero and García-Berthou, 2006; Collares-Pereira, 2021; Doadrio et al., 2011). This scenario of widespread and continuous exposure to NIS introductions, both from adjacent inland and marine ecosystems, poses serious risk to Spanish Mediterranean transitional waters and jeopardizes several ecosystem services provided to local people (e.g., mariculture production, fisheries, and recreational uses). Hence, updated and comprehensive NIS assessments are required to inform management strategies and to support legislative instruments aimed to mitigate impacts from biological invasions in transitional environments (Ojaveer et al., 2018). However, information on NIS occurrence, distribution and key introduction-related attributes (e.g., native origin and introduction pathways) in transitional waters from the Spanish Mediterranean coast appears notably scattered across several repositories and published literature, which is also applicable to other Mediterranean regions (e.g., Katsanevakis et al., 2014a, 2014b; Zenetos et al., 2017). In turn, to our knowledge, studies providing a comprehensive inventory of aquatic NIS across Spanish Mediterranean transitional waters are lacking so far, and the scarce available literature deals exclusively with some particular taxa (e.g., Clavero et al., 2022; Clavero et al., 2021; Gisbert and López, 2007; López and Richter, 2017) or focuses mostly on inland waters as target habitats while accounting for transitional waters in a secondary way (Muñoz-Mas and García-Berthou, 2020). In this context, previous research highlighted that biological invasions are not a sufficiently high priority for many scientists and managers dedicated to transitional and coastal environments (Williams and Grosholz, 2008). Therefore, this scenario of scattered information and insufficient research/management interest on NIS precludes an effective implementation of specific regulatory initiatives to properly deal with biological invasions in transitional waters.

Here, we conducted an extensive literature survey to compile available records on non-indigenous aquatic fauna distributed across transitional waters from the Spanish Mediterranean coast. Our specific objectives were: (1) to provide a comprehensive and updated inventory of the non-indigenous aquatic fauna recorded across transitional waters from the Spanish Mediterranean coast; (2) to assess main introduction pathways, temporal introduction trends and association patterns among key introduction-related attributes; and (3) to test whether the distribution of NIS across Mediterranean Spanish transitional waters shows a nested assemblage pattern. Outcomes from this comprehensive assessment could provide knowledge-based guidelines to implement effective management strategies at multiple spatial scales across Mediterranean transitional waters.

2. Material and methods

2.1. Study area

The Spanish Mediterranean coast extends over 3422 km -including Balearic Islands- and comprises one of the longest national coastal sectors across the Western Mediterranean region (Pauly et al., 2020). Several transitional waters occur along this sector and they are mostly associated to large coastal wetlands and lagoons (e.g., the Mar Menor coastal lagoon and Albufera de Valencia), but also to river mouths of some main Spanish Mediterranean rivers (e.g., Ebro and Segura), thus showing a wide array of geographic attributes (e.g., surface area), environmental conditions (e.g., salinity and flow regimes) and anthropogenic pressures (e.g., extractive, touristic and commercial activities). The main 30 transitional waters from the Spanish Mediterranean coast were selected here as study sites, which were further classified into five coastal regions: Catalan, Valencian, Balearic, Levantine and Alboran (Fig. 1). The Levantine coastal region corresponds to the Mediterranean Spanish coastline comprised between the provinces of Almería and Valencia, so this sector should not be confused with Levantine sea from the eastern Mediterranean. Most of these transitional environments extend over a surface area smaller than 50 km^2, whereas two of them were comparatively much larger (50–200 km^2; i.e., the Mar Menor coastal lagoon and Albufera de Valencia), and the Ebro Delta being the single one covering >200 km^2 (Supplementary material – Table S1).

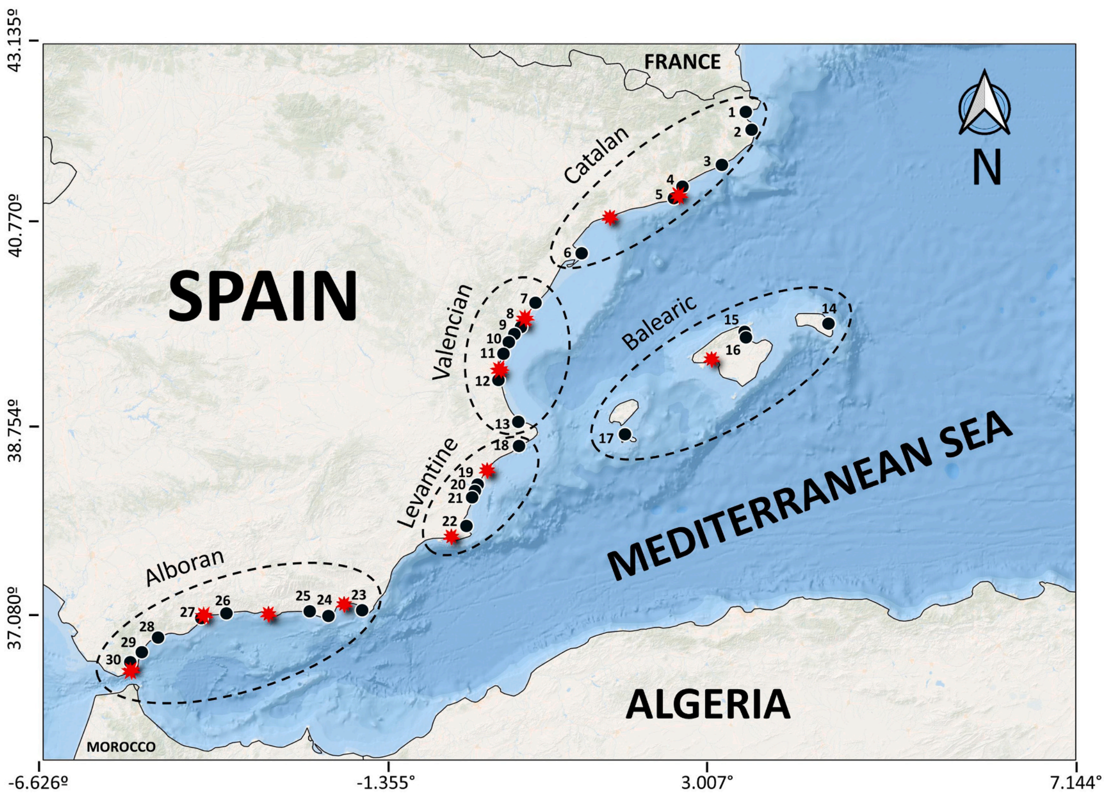

Fig. 1. Distribution of the 30 assessed transitional waters (black dots) and main commercial ports (red stars) along the Spanish Mediterranean coast. Dash-lined ellipses define the main five coastal regions established across the study area. Numerical codes are provided to refer each study site (see Supplementary material – Table S1). Geographic coordinates are indicated in decimal degrees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

These target sites were all influenced by freshwater flows (i.e., inland waters), so coastal environments exclusively influenced by marine waters (e.g., ports, marinas and coast shoreline) were excluded. The study sites presented a wide variability in terms of NIS introduction pressure. For instance, some transitional sites appeared very close to the most important Spanish commercial ports (Fig. 1; e.g., Barcelona, Valencia and Bahía de Algeciras), whereas the Balearic region supported the highest shipping-mediated touristic activity and many other sites were close to small commercial ports or marinas (IGN, 2019).

