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Non-indigenous species (NIS) of polychaetes (Annelida: Polychaeta) from the Atlantic and Mediterranean coasts of the Iberian Peninsula: an annotated checklist

E. López* and A. Richter

Abstract

This study provides an updated catalogue of non-indigenous species (NIS) of polychaetes reported from the continental coasts of the Iberian Peninsula based on the available literature. A list of 23 introduced species were regarded as established and other 11 were reported as casual, with 11 established and nine casual NIS in the Atlantic coast of the studied area and 14 established species and seven casual ones in the Mediterranean side. The most frequent way of transport was shipping (ballast water or hull fouling), which according to literature likely accounted for the introductions of 14 established species and for the presence of another casual one. To a much lesser extent aquaculture (three established and two casual species) and bait importation (one established species) were also recorded, but for a large number of species the translocation pathway was unknown. About 25% of the reported NIS originated in the Warm Western Atlantic region, followed by the Tropical Indo West-Pacific region (18%) and the Warm Eastern Atlantic (12%). In the Mediterranean coast of the Iberian Peninsula, nearly all the reported NIS originated from warm or tropical regions, but less than half of the species recorded from the Atlantic side were native of these areas. The effects of these introductions in native marine fauna are largely unknown, except for one species (*Ficopomatus enigmaticus*) which was reported to cause serious environmental impacts. In other cases, the displacement of native species or economic damages are suspected.

Keywords: Non-indigenous, Alien, Introduction pathway, Polychaeta, Iberian Peninsula

Background

Non-indigenous species (NIS) are defined as species introduced outside of their native distribution range (past or present) and outside of their natural dispersal potential by intentional or unintentional human activities [1]. Their translocation is one of the major drivers of biodiversity changes [2]. Global trade and the construction of land or water corridors to facilitate trade or human migration are causing the breakdown of biogeographic barriers leading to an increasing homogenization of the biota [3] in such a way that the occurrence of NIS is altering marine ecosystems all over the world. Some NIS may even become invasive in the recepient environment and when it happens they might displace native species and reduce biodiversity, thus modifying community structures, physical properties of the habitat, food webs and ecosystem function [4, 5]. In extreme cases, this process can lead to financial losses due to fishery decreases and to irreversible damage to vessels, water pipes, piers and other port and canalization infrastructures by fouling organisms [6].

Unfortunately, there is still a lack of information about marine NIS on a global scale and their ecological impacts on native biota as well as their current distribution ranges are not well known [7]. Any NIS that is released into a new recipient environment can potentially start an invasion process that consists of three progressive stages: the release and introduction of the species outside its

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native range of distribution through human activities, the establishment of a self-sustaining population in the new ecosystem, and the dispersal of this species outside of its site of introduction [8, 9]. It is thus important to asses in which phase of an invasion process an evaluation of the effects on the native biota is performed [10] and to make a follow up of the evolution of already established NIS and newly recorded ones to detect eventual sudden outbursts or blooms [11]. Since once NIS are established, their eradication is almost impossible [12, 13], early interception by controlling potential pathways is probably the most efficient method to prevent future impacts on native ecosystems [14]. This implies a correct taxonomic identification of new arriving NIS and distinguishing them from the native biota, which is sometimes problematic—misidentifications with native species or other NIS frequently occur [11, 15]—and knowledge of the pathways and vectors for NIS introductions with a high level of certainty. Although there are a few exceptions (i.e. [16]), the most common introduction mechanisms for marine NIS are (1) movement of fouling organisms on the hull of ships, (2) release of organisms in solid or liquid ship ballast, (3) movement or intentional release of aquaculture target species along with their associated organisms, (4) connection of water bodies through canals, and (5) release associated with pet industries or bait species [17].

In Europe, the European Strategy on Invasive Alien Species encouraged the implementation of a pan-European inventory of NIS [18]. Within this framework, marine NIS catalogues have been elaborated and published for several countries: France [19], Norway [20], United Kingdom [21, 22], Turkey [23, 24], Denmark [25], Greece [26], the Netherlands [27], Germany [4], Belgium [28], Ireland [29], Cyprus [30], Italy [31], and Portugal [32]. The situation in Europe encompasses a lively, yet fragmented, field of investigation [31]. Their results have been reviewed by a number of research projects funded by the European Commission such as DAISIE: Delivering Alien Invasive Species Inventories for Europe [33] or EASIN: European Alien Species Information Network [34]. From these datasets, the number of marine NIS recorded is estimated to be about 1400 [9]. When comparing to the nearly 33,000 registered European marine species [35], the share of NIS is slightly over 4%. This may represent an insignificant proportion, but the presence of NIS is strongly biased towards environments affected by natural disturbances and/or alterations caused by human activities like estuaries, lagoons, harbours and canals, where native species richness is low [10, 36, 37]. In Europe, the most altered environments, be it due to chemical or organic pollution, physical disturbances or a combination of both, seem to be the most favourable for NIS settlement [38, 39].

The class Polychaeta is the most important taxonomic group within Annelida in terms of species richness, with about 100 families and over 12,000 valid species [40]. They inhabit almost every benthic ecosystem, ranging from littoral environments down to bathyal and abyssal depths. In addition to their great biodiversity, polychaetes play a key role in benthic communities as they take part in the decay of organic sediment matter as well as in the transfer of nutrients to the water column [41]. Although some species are sensitive to high or medium levels of pollution and are useful for environmental monitoring programs [42], many of them are opportunistic species that can withstand high levels of perturbation [43]. Besides environmental tolerance [22], there are a series of biological traits that allow NIS to overcome the negative genetic effects of small founder populations therefore promoting their successful establishment and spread. These include a high genetic variability [44], short generation time, early sexual maturity, high reproductive capacity, and a broad diet [45]. Asexual reproduction [46], hermaphroditism and gregariousness [47] also seem to favour the successful establishment of NIS, as these sexual and behavioural strategies avoid or mitigate the mate finding Allee effect in situations of low population density [48]. Many opportunistic polychaetes show these features that justify them as the second most often detected group of marine animal NIS in Europe, just behind arthropods [9].