2.2. NIS database

Our assessment involved all aquatic animal NIS occurring in transitional waters from the study area. We considered non-indigenous aquatic fauna as all those animal species (both free-living and symbiont taxa) associated to aquatic ecosystems (both freshwater, estuarine and marine environments) during -at least- one part of their life cycle. A comprehensive literature review on NIS records was conducted by screening the following data sources: (1) scientific databases for peer-reviewed international publications (e.g., Web of Science and Google Scholar); (2) regional non-indexed journals for grey literature providing NIS records (e.g., bulletins, regular checklists and technical reports); and (3) online databases and institutional repositories for accepted NIS records as well as additional information on key species-specific attributes. For the literature search, we made a query for peer-reviewed publications in the Web of Science by including topics related to our interest either in the title, abstract or keywords. Boolean search terms included all words related with NIS or potential synonyms (i.e., non-native, non-indigenous, exotic, alien, allochthonous, introduced, invasive), as well as the name of the 30 transitional sites (e.g., Ebro Delta or Mar Menor) and the whole study area (Mediterranean). Resulting publications were exported and manually screened to select only those related to non-native aquatic fauna inhabiting any of the studied transitional waters. This process yielded a set of publications (Supplementary material – Appendix I) which were used to generate a list of animal NIS recorded in the study area. In addition, online databases included the European Alien Species Information Network (EASIN; http://easin.jrc.ec.europa.eu), the CABI's Invasive Species Compendium (CABI-ISC; http://www.cabi.org/isc/), the Global Invasive Species Database (GISD; www.iucngisd.org), the EXOCAT database (http://exocatdb.creaf.cat/base_dades/#), the AquaNIS database (http://www.corpi.ku.lt/databases/aquanis/) and the Global Biodiversity Information Facility database (GBIF; http://www.gbif.org/). Following Zenetos et al. (2017), all NIS names retrieved from the literature search were checked for validation and standardization with the World Register of Marine Species (WoRMS Editorial Board, 2016), FishBase (Froese and Pauly, 2018) and MolluscaBase (MolluscaBase, 2020). Doubtful records from online databases were thoroughly reviewed and validated upon taxa-specific expert consultation. The recorded NIS-specific attributes comprised relevant variables related to the introduction event (native origin, introduction pathway, year of detection/introduction, establishment status and distribution across the studied sites), trophic group and taxonomic group. The native origin of each recorded NIS was divided into the following ten geographic realms: Africa, Antarctica, Asia, Atlantic Ocean, Europe, Indo-Pacific, North America, Oceania, Pacific Ocean and South America. To facilitate comparative studies on introduction pathways, Hulme et al. (2008) proposed a pathway classification which was further developed and consequently adopted by the Convention of Biological Diversity (hereafter, CBD) (Turbelin et al., 2022). Following such standard classification (CBD, 2014), we established seven major introduction pathways: Release, Escape, Contaminant, Stowaway, Corridor, Unaided, and Unknown. Both attributes on native origin and introduction pathway are not encompassed by exclusive classes, so a given taxon may belong to two or more biogeographic realms (e.g., North and South America) as well as to show several introduction pathways (e.g., Release and Escape). The year of introduction of each recorded NIS in the study area was mostly retrieved from international peer-reviewed and grey literature providing first records on NIS occurrence, which generally included an accurate date of detection. When the detection date was unreported for a given NIS, then the year of the corresponding publication was considered as the year of introduction, following previous related studies (Cobo et al., 2010; Muñoz-Mas and García-Berthou, 2020). The year of introduction at European scale was retrieved from EASIN. On the other hand, the establishment status of each inventoried NIS was assigned based on the reported existence of self-sustaining populations within the study area. Hence, NIS clearly introduced in Spanish Mediterranean transitional waters and with known self-sustaining populations were classified as *established*, whereas NIS only reported to occur or occasionally breed within the study area but do not have self-sustaining populations were classified as *uncertain*. Following the precautionary principle applied by previous studies (Muñoz-Mas and García-Berthou, 2020; Nunes et al., 2014; Tsirintanis et al., 2022), we also considered all those taxa with uncertain biogeographic history in the study area by including them in the class *cryptogenic* (i.e., the native or non-indigenous condition in the study area still remains unclear or under debate). Though some cryptogenic taxa could be reclassified by further research as native species in the study area, other cryptogenic taxa inhabiting the study area are known to cause major economic impacts (e.g., Hoppe, 2002; Tsirintanis et al., 2022) or could become invasive in the near future, thus supporting our conservative approach.

2.3. Data analyses

Firstly, we used a descriptive approach to characterize overall patterns of NIS temporal introduction trend, establishment status per different NIS-specific attributes (taxonomic group, biogeographic realm of native origin and invaded coastal region), introduction pathway and trophic group. Compiled data on year of introduction were used to ascertain the NIS arrival rate in the study area. The descriptive approach involved the use of an alluvial diagram to highlight relationships among native origin, main taxonomic groups and introduction pathways. Alluvial plots are flow diagrams typically used to visually display associations across different dimensions or sets of variables (e.g., regions or life-history attributes), and they have been recently applied in invasion science (Koutsikos et al., 2021; Muñoz-Mas and García-Berthou, 2020). For those NIS with more than one origin biogeographic realm or introduction pathway, we kept all the assigned classes by downweighting these taxa in frequency-related analyses (see Muñoz-Mas and García-Berthou, 2020), thus avoiding an overrepresentation of these classes. We performed the alluvial diagram using the package *ggalluvial* (Brunson and Read, 2023) implemented in the R software environment (R Development Core Team, 2016).

Secondly, we used the metric *Nestedness measure based on Overlap and Decreasing Fills* (NODF, Almeida-Neto et al., 2008) to explore nestedness patterns in NIS assemblages across the selected sites. The NODF metric quantifies independently whether poorer assemblages comprise subsets of progressively richer assemblages (Ulrich et al., 2009), thus allowing identifying which sites may be under higher introduction pressure (e.g., secondary spread from nearby NIS gateways, such as ports or aquaculture facilities). Moreover, this analytical approach allows assessing whether rare or uncommon species occur in sites where the most common taxa are also found. Following Zamora-Marín et al. (2021), we generated a NIS presence/absence matrix across the studied sites, and then compared its NODF value with that resulted from 500 null matrices using the “Proportional column and row totals” algorithm within the online tool NeD (https://ecosoft.alwaysdata.net/; Strona et al., 2014). Moreover, this online tool was also used to retrieve a matrix packaged according to maximum nestedness, thus allowing a visual interpretation of assemblage patterns across the study sites.