In this study, our goals were firstly to elaborate a reliable updated inventory of NIS belonging to Polychaeta using data on their introduced distribution range and the invasion stage they have reached in the studied region, the Atlantic and Mediterranean coast of the Iberian Peninsula, following the unifying quality criteria proposed by Blackburn et al. [8] and Marchini et al. [49], and secondly to reveal eventual regional trends in their introduction pathways and biogeographic origins. The results obtained will provide a baseline to develop regional and national strategies to prevent new introductions of NIS of polychaetes and/or to control the demographic growth and spread of already introduced species.

Methods

For this work, the literature was thoroughly reviewed in search of polychaete NIS records all around the continental coast of Iberian Peninsula, including the Balearic and Chafarinas islands. The Canary, Madeira, and Azores Islands were excluded from this study. Following the quality criteria for establishing normalized inventories [49], only reliable sources that allowed for the validation of the taxonomic identity of the NIS, their time and spatial records and their status in the invasion process were considered for data extraction and analyses. Especial attention was paid to publications in scientific journals and academic works, such as PhD theses. Unpublished reports from monitoring programs, workshops and conferences were only considered when publicly available and their results testable through detailed descriptions or deposition of voucher specimens. Newly recorded species in the time period considered were regarded as true NIS following the published criteria [15]. Thus, species previously known to be absent from the region based on convincing archaeological or historical evidence and whose new record could be directly linked in space and time with a human mediated vector was considered NIS. In the absence of direct evidence of a human-mediated introduction and provided that the natural distribution range was known, the species were considered NIS only if their new records were located clearly beyond their current known distribution limit and outside their natural dispersal potential, rendering intentional or unintentional human mediated introductions as the only translocation mechanisms. Consequently, deep-water and interstitial species whose occurrence cannot be linked to any human activity and those that might be able to reach the Atlantic and/or Mediterranean coasts of the Iberian Peninsula by natural dispersal from neighbouring areas in which they are native or cryptogenic species sensu Carlton [50] were excluded. For nomenclatural purposes, names were updated according to the World Register of Marine Species [51], but in some instances older names or misidentifications were also mentioned. The records were cited in strict chronological order and registered separately for the Atlantic and the Mediterranean coasts of the Iberian Peninsula in order to detect a biogeographic effect, if present. In addition, they were assigned to administrative divisions such as Spanish Marine Demarcations [52] and Portugal (Fig. 1). For each area, the stage of the invasion process for the recorded species was categorized according to the conceptual framework proposed by Blackburn et al. [8], which is summarized in Table 1. Species were considered as established in one location when they were recorded with certainty in the same site or close locations successively over a reasonably long period, assuming that the short life-span of most species implies the presence of self-sustaining populations in these cases. Otherwise, the species was recorded as casual. When vouchers and/or complete descriptions were given with the bibliographic report allowing corroboration of the taxonomic identity, it was clearly mentioned. The casual records not fulfilling this requirement should be considered questionable and were excluded from the checklist, as well as doubtful (cf.) ones. The native distribution of all NIS was assigned to broad oceanic regions according to the classification proposed by Briggs and Bowen [53]. It must be stressed here that unlike animals with hard endo or exoskeletons, such as molluscs, polychaetes hardly ever fossilize and leave remains in archaeological findings, so their native

Fig. 1 Map of Iberian Peninsula showing the limits between administrative marine demarcations. *NOR* North-Atlantic Demarcation (*Demarcación Marina Noratlántica*); *PT* Portuguese mainland; *SUD* South-Atlantic Demarcation (*Demarcación Marina Sudatlántica*); *ESAL* Gibraltar and Alborán Sea Demarcation (*Demarcación Marina del Estrecho y Alborán*); *LEBA* Levantine and Balearic Demarcation (*Demarcación Marina Levantino-balear*). Derivative of "Positionkarte von der Iberische Halbinseln" © NordNordWest/Wikimedia Commons/CC BY-SA 3.0

Table 1 Categorization scheme for the stages in the invasion process, modified from Blackburn et al. [8]

Category	Definition
A	Not transported beyond limits of native range
B	Individuals transported beyond limits of native range, but not released in the wild
C0	Individuals released in the wild, but incapable of surviving for a significant period
C1	Individuals surviving in the wild in location where introduced, no reproduction
C2	Individuals surviving in the wild in location where introduced, reproduction occurring, but population not self-sustaining
C3	Individuals surviving in the wild in location where introduced, population self-sustaining
D1	Self-sustaining population in the wild, with individuals surviving a significant distance from the original point of introduction
D2	Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction
E	Fully invasive, with individuals dispersing, surviving and reproducing at multiple sites across a significant spectrum of habitats

or non-indigenous status is often difficult to assess with certainty [15]. Thus, the present list may grow or shrink when more information on the life cycle and larval development, ecology and evolutionary biology of the polychaetes inhabiting the studied region becomes available. The introduction pathway to the Iberian Peninsula of each species was cited from literature when available, considering it the most likely mechanims. When it was not stated for the Iberian Peninsula, reported pathways to nearby countries were proposed.

Results

According to literature, a total of 23 polychaete NIS have been able to establish in the Iberian coasts (Table 2), with an additional 11 casual records (Table 3). The Atlantic coast of the Iberian Peninsula accounted for 11

Table 2 Established NIS of polychaetes in the Iberian Peninsula

Taxa	NOR	Stage in the invasion process				Native origin	Pathway	References
		PT	SUD	ESAL	LEBA			
Ampharetidade								
Isolda pulchella Müller in Grube, 1858		D2				Warm Western Atlantic	Uk	[145, 168]
Capitellidae								
Notomastus aberans Day, 1957				C3	D2	Warm Eastern Atlantic	BW	[169, 170]
Eunicidae								
Lysidice collaris Grube, 1870				C1	D2	Tropical Indo-West Pacific	Uk	[135, 171]
Fabriciidae								
Novafabricia infratorquata (Fitzhugh, 1973)	C1				D2	Warm Western Atlantic	Aq	[172, 173]
Goniadidae								
Goniadella gracilis (Verrill, 1873)		D2				Cold-Temperate Western North Atlantic	BW	[145, 168]
Hesionidae								
Parasyllidea humesi Pettibone, 1961			D2			Warm Eastern Atlantic	Uk	[174]
Nereididae								
Perinereis linea (Treadwell, 1936)					C3	Cold-Temperate Western North Pacific	Bt	[113]
Phyllodocidae								
Hesionura serrata (Hartmann-Schröder, 1960)					C3	Tropical Indo-West Pacific	Ls	[175]
Sabellidae								
Amphicorina pectinata (Banse, 1957)	C3			C3		New Zealand-Australian	BW	[88, 176]
Branchiomma bairdi (McIntosh, 1885)					E	Warm Western Atlantic	HF	[82]
Branchiomma luctuosum (Grube, 1869)					D2	Tropical Indo-West Pacific	HF	[81]
Desdemona ornata Banse, 1957	D2	D2				Warm Eastern Atlantic	BW	[177, 178]
Serpulidae								
Ficopomatus enigmaticus (Fauvel, 1923)	E	D2	E		E	Warm Western Pacific	HF	[92, 179–181]
Hydroides dirampha Mörch, 1863					C3	Warm Western Atlantic	HF	[182]
Spirorbis marioni Caullery & Mesnil, 1897					C3	Warm Eastern Pacific	HF	[183]
Spionidae								
Boccardia proboscidea Hartman, 1940	C3					Cold-Temperate Eastern North Pacific	BW	[166]
Dipolydora socialis (Schmarda, 1861)	C3					Cold-Temperate South American	Aq	[99]
Dipolydora tentaculata (Blake & Kudenov, 1978)	C3					Cold-Temperate Eastern North Pacific	Uk	[87]
Polydora colonia Moore, 1907				C3		Warm Western Atlantic	BW	[184]
Polydora cornuta Bosc, 1802		C1			C3	Warm Western Atlantic	BW	[103, 120]
Prionospio pulchra Imajima, 1990	E	C3				Cold-Temperate Western North Pacific	Aq	[97, 98]
Pseudopolydora paucibranchiata (Okuda, 1937)	E	D2				Cold-Temperate Western North Pacific	BW	[101, 185]
Terebellidae								
Pista unibranchia Day, 1963	C1				D2	Warm Eastern Atlantic	BW	[99, 186]

Atlantic demarcations: NOR, PT, SUD; Mediterranean demarcations: ESAL, LEB. Abbreviattions for demarcations as in Fig. 1; Stages in the invasion process as in Table 1

Pathway: *Aq* aquaculture; *Bt* bait commerce; *BW* ship ballast water; *HF* ship hull fouling; *Ls* Lessepsian migrant; *Uk* unknown

Table 3 Casual NIS of polychaetes in the Iberian Peninsula

Taxa	NOR	Stage in the invasion process				Native origin	Pathway	References
		PT	SUD	ESAL	LEBA			
Capitellidae								
Leiochrides australis Augener, 1914					C1	Warm Western Pacific	BW	[81[a]]
Neopseudocapitella brasiliensis Rullier & Amoureux, 1979				C1	C1	Warm Western Atlantic	Uk	[170, 187[a]]
Fauveliopsidae								
Fauveliopsis glabra (Hartman, 1960)				C1		Warm Eastern Pacific	Aq	[112[a]]
Lumbrineridae								
Lumbrineris crassicephala (Hartman, 1965)		C1				Warm Western Atlantic	Uk	[168[a]]
Maldanidae								
Metasychis gotoi (Izuka, 1902)	C1	C1		C1	C1	Warm Western Pacific	Uk	[68, 70, 170, 188[a]]
Polynoidae								
Lepidonotus carinulatus (Grube, 1870)				C1		Tropical Indo-West Pacific	Aq	[189[a]]
Sabellidae								
Euchone incolor Hartman, 1965	C1	C1				Warm Western Atlantic	Uk	[69, 188[a]]
Spionidae								
Prionospio aluta Maciolek, 1985		C1				Cold-Temperate Western North Atlantic	Uk	[168[a]]
Spiophanes wigleyi Pettibone, 1962	C1					Cold-Temperate Eastern North Pacific	Uk	[188[a]]
Syllidae								
Erinaceusyllis serratosetosa (Hartmann-Schröder, 1982)					C1	Tropical Indo-West Pacific	Uk	[122[a]]
Syllis pectinans Haswell, 1920	C1			C1	C1	Tropical Indo-West Pacific	Uk	[73[a], 190, 191[a]]

Atlantic demarcations: NOR, PT, SUD; Mediterranean demarcations: ESAL, LEB. Abbreviattions for demarcations as in Fig. 1; stages in the invasion process as in Table 1

Pathway: *Aq* aquaculture; *BW* ship ballast water; *Uk* unknown

[a] Indicates that voucher location and/or complete description of the material is provided in the report

established and nine casual NIS of polychaetes, whereas in the Mediterranean coast they numbered 14 and seven, respectively (Fig. 2). Not only were the numbers different, but also the species. Only *Ficopomatus enigmaticus* and *Amphicorina pectinata* were established NIS in both the Atlantic and Mediterranean coasts; another three species (*Novafabricia infratorquata*, *Polydora cornuta* and *Pista unibranchia*) were reported from the two coasts, but were only established in the Mediterranean. Two species (*Metasychis gotoi* and *Syllis pectinans*) were cited as casual records in both of the two areas. Considering administrative divisions, in Spain 21 established NIS of polychaetes and nine casual ones were found, whereas five established and five casual species have been reported from Portugal.