3. Results

3.1. NIS richness and distribution in transitional waters

We compiled records for a total of 129 animal NIS inhabiting transitional waters from the Spanish Mediterranean coast (Supplementary material – Appendix I). From this pool of NIS, 93 taxa (72 %) were clearly established in the study area maintaining self-sustaining populations in -at least- one of the assessed sites, whereas 30 and 6 taxa were classified as uncertain and cryptogenic, respectively. Recorded NIS represented most of the animal taxonomic groups (i.e., phyla) potentially inhabiting transitional waters. Chordata was the richest taxonomic group (53 NIS), followed by Mollusca (34) and Arthropoda (26), whereas the remaining phyla had a markedly lower NIS richness (< 5 NIS) (Fig. 2). At lower taxonomic resolution, the class Actinopterygii (i.e., fish) was the dominant group with 28 recorded NIS, followed by Gastropoda (19 NIS), Bivalvia (15 NIS) and Ostracoda (12). Aves (8), Malacostraca (8) and Reptilia (7) showed a lower richness, whereas all the remaining animal classes ($n = 15$) were represented by less than five NIS (Supplementary material – Fig. S1). Among the inventoried NIS within each phylum, the ratio established/uncertain varied notably from some groups whereby all the recorded species were established, such as Cnidaria, Ctenophora and Platyhelminthes, to other phyla for which uncertain species were dominant, such as Annelida (Fig. 2). The dominant phyla (Chordata, Arthropoda and Mollusca), which accounted together for about 88 % of the overall NIS richness, presented all a high proportion of established NIS (66 %, 69 % and 91 %, respectively). A similar pattern was observed at class level, with established NIS being clearly dominant in most cases, while a higher proportion of uncertain NIS was only recorded for Aves, Reptilia, Polychaeta and Malacostraca (Supplementary material – Fig. S1).

At species level, the Asian tiger mosquito (*Aedes albopictus*) was the most widespread NIS among the inventoried taxa (Fig. 3), being recorded in all the evaluated sites. Other five NIS (*Gambusia holbrooki, Procambarus clarkii, Callinectes sapidus, Cyprinus carpio* and *Trachemys scripta*) were recorded in most (>20) of the sites, whereas the vast majority of recorded taxa were reported for less than half of the assessed waters. Interestingly, about half of the inventoried NIS was exclusively recorded at a single study site (Fig. 3).

From a geographic perspective, meaningful differences in NIS richness were found among the five established coastal regions (Fig. 4). The Catalan region (101 NIS) was clearly the richest one because it hosted more than twice as NIS as the second dominant region (Valencian, 47 NIS). Overall NIS richness per region slightly decreased southwards, with the Levantine and Alboran regions harboring 35 and 16 NIS, respectively, whereas the Balearic region hosted 22 taxa. NIS richness varied largely (range 84–2 taxa) among the 30 assessed sites (Supplementary material – Table S1), with the highest NIS richness being recorded in the Ebro Delta Natural Park (84 NIS). In turn, richness values from this NIS hotspot were almost twice as those from the second richest site (Albufera de Valencia Natural Park, 44 NIS). A pool of 14 sites hosted intermediate values of NIS richness (35–10 species), the vast majority of them belonging to the Catalan, Valencian and Levantine regions. NIS poorer sites (i.e., < 5 species) were all placed in the Alboran and Balearic regions.

3.2. Introduction pathways, temporal trend and NIS-specific attributes

Compiled NIS records were associated to all the established introduction pathway classes. Two groups of introduction pathways were clearly distinctive in terms of their contribution to the NIS arrival to transitional waters from the Spanish Mediterranean coast (Fig. 5). Stowaway (78 NIS), Escape (75), Contaminant (68) and Release (61)

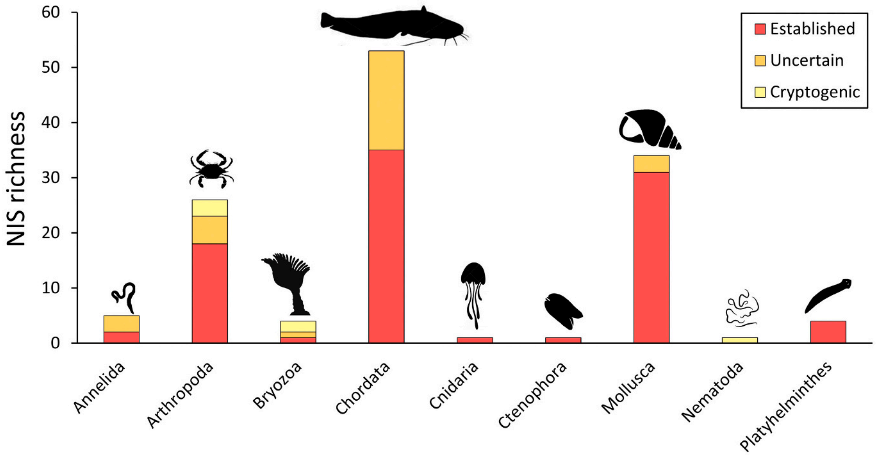

Fig. 2. Number of non-indigenous animal species (NIS) per phylum recorded in the 30 transitional waters assessed along the Spanish Mediterranean coast. Color indicates the proportion of NIS which maintain self-sustaining populations (established), do not maintain self-sustaining populations but have been already recorded in the study area and are clearly non-indigenous (uncertain) or their biogeographic origin remains unclear (cryptogenic).

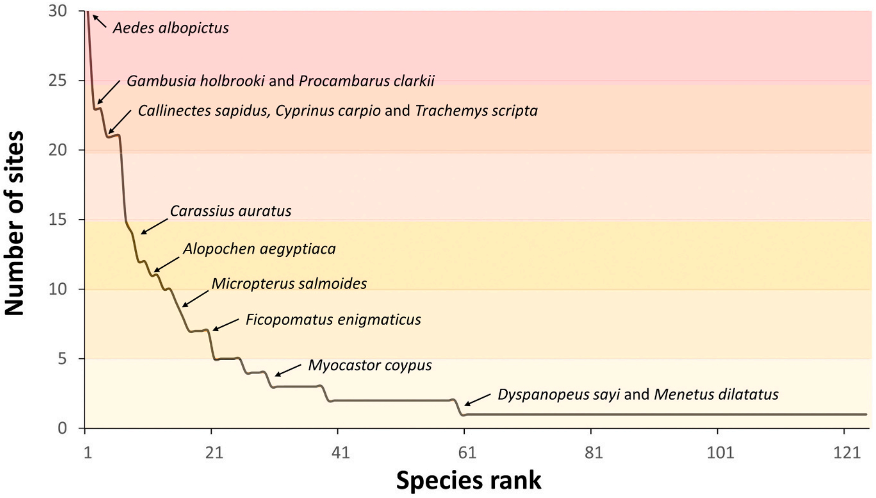

Fig. 3. Rank frequency curve for the non-indigenous animal species (NIS) recorded at the 30 transitional waters assessed along the Spanish Mediterranean coast. NIS are ranked from highest to lowest extent of occurrence across the assessed sites (i.e., the most widespread species appear at the top, whereas the uncommon ones are ranked at the bottom). The position of some representative NIS is indicated with arrows along the curve. A yellow-red color gradient is included at the background as an indication to the dispersal ability of the inventoried NIS. Note that symbiont invertebrate NIS ($n = 5$) were excluded from site-specific analyses, so an overall richness of 124 NIS is represented. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

were the main introduction pathways in the study area, accounting together for about 84 % of the total compiled records. Most of the inventoried NIS (67 %) were associated to more than one introduction pathway, this pattern being equally homogenous across the recorded animal taxa. Within taxonomic groups, Escape and Release were the dominant introduction pathways for vertebrates (mostly for fish, birds and reptiles), whereas the seven established pathways contributed similarly to the arrival of non-indigenous molluscs (both Bivalvia and Gastropoda) and Malacostraca, being ostracods mostly introduced as Contaminant or Corridor (Supplementary material – Fig. S2). With the single exception of Corridor, the proportion of established NIS was notably higher as compared to that from uncertain species for all introduction pathways (Fig. 5).

The temporal introduction trend was assessed at two different spatial scales: Europe and Spanish Mediterranean coast (Fig. 6.). Information on introduction date was missing for about 5 % of the recorded NIS. The introduction rate of the inventoried NIS at European scale homogenously increased since the 1800s, though a slightly steeper growth was experienced from the middle of the last century. A similar pattern was also observed at the scale of the study area (Spanish Mediterranean coast), but the turning point from the 1950s was even more pronounced here. Temporal variation into the overall contribution of introduction pathways to NIS arrival showed that Release and Escape were the main introduction pathways in the earliest assessed period (1800–1940), being responsible for about 62 % of the total NIS introductions, whereas Stowaway and Contaminant explained respectively 17 % and 12 % of the NIS introductions (Fig. 7). Similar values per introduction pathway were observed in the second assessed period (1941–1980). However, some changes in the contribution of different introduction pathways were evident for the latest assessed period (1981–2022), whereby Stowaway (25 %) was the most important introduction pathway followed by Contaminant (21 %) (Fig. 7).

Native distribution range (i.e., native origin) for the recorded NIS corresponded to all the established biogeographic realms, with the exception of Antarctica (Supplementary material – Fig. S3). Asia and North America were the most common origin among the inventoried NIS, accounting together for about 51 % of the compiled records. Lower values were observed for Europe (15 %), Africa (10 %) and South America (8 %), whereas Oceania (7 %), Pacific (4 %) and Atlantic Ocean (4 %) were minority native origins. Most NIS (74 %) were native from a single biogeographic realm (a pattern particularly evident in Chordata). With regard to the functional group of the recorded NIS, filter-feeders (33 %), omnivores (28 %) and predators (22 %) were the dominant dietary groups (Supplementary material – Fig. S4).

The alluvial diagram showed some clear association among taxonomic groups, native origin and introduction pathways (Fig. 8). Non-

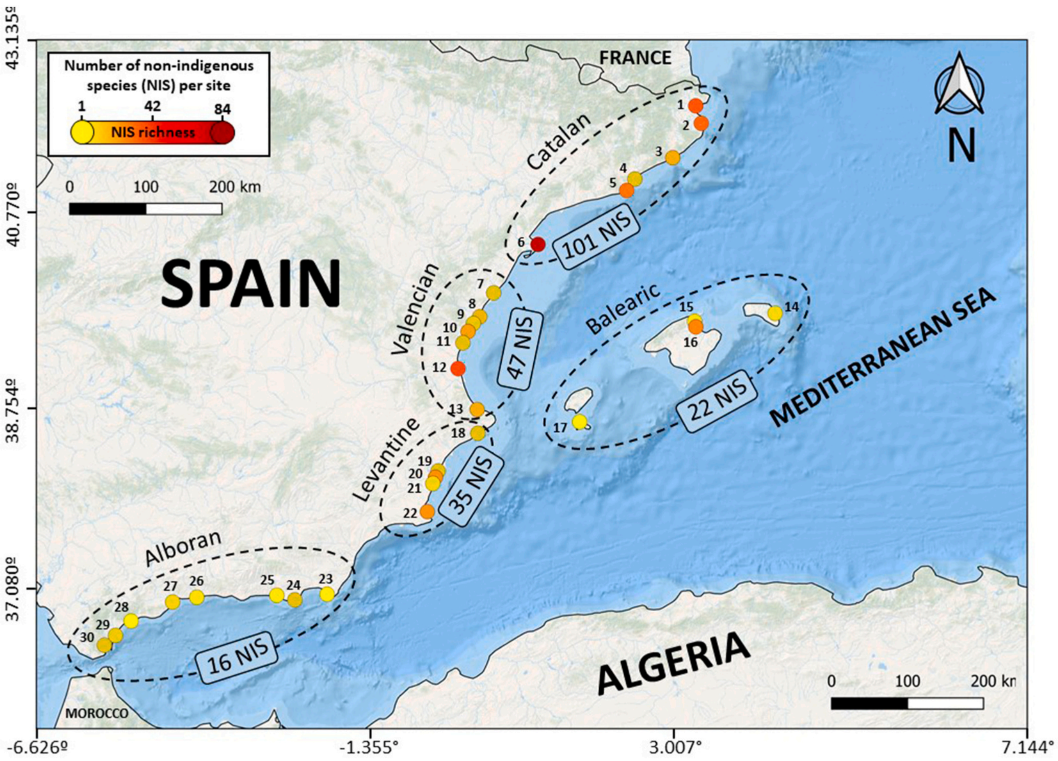

Fig. 4. Richness of non-indigenous animal species (NIS) recorded within transitional waters belonging to the five coastal regions established along the Spanish Mediterranean coast. Dash-lined ellipses define the main five regions established, and NIS regional richness values are indicated beside ellipses. NIS richness at each study site is represented by a yellow-red color gradient. Numerical codes are provided to refer each study site (names of sites are provided in Supplementary material – Table S1). Geographic coordinates are provided in decimal degrees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

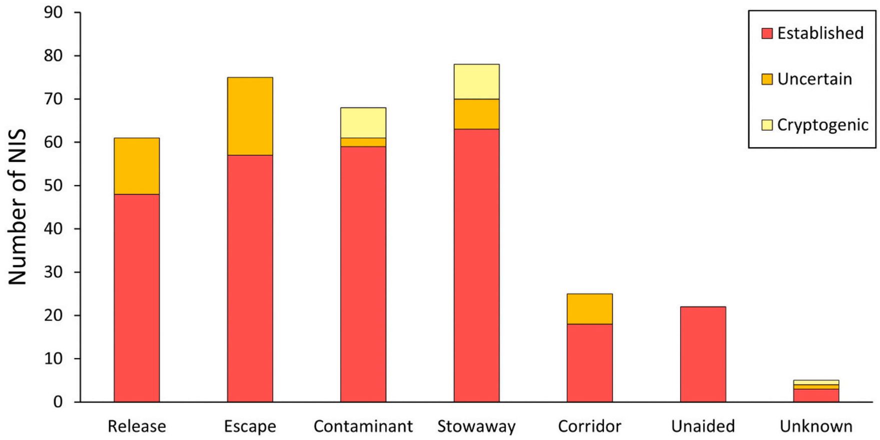

Fig. 5. Contribution of different introduction pathways to the arrival of non-indigenous animal species (NIS) to transitional waters from the Spanish Mediterranean coast. Note that most of the recorded NIS (67 %) were associated to two or more introduction pathways. Color indicates the proportion of species which maintain self-sustaining populations (established), do not maintain self-sustaining populations but have been already recorded in the study area and are clearly non-indigenous (uncertain) or their biogeographic origin remains unclear (cryptogenic).

indigenous Chordata were almost exclusively introduced through Escape and Release, and they mostly came from North America (36 %), Asia (25 %) and Europe (19 %). Major introduction pathways for Arthropoda were Stowaway (37 %) and Contaminant (35 %), and they arrived mostly from Asia (27 %) and North America (20 %). A similar pattern in introduction pathways and native origin was observed for Mollusca, with the remaining taxonomic groups being associated to diverse introduction pathways and realms of origin.