The historical evolution of new records of NIS of polychaetes shows that the reports of new polychaete species were just incidental prior to 1980, but their number increased dramatically in the following 10 years. After this point in time, the new records of established

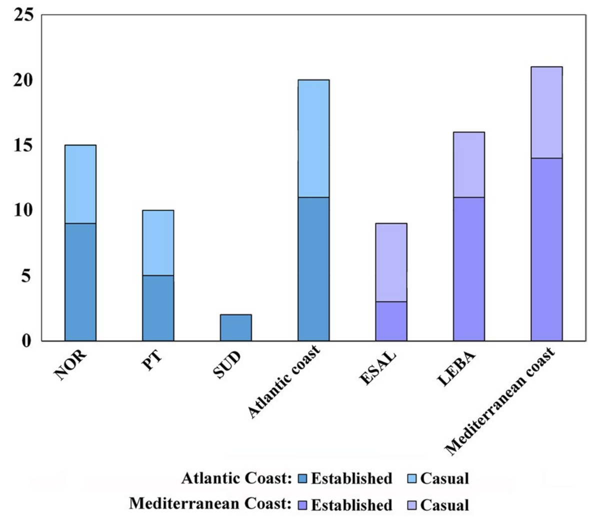

Fig. 2 Number of polychaete NIS recorded from each administrative demarcation of the Iberian Peninsula and from the Atlantic and Mediterranean coasts

NIS have remained stable (Fig. 3). Regarding their origin (Fig. 4), slightly above 25% of the NIS reported for the Iberian Peninsula originated in the Warm Western Atlantic region, followed by the Tropical Indo-West Pacific region (nearly 18%) and the Warm Eastern Atlantic region (about 12%), The remainder of the species are native to an array of biogeographical regions and it must be noted that none were translocated from the Polar Arctic or Antarctic regions. Furthermore, the species originating in Warm Western Atlantic are seemingly the most successful ones, considering that six of the established species came from this region. The Warm Eastern Atlantic region and the Tropical Indo-West Pacific region provided four and three established species, respectively. If the two slopes are considered separately, a clear difference can be noticed. Almost all the species reported from the Mediterranean coast were native from warm or tropical areas, with the Warm Western Atlantic (five established and one casual) and the Tropical Indo-West Pacific (three established and three casual) regions as the main sources. However, the origin of the NIS reported from the Atlantic coast of the Iberian Peninsula is more diverse, since seven established and two casual species are native from cold-temperate regions while four established and seven casual ones originated from warm or tropical areas.

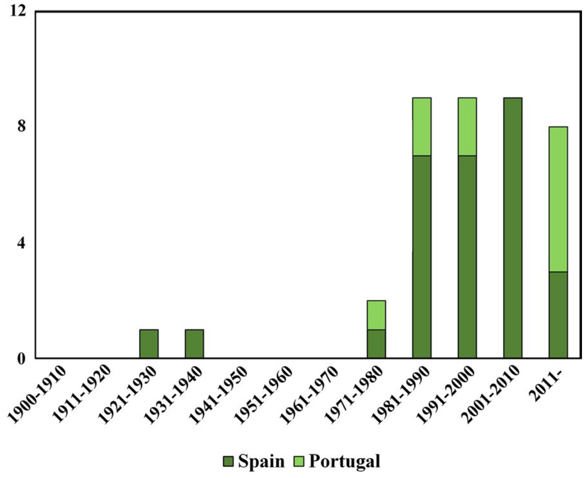

Fig. 3 Numbers of new records of polychaete NIS reported from the Iberian Peninsula in each decade of 20th and 21st centuries

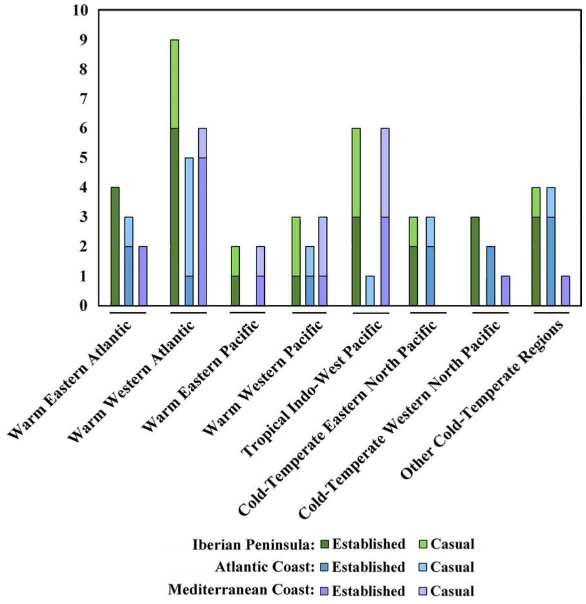

Fig. 4 Native distribution of NIS of Polychaeta introduced to the Iberian Peninsula

According to availbale literature, shipping was the most common way of translocation as it was the most likely pathway for 14 species (nine with ballast water and five as part of the hull fouling community), although no experimental studies have been conducted. Aquaculture related activities accounted for five introductions and bait industry for another one. Finally, one species is considered a Lessepsian migrant that spread along the Mediterranean basin and eventually arrived to the Spanish coasts. However, for more than one third of the reported species (four established and eight casual) the exact mechanism that facilitated their transport remains unknown (Fig. 5). The most remarkable difference between the Atlantic and Mediterranean coasts is the higher number of fouling species in the latter. In addition, there were a Lessepsian migrant and an introduction related to the fish bait commerce in the Mediterranean, pathways which are to date still unreported from the Iberian Atlantic slope (Tables 2, 3).

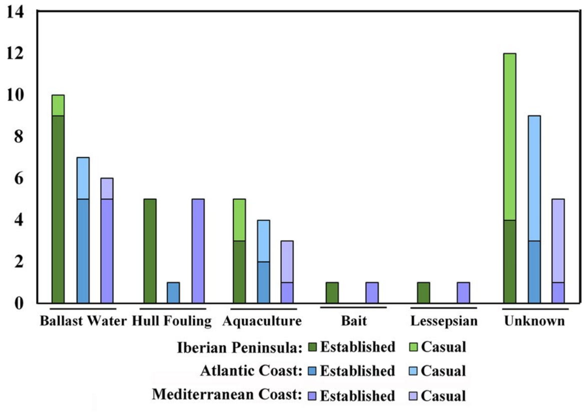

Fig. 5 Introduction pathway of polychaete NIS to the Iberian Peninsula

Discussion

Is the situation in Spain and Portugal worse than in other European countries?

From the literature examined, we found that 30 polychaete NIS have been recorded from continental Spanish and ten from mainland Portuguese coasts, of which about two thirds were established in one or more locations. Taking into account the Atlantic coast of the Iberian Peninsula, where 20 species were cited, the number was higher than that of other Europeans countries of the Atlantic slope, such as the United Kingdom [22] and France [19, 54] with ten NIS of polychaetes, Germany [4] with nine, Belgium [28, 55] with five, or Ireland [29] with just three. Not only can differences among the countries in the quantity be mentioned, but also in the species involved, with *Ficopomatus enigmaticus* as the only one present in all these countries. Other shared Iberian polychaetous NIS were *Desdemona ornata* and *Goniadella gracilis*, which were also recorded from the United Kingdom.

The number of NIS in the Mediterranean side of the Iberian Peninsula was similar to those from other countries from the Central and Eastern Mediterranean, where 19 NIS of polychaetes were recorded from Cyprus [30], 16 were reported from Greece [26] and 37 are established along Italian coasts [31, 56–58]. With just two NIS, the inventory is much less in Malta [59], but it is a much smaller country, whereas the list from Turkey of 66 species is by far the largest, [24]. In fact, compilations for the Mediterranean Sea are more complete as 132 NIS polychaete species [60, 61] have been recorded, of which at least 26 are known to be established in the western area of this sea [62]. Some of the species herein recorded as established are present in all the aforementioned countries except Malta, namely *S. marioni*, *L. collaris* and *Notomastus aberans,* whereas *D. ornata* and *F. enigmaticus* have been reported from Turkey, Greece and Italy; *Pista unibranchia*, *Branchiomma luctuosum* and *B. bairdi* from Turkey, Cyprus and Italy; *Metasychis gotoi* from Turkey, Cyprus and Italy; and *Syllis pectinans* from Turkey and Italy. The presence of *S. marioni*, *D. ornata*, and *F. enigmaticus* in several Atlantic countries points to their great colonization ability.

The great difference between the Mediterranean and Atlantic national inventories might suggest that the former is under a stronger invasion pressure. In fact, the Mediterranean Sea is among the most affected marine areas in the world where about 820 NIS have been recorded [61], accounting for at least 4.8% of its total biodiversity. This figure might be an underestimation, since a number of species belonging to the smallest fraction of plankton or benthos might have passed overlooked [63]. However, when comparing our data for the Mediterranean and Atlantic Iberian coasts, it can be observed that the difference is not so great, indicating that the number of polychaete NIS is more or less equal when sampling efforts are similar and that lower number in the Atlantic countries can be caused by poorer knowledge of the current situation of polychaete fauna.

Chronological trends in NIS reports

The temporal dynamics of new NIS records of polychaetes shows that prior to 1970 the number of reports of new polychaete species was negligible. Rather than concluding an acceleration of the introduction rates, this fact reflects the poor knowledge of the polychaete fauna in the Iberian coasts at the time. After the most important polychaetologist in Spain, Enrique Rioja was exiled to Mexico at the end of the Spanish Civil War [64], just a handful of local publications were devoted to this group and the main effort in data gathering relied on the work of French scientists [65–70]. With the coming of a new generation of researchers, in the 70's and 80's, a number of PhD theses and their associated papers [71–76] resumed the study of these animals in an exhaustive way. This accounts for the high number of newly recorded species in the following years (Fig. 3). Subsequently, the investigations lead by some of these scientists and the students they trained, together with an increasing concern on environmental issues has maintained the number of new records more or less stable every year.

To what extent are these species harmful?

Thus far, the effects of the settlement of most of these new polychaete species are very poorly understood, mostly as a consequence of the insufficient development of research projects, although the lack of investigation does not justify the assumption that these species have no impact [31]. Streftaris and Zenetos [77] gave a list of invasive species in the Mediterranean biota and established which ones were the worst on account of their known impact. Five of these species have been recorded in our compilation, namely *B. luctuosum*, *F. enigmaticus*, *Hydroides dirampha*, *Polydora cornuta* and *S. marioni*.

The NIS belonging to the genus *Branchiomma* Kölliker, 1858 are relatively large sized tubiculous fan-worms (Sabellidae). They present a very high risk of invasion because they are hermaphrodites with a very short pelagic phase that may produce high population densities starting from only a few individuals [78]. *Branchiomma luctuosum* was first recorded in Europe from Italy [79], where it was found in littoral lagoons, marinas and other significantly disturbed habitats. In these environments, it seemingly displaced native species [80]. A well-established population is also known from the port of Valencia, but no negative effect was observed [81]. In Spain, *B.*

bairdi was first recorded from Mar Menor Lagoon, where it was especially abundant in meadows of *Caulerpa prolifera* (Forsskål) J.V. Lamouroux [82], and within a few years it was present in several localities of south-eastern Spain [83] as well as in other parts of the western Mediterranean basin [56, 84]. In Portugal, the species has been reported only from the island of Madeira [85], but not from the mainland coasts. Competition with native suspensions feeders and interfernce with recruitment processes were observed for *B. luctuosum* [80] and *B. bairdi* [86] in the Mediterranean Sea. For *D. ornata* no effect on native species has been observed in British coasts [22], although it has been considered a potential competitor of the native *Manayunkia aestuarina* (Bourne, 1883) in Northern Spain because they have similar ecological requirements [87]. Albeit no impact is described for *Amphicorina pectinata*, it is by far the dominant sabellid in the area [88], indicating a probable replacement of native small species of the family.

Serpulid tubeworms settle and build their calcareous tubes on various natural substrates, as well as on artificial ones, forming an important part of the biofouling pests on submerged marine structures with a significant economic impact [77, 89]. In this respect, *F. enigmaticus* is considered a real conservation threat, as it is the only annelid included in the Spanish official catalogue of invasive species (Real Decreto 630/2013. BOE, 185: 56764). It is a eurihaline species dwelling in estuaries and coastal lagoons. Its highest population densities are achieved in locations with salinities below 30 ppm [90], mild hydrodynamic conditions and high content of organic matter [91]. Under these conditions, it forms large circular reefs that can exceed 1 m in diameter and they have been observed to alter natural water circulation in tidal marshes of southern Atlantic coast of Spain [92]. When populations are very dense, their filter feeding can disturb the natural concentration of nutrients and phytoplankton [93], although the very same effect has also been considered to be beneficial, acting as natural bioremediation in high organic pollution situations [94]. The reefs are structurally stable over time, providing complex three-dimensional habitat in a soft sediment environment, and this biogenic habitat hosts an abundant associated fauna, distinct from nearby mudflats in species composition and relative abundance [95]. NIS belonging to the genus *Hydroides* also form dense aggregations that cause economic problems [96] and can constitute a major part of the fouling communities in ports and marinas where they displace native species [38, 96]. *Spirorbis marioni* also build calcareous tubes, but being a minute species its physical impact is much lesser. Nevertheless, alterations on native biodiversity have been reported from the Mediterranean Sea [77].