3.3. *NIS assemblage patterns*

An overall nested pattern was observed for NIS assemblages across the assessed sites (Fig. 9). The nestedness matrix highlighted that NIS poorer sites were inhabited by species already present in progressively richer transitional waters, then supporting a nested structure (i.e., subsets) in relation to the NIS distribution across the study area. Rarer NIS tended to occur exclusively in richest sites, which were also inhabited by most widespread NIS. For instance, 54 out of the 65 NIS occurring in a single site were recorded in any of the three NIS-richest sites (Ebro Delta, Albufera de Valencia and Aiguamolls de l'Empordá). The five NIS richest sites collected 90 % of the overall NIS richness. As revealed from the NODF analysis, NIS assemblages were significantly more nested than expected by chance ($p < 0.0001$; 500 null matrices). The relative contribution of species nestedness (NODF$_c$) to the overall nestedness was considerably higher than that of site nestedness (NODF$_r$) (Supplementary material – Table S2). Most transitional waters from the Catalan

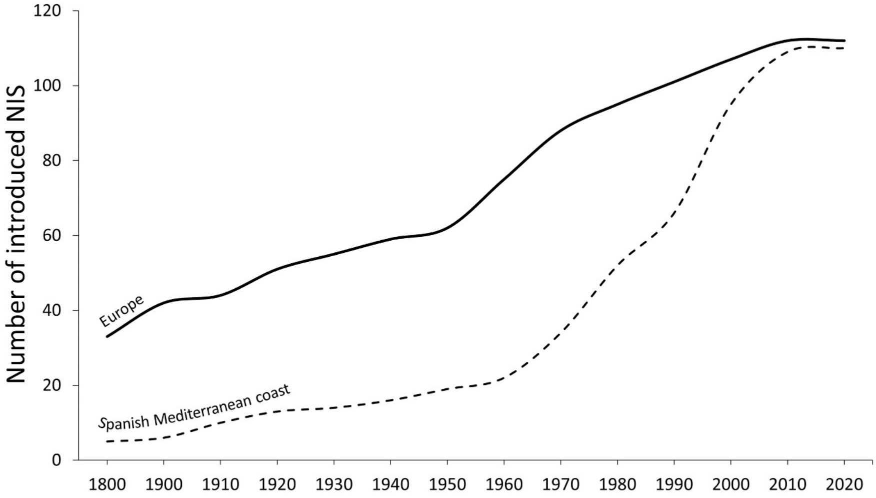

Fig. 6. Temporal introduction trend showing the cumulative number of non-indigenous animal species (NIS) introduced in transitional waters from the Spanish Mediterranean coast. Cumulative number of introduced NIS is shown at two different spatial scales: Europe and Spanish Mediterranean coast. Year of first introduction in Europe and Spanish Mediterranean coast was retrieved from EASIN and published literature, respectively.

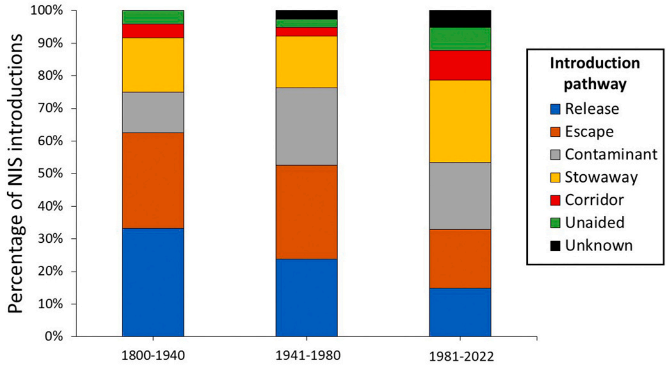

Fig. 7. Temporal variation into the contribution of introduction pathways to the arrival of non-indigenous animal species (NIS) to transitional waters from the Spanish Mediterranean coast. Three major time intervals were established according to the most relevant periods for industrial and commercial development in the study area.

region ranked at the top of the nestedness matrix, thus highlighting the relevance of this coastal region to the NIS arrival and introduction in the study area.

4. Discussion

4.1. NIS occurrence in Spanish Mediterranean transitional waters

The introduction and spread of NIS is a major driver of impairment in estuaries and transitional waters worldwide (Bailey et al., 2020; Preisler et al., 2009; Williams and Grosholz, 2008). Here, we reported the occurrence of 129 aquatic animal NIS inhabiting 30 transitional waters along the Spanish Mediterranean coast. Up to date, comprehensive inventories on NIS occurrence in transitional waters are lacking for Spain. At regional scale, a few studies have assessed NIS assemblages in transitional waters but focused on particular animal groups (e.g., Zorita et al., 2013). Extensive assessments providing NIS inventories at Iberian or national scale are extremely scarce and rarely target transitional environments (Cobo et al., 2010; ICES, 2018; Muñoz-Mas and García-Berthou, 2020; Oficialdegui et al., 2023). For instance, a recent global review conducted across marine and estuarine ecosystems reported a total of 90 aquatic animal NIS for the Iberian coast (Bailey et al., 2020), but no indication was provided on the proportion of NIS inhabiting separately transitional and purely marine environments. A similar issue was found in two scientific reports recently published by international panels of experts in aquatic NIS introductions, respectively, where the Iberian coastline was indicated to support 137 introduced NIS (Chainho et al., 2020) and Iberian waters (both transitional and inland) were reported to support 306 NIS (Oliva-Paterna et al., 2020), but no detailed information was provided on NIS richness and invaded habitat types. More recently, Oficialdegui et al. (2023) provided a concern list of 126 taxa as the most impactful IAS already established in Iberian inland waters, but they excluded those NIS which did not score high enough. A total of 144 NIS have been also recently recorded as established in marine waters from the Macaronesian region, with differences in NIS richness among islands being strongly influenced by the minimum distance to the mainland and the total number of ports (Castro et al., 2022). On the other hand, Muñoz-Mas and García-Berthou (2020) conducted an extensive review of animal NIS in Iberian inland waters, which included also estuaries and transitional waters, but their mostly focused on freshwater environments. These authors reported 59 aquatic animal NIS occurring in Iberian estuaries and brackish waters (excluding Balearic and Macaronesian islands), which is less than half the overall NIS richness compiled in our study, despite their target area was notably larger because it included also Iberian transitional waters from the Atlantic and Cantabrian coastlines. This meaningful difference in NIS richness between both studies is likely due to these authors retrieved NIS records exclusively from published scientific literature, thus overlooking unpublished but validated NIS records from institutional repositories and official databases. Over the last years, official data repositories have become essential management tools for regularly updating NIS records across large marine and estuarine areas, because of scientific literature takes some years from the field detection to publication (Zenetos et al., 2017). Then, future systematic reviews on NIS should account jointly for both data sources (online repositories and published literature) to not underestimate NIS richness values. In turn, NIS richness is already often underestimated due to limited search effort, uncertainty about historical biogeography and insufficient taxonomic expertise (Bailey et al., 2020), constraints becoming more evident in transitional environments (Ojaveer et al., 2017). Nevertheless, dedicated research efforts in invasion ecology have undoubtedly increased over the last years due to policy requirements and management concerns (Zenetos et al., 2022a), so NIS introductions can be now more rapidly detected and reported. Accounting for the scarce and scattered data previously available to the study area, we provide the first comprehensive assessment on aquatic animal NIS occurring across Spanish Mediterranean transitional waters.

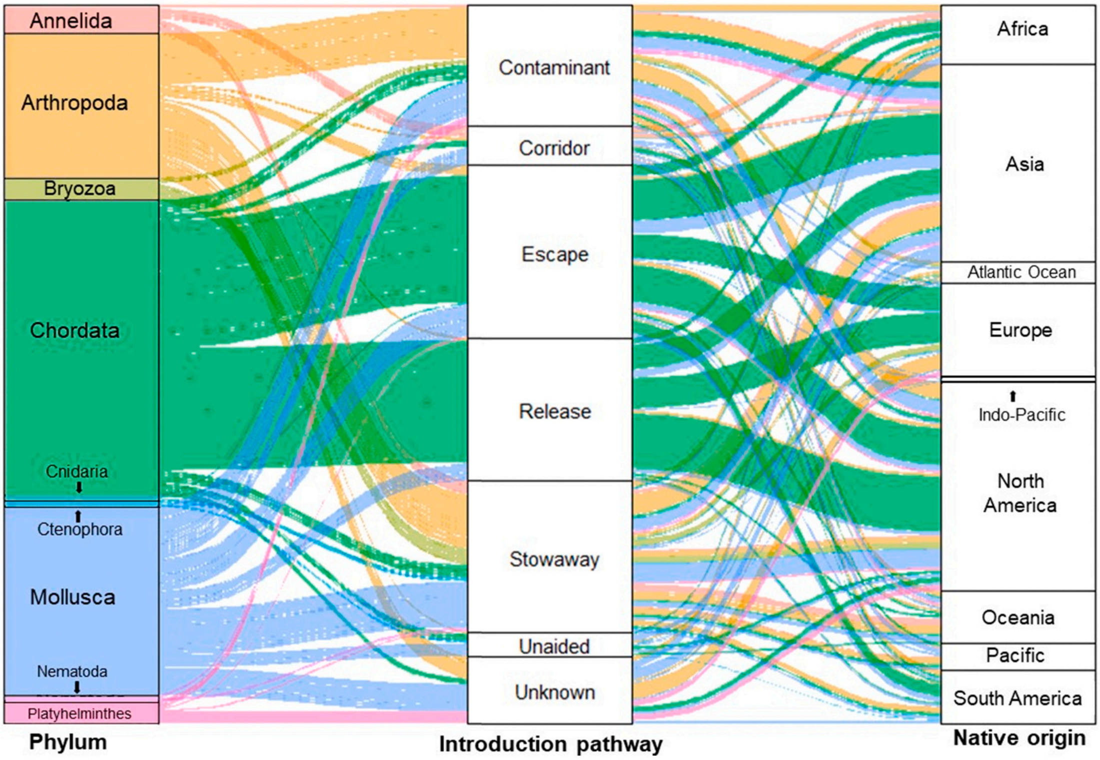

Fig. 8. Alluvial diagram showing relationships among introduction pathways, native origin, and taxonomic groups (phyla) of aquatic animal non-indigenous species recorded in transitional waters from the Spanish Mediterranean coast. Data has been down-weighted to account for species showing two or more regions of origin and introduction pathways. Flows among the three stratums (columns) are colored according to each phylum.

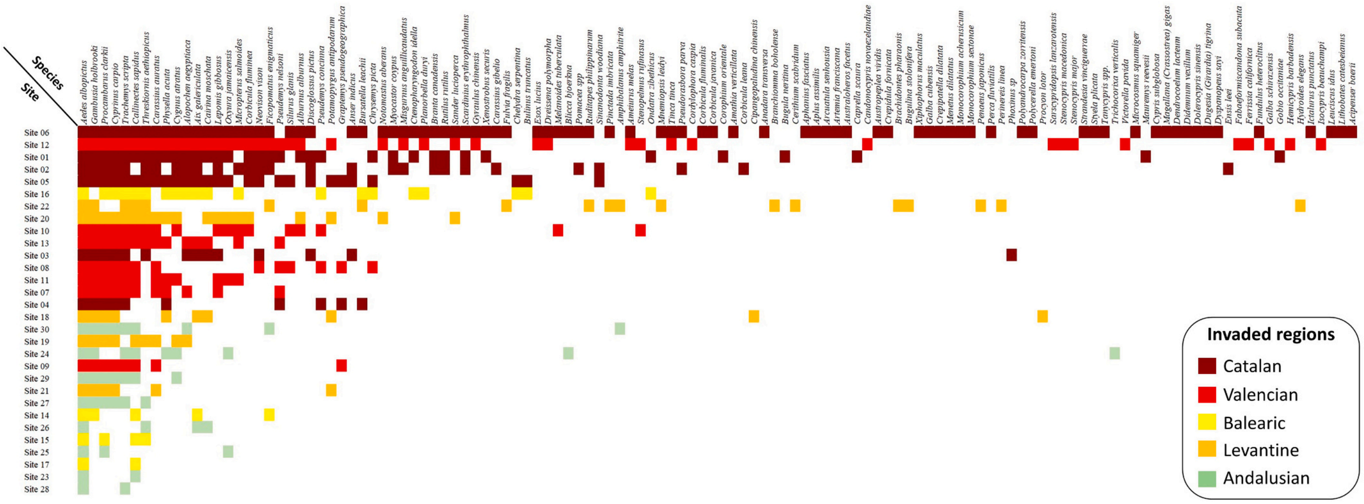

Fig. 9. Species-by-site matrix arranged according to maximum nestedness (nestedness matrix) and representing assemblages of non-indigenous animal species (NIS) recorded in transitional waters from the Spanish Mediterranean coast. From left to right, NIS are ranked from the most common to the rarer. From top to bottom, transitional waters (sites) are ranked from the NIS richer to the poorer. Empty (white) cells indicate the absence of the species in a given site. Cell color indicates to which coastal region belongs each of the assessed sites.

Within the Iberian Peninsula, a greater effort on providing NIS checklists in transitional waters have been conducted in Portugal (Cabral et al., 2020; Chainho et al., 2015), with the last updated version supporting the occurrence of 182 NIS (including both macroalgae and fauna) across Portuguese estuarine and marine waters (Chainho et al., 2020). Among the Mediterranean countries, published data on estuarine NIS occurrence and distribution are also scarce and does target only some particular biotic groups (i.e., Orlando-Bonaca et al., 2021; Piria et al., 2018), with the exception of Greek marine xenodiversity which has been thoroughly quantified and characterized (Zenetos et al., 2018). These latter authors compiled records for 247 aquatic animal NIS inhabiting Greek seas, but the authors did not provide indications to what habitat types (e.g., estuaries, ports or open sea) were invaded, thus hampering a detailed comparison with our NIS richness values. In this context, high-quality standardized data on NIS occurrence across estuaries and transitional waters are urgently required for a global comprehensive assessment on the magnitude of biological invasions in these vulnerable environments. Through this approach, NIS richness values could be compared among different transitional waters worldwide with the aim of assessing overall introduction patterns and identifying major pathways, allowing to inform international NIS management programs and to assess policy effectiveness (Bailey et al., 2020).