A third major group of polychaetous NIS is formed by members of the family Spionidae Grube, 1850. In some cases, the colonization of the Iberian coasts has been rapid. For instance, *Prionospio pulchra* quickly spread along the Atlantic Iberian coast [87, 97] after being reported from its first location in Spain [98] and *Pseudopolydora paucibranchiata* has also been steadily spreading to the Bay of Biscay [99] and Portugal [97, 100] after its first cite from NW Spain [101]. The successful colonizations by these species seem to be related to their tolerance to severe pollution, as is the case of *P. paucibranchiata* in some Mediterranean [102] and Atlantic [87] locations, as well as the Spanish population of *P. cornuta* [103], or of *P. pulchra*, both within its Japanese native range [104] and in its Mediterranean locations [105]. Regarding the effect on native biota, the extent of the impact differs between species. In Aegean Turkish [106] and Black Sea [107] harbours, where *P. cornuta* constitutes one of the most conspicuous NIS, massive colonization and replacement of native species with the same ecological requirements have been reported. Similarly, large populations of *P. paucibranchiata* were reported from locations in NW Spain [101] and southern Portugal [97], where it might replace native species. However, coexistence without replacement of autochthonous taxa has been reported for *P. pulchra* from colonized locations in California [108]. Thus far, only one shell-boring species has been reported from Spanish coast, *Dipolydora socialis* [99] and no economic damage was recorded. However, the species is a well-known pest of mollusc aquaculture, both within its native range and in new locations [109].

What is their origin and how did they arrive?

The majority of NIS introduced to European Atlantic waters were found to originate from the North Pacific, particularly the western area, followed by the North-West Atlantic. This suggests that introductions from regions with similar temperature regimes are more likely to become established and widespread, as they would be physiologically adapted to the environmental conditions experienced in the recipient waters [22]. Nevertheless, introductions in the Iberian Peninsula as a whole showed a different pattern. Less than 25% of the established NIS originated in cold temperate regions and the region that provided the higher number of species was the Warm Western Atlantic, where the tropical component is also important, in addition to nine species originating from other warm areas. However, the patterns in the Atlantic and Mediterranean coasts were noticeably different. The Atlantic NIS were a mixture of species with warm and cold-temperate origins, although species from cold-temperate regions were more successful in terms of establishment. It pointed to a condition not so divergent from that described above for the northern European countries. On the contrary, nearly all the reported NIS from the Mediterranean side were native from warm or tropical regions. In this respect, the situation in the Mediterranean coast was more similar to that in some Mediterranean countries, such as Italy, where marine NIS of tropical origin account for half of the total number [31], or to that of the easternmost area of this sea, where 49 out of 52 established polychaete NIS are of tropical origin [62]. Thus, it can be concluded that the Iberian Peninsula is divided in two clear biogrographic units regarding NIS polychaetes. This fact should be considered in order to implement future research and control procedures.

Based on the present records, the principal pathway for the introduction of the established NIS of polychaetes in the Iberian coastal waters was being transported by shipping activities. It involves translocation via commercial or recreational vessel hulls and ship sea-chests (used during ballast water exchange), either as sessile (fouling), boring, vagile, or clinging species [22]. Most of these species were first cited in ports and then expanded to other environments or in some cases even stayed restricted to such localities. *Branchiomma bairdi* [78], *B. luctuosum* [81], *F. enigmaticus*, *H. dirampha* [110] and *S. marioni* [31] have been considered as belonging to the hull fouling community and having this mechanism as their more likely way of introduction. Ballast water has also been highlighted in numerous studies as an important transmission vector for NIS, particularly plankton [22], thus being especially important for those species with life cycles involving long planktonic larval stages. This vector is proposed for several members of Spionidae, namely the established *Polydora colonia* [63], *P. cornuta* [62], *P. paucibranchiata* and *Boccardia proboscidea* [99], but also by some small sabellids, such as *A. pectinata* and *D. ornata* [31], and members of other families, including the capitellids *N. aberans* and *Leiochrides australis*, and the terebellid *P. unibranchia* [81]. Thus, introduction via ballast water seems to be the most common pathway. Again, some differences arose between the coasts of the Iberian Peninsula, since the number of introductions related to hull fouling was proportionately fewer in the Atlantic coasts.

Aquaculture was identified as the second major pathway for the importation of marine NIS to European coastal waters [19, 22]. Introductions have occurred, either through the deliberate movement of a target species for culture or unintentional introduction as a 'hitchhiker'. Considering they have no commercial value, the latter seems the more likely pathway for polychaetes. Only three of the 39 species recorded in this report as established have been related with aquaculture for their introduction: *P. pulchra* [98], *Novafabricia infratorquata* [31] and *D. socialis* [109]. Another two casual ones have also been related to aquaculture activities: *Lepidonotus carinulatus* [111] and *Fauveliopsis glabra* [112]. It is much lesser than expected since roughly 20% of the polychaete NIS introduced in Europe as a whole arrived via vectors related to aquaculture in some way [9]. Another unintentional way of introduction is the accidental release of imported bait worms, which apparently caused the establishment of *Perinereis linea* in SE Spain [113]. Finally, there are possible transmission routes that might include secondary spread from neighboring countries where the NIS arrived via the Suez Canal, as seems to be case of *Hesionura serrata* [114]. Thus far, the two last mechanisms have been reported only from the Mediterranean coast. However, for the remaining NIS it is still unclear how they arrived.