About two thirds of the inventoried NIS (72 %) in the present study were established in -at least- any of the 30 assessed sites across the Spanish Mediterranean coast. This proportion of established taxa is similar to that reported jointly from Iberian inland and transitional waters (Oliva-Paterna et al., 2020), but slightly higher than that observed for aquatic NIS (both marine and estuarine) along the Iberian coast (55 %) (Sup. Mat. in Bailey et al., 2020), and very similar to that reported by the same authors at global scale (74 %) and for the Mediterranean region (74 %). However, in the absence of routine NIS monitoring programs, established NIS populations are more likely to be detected in comparison to casual-introduction taxa due to a greater species conspicuousness mediated by higher population density and more widespread occurrence within the colonized environment (Zenetos et al., 2017). As a consequence, the proportion of uncertain NIS (i.e., non-indigenous taxa recorded in the study area but with no self-sustaining populations detected) may be slightly underestimated. Here, NIS with uncertain status comprised about 23 % of the inventoried taxa, so this set of potentially established species should not be overlooked from a management point of view, since they may thrive and become invasive in the near future. In this context, we recommend particular surveillance efforts (e.g., regular monitoring) to be focused on these species with the aim of implementing effective control measures (Ojaveer et al., 2018), such as EWRR protocols.

Our assessment highlighted that Chordata was the most represented phylum, with almost half of these species being fish. The other two dominant phyla were Mollusca and Arthropoda, and these three best represented phyla have been also identified as the main animal taxonomic groups contributing to the overall aquatic xenodiversity in Iberian marine (Bailey et al., 2020; Nunes et al., 2014), transitional (Chainho et al., 2015; Oliva-Paterna et al., 2020) and freshwater ecosystems (Muñoz-Mas and García-Berthou, 2020; Nunes et al., 2015). The same dominance pattern has been reported at global scale for marine, estuarine and freshwater environments (Bailey et al., 2020). Our target environments (transitional waters) were variably influenced by freshwater flows, thus promoting a wide within-site salinity gradient and allowing the occurrence of typically freshwater species. Indeed, most of the recorded fish show freshwater habitat preferences (e.g., *Sander lucioperca* and *Lepomis gibbosus*), and the five most widespread NIS were also typically freshwater taxa (e.g., *Gambusia holbrooki, C. carpio, Procambarus clarkii* and *Trachemys scripta)*, though these latter taxa are habitat generalists and able to thrive under salinity conditions.

4.2. Main introduction pathways, donor regions, recipient sites and arrival rate

The arrival of inventoried NIS was mediated by all the introduction pathways, but four dominant classes were clearly identified: Stowaway, Escape, Contaminant and Release. These dominant pathways have been also identified as major vectors of aquatic NIS introduction by previous studies in the Iberian Peninsula (Muñoz-Mas and García-Berthou, 2020) and other Mediterranean regions (Gravili et al., 2010; Zenetos et al., 2018), as well as at European (Nunes et al., 2015) and global scales (Bailey et al., 2020; Stranga and Katsanevakis, 2021; Turbelin et al., 2022). The two intentional pathways (Escape and Release) were mostly responsible for the introduction of vertebrates and -into a lesser degree- molluscs, whereas unintentional pathways (Stowaway and Contaminant) assisted the arrival of most invertebrates, such as crustaceans and bryozoans (Supplementary material – Fig. S2). For intentionally introduced NIS, recreational fishery and pet/aquarium trade in the wild were the major introduction vectors, with freshwater fish and turtles being respectively spread through these human-aided pathways. Both large piscivores (e.g., *Sander lucioperca* and *Silurus glanis*) and bait small-sized fish (e.g., *Lepomis gibbosus* and *Alburnus alburnus*) have been widely introduced across Iberian inland basins (Clavero and García-Berthou, 2006). This situation poses transitional waters under a high NIS colonization pressure, because of such fish species can reach river mouths through secondary spread, which may encompasses both natural dispersal (e.g., active swimming or passive larval transport) and human-mediated dispersal mechanisms (e.g., aquaculture, recreational and fishing activities) (Bailey et al., 2020). In addition, previous studies highlighted some of the inventoried non-indigenous fishes, such as *Fundulus heteroclitus* and *Australoheros facetus*, and turtles of the genus *Trachemys* as the most commonly released taxa in Iberian inland waters by pets owner (Banha et al., 2019), thus increasing even more the introduction pressure on our study environments.

Stepping-stone invasion patterns have already been identified for aquatic NIS in Iberian inland waters, with many North American NIS entering Europe through France and other midlatitude European countries (e.g., Germany and the UK), thus leading to a strong introduction pressure from France to Spain (García-Berthou et al., 2005). This introduction route makes the northeastern Iberian basins much more prone to aquatic invasions (increased colonization pressure), which consequently promotes the NIS secondary spread to transitional waters from the Catalan region (Clavero and García-Berthou, 2006). According to this assumption, our results highlight transitional waters from the Catalan region were the NIS richest ones (Fig. 4). Hence, Catalan transitional waters -and particularly the Ebro Delta- can be considered as major gateways (i.e., main recipient sites) for aquatic NIS in the study area, either by acting directly as ground for first introduction events (e.g., some fish and molluscs were recorded for the first time in the Ebro Delta; Clavero et al., 2021; Schniebs et al., 2018) or by receiving new NIS through secondary spread from adjacent inland waters. This assumption is further supported by the nestedness matrix (Fig. 9) and NODF analysis (Supplementary Material - Table S2). However, these results on nestedness should be carefully interpreted because we did not assess environmental drivers of animal NIS occurrence in transitional waters, and tolerance to salinity may act as an important factor explaining the invasibility of transitional waters (Cuthbert et al., 2020). In addition, the higher NIS prevalence in Catalan transitional waters may be driven by other relevant socioeconomic and geographic aspects acting synergistically. Firstly, the enormous contribution of the Ebro Delta may be an effect of the large surface area occupied by this coastal wetland. The Ebro Delta expands over 350 km^2, this size being almost twice than that of the two following largest transitional waters (Albufera de Valencia and Mar Menor coastal lagoon). Previous studies have described a clear and direct relationship between surface area and NIS richness (Baiser and Li, 2018; Blackburn et al., 2020), with larger sites supporting richer NIS assemblages into a similar way than observed for native assemblages. Secondly, the Ebro Delta is an important core for Spanish mariculture, as well as one of the most relevant shellfish production places in the Mediterranean region (Ramón et al., 2005), thus exposing transitional waters to a strong introduction pressure through escape of cultivated species (e.g., the already established bivalves *Magallana gigas* and *Ruditapes philippinarum*), but also through contaminant within internationally imported shellfish products (López-Soriano and Quiñonero-Salgado, 2016). Moreover, the high NIS richness observed in Catalan transitional waters may be additionally due to increased NIS survey and recording efforts, as highlighted by the long-lasting research background in invasion science in this region (Riera et al., 2021) and the availability of an updated and consolidated public online database aimed to collect NIS records (EXOCAT; http://exocatdb.creaf.cat/base_dades/#). In this context, future assessments should consider associated levels of search effort to properly assess spatio-temporal dynamics of NIS (Bailey et al., 2020).