Some cryptogenic species

During the last 20 years, more than 70 species of polychaetes belonging to different biogeographical regions were newly cited in the Iberian Peninsula. Sometimes difficulties were faced when trying to assess their stages in the invasion process and even when trying to determine if new reports were real introductions of NIS. For several new records of polychaete species found in the literature, it was uncertain whether the extension of their biogeographic distribution and their presence in new localities beyond their known distribution limits was caused by a human mediated dispersal or represented a natural range expansion.

A good example of this is *D. marocensis*, whose status as NIS is somewhat controversial. The species was first described from the Atlantic coast of Morroco and was subsequently found in at least two separated locations in Portugal [115, 116] and three estuaries from Northen Spain [117], where it can be found sympatrically with the native *Diopatra neapolitana* Delle Chiaje, 1841. However, *D. marocensis* is absent from the Atlantic coast of SW Spain [116], the closest Iberian estuarine region to the Moroccan coast. The species has also been recently recorded in the Aegean and Levantine coasts of Turkey [118], but is currently unknown to any other location from the Medditerranean. Berke et al. [116] considered the presence of *D. marocensis* in the Iberian Peninsula as the result of a human-mediated introduction, probably through the fishing bait trade, since harvesting and selling *Diopatra* species as a bait is a common resource in Atlantic areas of the Iberian Peninsula [119]. Berke et al. [116] based their statement in the tube brooding of the larvae and the lack of planktonic stages that might facilitate dispersal between locations several hundred kilometers away, rendering all the Iberian populations as virtually isolated as long as only natural means of transport are involved. However, Gil [120] considered these statements mainly speculative and the species was not included in the recently published list of NIS marine species in Portugal [32]. In addition, the populations from the Iberian Peninsula might be relicts from a previous larger population with a wider and more continuous distribution range cannot be excluded. Prospections in suitable locations between the known ones coupled with genetic analyses of representative samples from populations covering the current range of distribution, a powerful tool that helps in unravelling the source and history of human mediated introductions [15, 121], might clarify this issue.

For some cases with a remarkably disjunct distribution and a still poorly known natural geographic distribution, it is difficult to assess whether the species is native or not and therefore they must be considered as cryptogenic, following the definition of the term by Carlton [50]. This may be the case of 15 out of the 17 new records of species belonging to Syllidae reported since 1980 and summarized by San Martín [122], which apart from their type localities are widespread around the Mediterranean basin and Atlantic coast of the Iberian Peninsula. All these records might belong to undescribed crytogenic species that might actually be native of the supposedly colonized habitats. The existence in Syllidae of complexes of sibling species that are morphologically identical and occupy disjunct or extremely wide distribution areas has been demonstrated a number of times by more detailed morphological studies [123] or molecular methods [124]. However, *Erinaceusyllis serratosetosa* and *S. pectinans*, which are known from a few localities of the Iberian Peninsula, seem to be true NIS [24, 62], although no human-mediated pathway has been identified for these species. The family Syllidae is not unique in this respect. Some species, newly reported from the Iberian Peninsula and with disjunct distribution, belonging to Pilargidae, such as *Ancistrosyllis hamata* (Hartman, 1960) and *Sigambra parva* (Day, 1963), and to Capitellidae, such as *Mediomastus capensis* Day, 1961, might fall into this category, provided that cryptic species complexes have been detected within both families [125, 126]. The spionid *Paraprionospio coora* Wilson, 1990, described from eastern Australia, has been considered as cryptogenic in the Mediterranean basin [127] and accordingly we consider the reports from Portugal [120] and the Bay of Biscay [128] in the same way.

Some problems arise when the identity of the species remains unclear. *Harmothoe notochaetosa* López & San Martín, 1996, a member of Polynoidae, was described based on material from the southern Alborán Sea [129]. The authors stated that the taxon was morphologically very similar to the South-African species *H. serrata* Day, 1963, but they considered the anatomical differences enough to erect a new taxon. Subsequently, Barnich and Fiege [130] revised the type material of the two taxa and regarded the observed differences of lesser importance, dismissing the new specific name. Nevertheless, because of the extreme distance between the two known localities and the absence of any introduction pathway, the species is herein treated as cryptogenic, awaiting further analyses that might resolve the uncertainty. Another case of likely misidentification is that of *Namanereis littoralis* (Grube, 1871), a species originally described from Brazil. In the Iberian Peninsula, it has been reported as *Namalycastis brevicornis* from the Tagus estuary [131] and as *N. littoralis* from the Basque Country [132]. However, in his revision of the subfamily Namanereidinae, Glasby [133] realized that specimens collected worldwide and referred to as this species and collected worldwide showed great variation in morphological characters. An informal group was created for all these taxa, but a thorough revision of material from the various locations is much needed to assess the number of species forming it. Taking this into account, the species is herein treated as cryptogenic. *Lysidice collaris* was first reported from the Eastern Mediterranean [134] and was considered a Lessepsian migrant. Some years later it was recorded from Spain [135] and subsequently from a number of Mediterranean countries, being listed as a NIS from Turkey [23], Greece [26], Cyprus [30], and Italy [31]. A comparison of material of the genus with the type series of *L. collaris* [136] proved that specimens from the Eastern Mediterranean actually belonged to the native Mediterranean *L. margaritacea* (Claparède, 1868), whereas those of the Iberian Peninsula actually corresponded to *L. collaris*. Furthermore, an evaluation based on genetic features [137] proved that specimens from Spain and Italy (including Adriatic Sea) were virtually identical, indicating a recent colonization. According to these studies, the species is herein reported as a real NIS for the Iberian Peninsula although it is probably absent from countries of the Eastern Mediterranean, so its Lessepsian introduction is rejected.

Species considered elsewhere as NIS and excluded from the present inventory

In some cases, NIS records result from misidentifications. This is especially frequent for polychaetes [138], resulting in an overestimation of the number of NIS. *Nereis jacksoni* Kinberg, 1866 is a clear example of this. The species, native of the Southern Australia region, was first recorded from the Mediterranean coast of France [139] and later from Spanish coast near Gibraltar Strait [140]. It has also been reported from Turkey [24, 86], where it is considered a Lessepsian migrant. As a result, Zenetos et al. [62] assumed the species as established in both eastern and western extremes of the Mediterranean Sea. However, a thorough revision of material from the Iberian Peninsula [141] pointed out that the specimens from the western Mediterranean Sea were juveniles of the native *Nereis funchalensis* (Langerhans, 1880). The real identity of the specimens from the Levantine Sea is still to be clarified, but for Spain *N. jacksoni* must be excluded from NIS catalogues.