Here, we used the temporal trend in NIS introduction as a proxy of the arrival rate of new aquatic taxa at Spanish Mediterranean transitional waters. Regardless of their real impact, an increasing trend in the

NIS occurrence and an extending non-native distribution range must be considered negative, whereas negative introduction trends should be viewed as acceptable (Zenetos et al., 2017). The rate of NIS introductions at both European and Spanish Mediterranean coast scales was similar to that recorded in the Mediterranean sea (Zenetos et al., 2017), with a clearly increasing trend since 1950. By 1960, Spanish Mediterranean transitional waters hosted only 20 % out of the 129 NIS currently inventoried, thus highlighting most introduction events have occurred over the last 60 years. This increase is congruent with that observed in the Gulf of Cadiz (González-Ortegón et al., 2020), which comprises the natural connection between the Mediterranean Sea and the Atlantic Ocean. However, the introduction rate has experienced a decrease over the last two decades and achieved stabilization, a pattern also observed by previous studies, (Muñoz-Mas and García-Berthou, 2020), but this negative trend remains to be thoroughly assessed by further research. Nevertheless, the introduction rate reported here should be carefully interpreted because of NIS monitoring efforts have increased during the last decades (Zenetos et al., 2022a), so this could lead to potential biases in the observed trend. Interestingly, the contribution of intentional pathways has progressively decreased during the last decades (Fig. 7), likely pointing to increased surveillance efforts and improved social perception on biological invasions. In fact, impacts from marine and estuarine NIS began to be widely considered from the early 1980, which helped to raise public awareness and assisted the implementation of pioneering NIS policy instruments (Ojaveer et al., 2018).

4.3. Implications for NIS management in transitional waters

Our results provide baseline information to assist NIS management in Spanish transitional waters, which is also applicable to other countries from the Mediterranean basin and other highly invaded coastal regions. In this context, a recent bibliometric review showed that information on NIS management in Spain is strongly biased towards terrestrial or freshwater ecosystems at the expense of marine and coastal waters (Muñoz-Mas et al., 2021), so our study contributes to fill this knowledge gap. Up to date, comprehensive studies providing high resolution data (i.e., species-by-site) on NIS occurrence along different transitional or coastal environments are extremely scarce (e.g., Cabral et al., 2020; Orlando-Bonaca et al., 2021), thus precluding comparative analysis and site-based management recommendations. With some exceptions (Anderson, 2005), NIS eradication measures are almost always unsuccessful once NIS become established (Nunes et al., 2014). Therefore, a holistic and preventive pathway-based management is an absolute priority for effectively combating NIS in marine and transitional waters, as supported by wide international consensus (Ojaveer et al., 2018). Owing to the growing trend of Contaminant and Stowaway as major introduction pathways over the last decade, an increased management effort should be focused on these unintentional pathways. In turn, shipping activity has already been considered a major vector of NIS introduction in estuarine environments from other Iberian coastal regions (Cabral et al., 2020). Importantly, management and damage costs of unintentionally introduced NIS tend to be much higher than species introduced intentionally, so managing unintentional pathways should be a keystone for future biosecurity efforts (González-Ortegón and Moreno-Andrés, 2021; Turbelin et al., 2022). For instance, the zebra mussel (*Dreissena polymorpha*) was unintentionally introduced in the Ebro Delta at the beginning of this century, causing large economic impacts for energetic companies and irrigation facilities (Durán et al., 2012). These authors quantified in 11.6€ million the overall costs (both related with control and damage) associated to the zebra mussel management only over the period 2005–2009 in the Ebro Delta. The Atlantic blue crab (*C. sapidus)* was also initially introduced in the Ebro Delta, spreading rapidly across all the study regions and displaying a causal role in the decline of some endangered (e.g., *Aphanius iberus* and *Anguilla anguilla*) and commercially exploited (e.g., *Atherina boyeri* and *Carcinus aestuarii*) animal species (Clavero et al., 2022). Then, more effective and targeted NIS surveillance programs should be urgently implemented to improve EWRR protocols in transitional waters. In this context, a cost-effective NIS monitoring protocol developed in the USA has been successfully implemented in Mediterranean coastal waters, showing a high performance for detecting new fouling NIS and even for providing quantitative data in a relatively short-time (Tamburini et al., 2021).

Conversely to well-consolidated and coordinated initiatives to track other anthropogenic drivers (e.g., climate change or pollution), programs monitoring biological invasions are frequently reactive, poorly coordinated and geographically limited (Pergl et al., 2020). Where surveillance is specifically designed to detect targeted taxa and implemented regularly, new NIS can be detected at relatively small population sizes, thus reducing time-lags between introduction and detection (Hayes et al., 2019). These increased surveillance efforts should account also for those already introduced NIS, which have not yet become established in the target area. In this context, a non-negligible proportion (23 %) of our inventoried NIS were classified as uncertain status in the study area, thus supporting the need for routine NIS monitoring programs to assess temporal trend of these potentially established populations. Future biosecurity efforts in transitional waters should be consequently adapted to the growing global shipping and the increased survivability of stowaways due to climate change (Turbelin et al., 2022). Port authorities and state coast demarcations should reinforce NIS surveillance through, for instance, (1) implementing novel eDNA detection techniques for a safer shipping (e.g., Fernandez et al., 2021), (2) promoting EWRR protocols (targeting particularly ballast water) for a more effective management (Kraus et al., 2019), and (3) encouraging the application of eco-friendly antifouling paints to ship hulls (e.g., Vilas-Boas et al., 2021). Furthermore, extensive educational and training campaigns should be simultaneously conducted to engage key stakeholders and users of transitional waters in NIS management. These measures could also improve the effectiveness of surveillance programs targeting non-indigenous flora in the study area. Though our study exclusively focused on animal NIS, several non-indigenous plants are also widespread across Mediterranean Spanish transitional waters, some of them causing major impacts on native biota (Campos et al., 2004; Sempere-Valverde et al., 2021), so further research is needed to provide comprehensive assessments on non-indigenous plant assemblages across transitional waters. The implementation of these management actions could be centralized through international agreements for establishing a worldwide standard to mitigate impacts and spread of NIS in transitional environments.

5. Conclusions

Understanding causes of spatial variation in NIS richness and distribution is a key goal in invasion biology (Blackburn et al., 2020). Comprehensive assessments providing high-resolution data (e.g., quantitative or species-by-site) in both marine and estuarine waters are scarce (Ojaveer et al., 2018). Our study provides the first comprehensive assessment on NIS richness and spatio-temporal dynamics across Spanish Mediterranean transitional waters. We quantified a total of 129 NIS inhabiting 30 transitional waters along the Spanish Mediterranean coast, as well as identified the most NIS-invaded sites and assessed main introduction pathways, geographic realms of origin and NIS assemblages. Overall, transitional waters from the Catalan region were more invaded than sites placed further south, likely as a consequence of the greater mariculture and shipping activity, but also of the secondary spread of freshwater NIS. While patterns depicted here refer only to Spanish Mediterranean transitional waters, our results are strongly aligned with recent studies from other regions, so management recommendations provided here must be easily applicable to other Mediterranean countries. In this context, a pathway-based approach should be properly implemented to mitigate spread and impacts of NIS in transitional environments, with management measures being centralized through internationally coordinated programs.

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CRediT authorship contribution statement

José M. Zamora-Marín: Conceptualization, Investigation, Formal analysis, Writing – original draft. **Antonio A. Herrero-Reyes:** Investigation, Formal analysis, Writing – original draft. **Ana Ruiz-Navarro:** Investigation, Writing – review & editing. **Francisco J. Oliva-Paterna:** Conceptualization, Investigation, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that there is no conflict of interest with any financial organization regarding the topics discussed in the manuscript.

Data availability

We attach an Appendix with all the raw data used in this study

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Appendices. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2023.114893.

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