The presence of the South-African hesionid *Podarkeopsis capensis* (Day, 1963) in the European coasts has been questioned. First reported from the British Isles [142], it has been recorded several times from the Spanish Atlantic coast [143, 144] and Portugal [69, 145]. Some years after its first European report, it was cited from Italy [146] and in the subsequent years was reported from several Mediterranean locations, including the Catalonian coast [147]. Zenetos et al. [62] and Çinar et al. [120] catalogued it as NIS, although some authors consider the identification questionable stating that specimens belonging to the native *P. galangaui* Laubier, 1961 were erroneously referred to *P. capensis* [24]. A thorough revision of material from each locality is needed in order to resolve that question. With the same disjunct distribution, *Neanthes agulhana* (Day, 1963) was reported as a single specimen from the area of the Gibraltar Strait [148] and later as an abundant species from the Balearic Islands [149, 150]. More recently it has been reported from Italy [31]. Apart from the type locality and the Mediterranean ones, the species has never been recorded elsewhere, but when comparing the original description [151] with that of Iberian specimens it can be observed that posterior parapodia are represented with distinctly short neuropodial lobes in the latter, while they are longer in South African specimens [141]. It probably indicates the presence of a cryptogenic taxon instead of a true NIS.

In some other cases, misidentifications are due to a lack of knowledge of the actual native fauna. For instance, *Onuphis geophiliformis* (Moore, 1903), a Japanese species, was recorded from SW Spain as early as the 70's [152] and subsequently it was reported as a NIS in the Bay of Biscay [99]. However, a careful examination of material from southern Portugal identical to that described by the former author, demonstrated that it belonged to a new species [120, 153], *Onuphis farensis* Gil & Machado 2014. This might also be the case of *Dispio uncinata* (Hartman, 1951), a species native of the Gulf of Mexico. After its first record from NW Spain [154], it has been cited many times from most of the Spanish demarcations: NOR [155], SUD [156, 157] and LEBA [158], although it has not been cited from Portugal. In addition, it has been recorded as a NIS polychaete in a number of Mediterranean countries [62]. However, a recent revision of the genus states that *D. uncinata*, as currently considered, hides a complex of sibling cryptogenic species; therefore, records from localities different of the type one, including specifically the Iberian Peninsula, should be re-examined [159]. The cirratulid *Kirkegaardia dorsobranchialis* (Kirkegaard, 1959), described from Southern Africa, was first reported from the Spanish Mediterranean coast in 1972 [70]. Subsequently, it has been recorded several times as a NIS from other locations in the Mediterranean basin [81, 160] although, other authors consider it as a native species [24, 96]. A complete revision of the genus including an examination of the type-series of this species [161] suggests that records of *K. dorsobranchialis* out of the type locality are likely to belong to a number of new undescribed taxa.

The case of *Hydroides dianthus* (Verrill, 1873) deserves special attention. It is one of the most documented invasive foulers worldwide and can form dense populations in polluted areas [62], even able to build reef-like aggregations similar to those of *F. enigmaticus*, although within a narrower range of salinity [91]. The species was originally described from Massachusetts and it has been considered native of the eastern coast of North America, from the type locality to Florida and the Caribbean [162]. In Europe, it was reported from Mediterranean localities of France [163], Spain [164], Cyprus [30], Greece [26], and Turkey [24], and from the French Atlantic coast [165] and the British Isles [22]. Due to its fouling abilities, it was listed within the most harmful invasive species in the Mediterranean [77]. Nevertheless, some authors questioned the identity of the Mediterranean specimens and Zenetos et al. [96] treated the species as a questionable alien. In a recent study, Sun et al. [121] studied the genetic structure of a number of populations of the species and concluded that it encompassed several clades and that the Mediterranean one (excluding populations from the Black Sea) was autochthonous, pending the evaluation of the status of the populations inhabiting the Atlantic European coasts. It must be stressed that some catalogues of NIS are very locally focused, narrowing the concept of "native" species. Spain and France are the only European countries having Atlantic and Mediterranean coasts and in some instances species that are native to the Mediterranean Sea have been recorded as NIS in the Atlantic Ocean. For example, *Boccardia semibranchiata* Guérin, 1990, that was described from the Gulf of Lyon, in the Mediterranean coast of France, was reported as a NIS from Arcachon Bay [19] and San Sebastián [166], both in the Bay of Biscay. This is also the case of the catalogues for the Basque Country and Bay of Biscay [87, 99] in which as many as another 10 species (*Arichlidon reyssi* (Katzmann, Laubier & Ramos, 1974), *Dasybranchus gajolae* Eisig, 1887, *Dialychone longiseta*

(Giangrande, 1992), *Microphtahlmus similis* Bobretzky, 1870, *Nereiphyla pusilla* (Claparède, 1870), *Oriopsis eimeri* (Langerhans, 1881), *Paleanotus chrysolepis* Schmarda, 1861, *Paralacydonia paradoxa* Fauvel, 1913, *Sabella spallanzanii* (Gmelin, 1791) and *Syllis westheidei* San Martín, 1984) that are native to the Mediterranean coast of Spain are listed as NIS. However, it is well known that the Bay of Biscay, especially in its inner part, shares many species with the Mediterranean biota [167]. Thus, considering Mediterranean species present in the Bay of Biscay a priori as NIS is incorrect and the term cryptogenic (or just native) is more adequate to describe them. Therefore, the taxa mentioned above should be excluded from NIS inventories in the absence of other evidence. In addition, these regional catalogues mention *Paranaitis speciosa* (Webster, 1879), a phyllodocid, and *Asclerocheilus ashworthi* Blake, 1981, belonging to Scalibregmatidae, without providing an adequate description or voucher specimens. Thus, they are considered as questionable records. Some of the species of syllids herein described as cryptogenic, namely *P. brevicirra*, *P. wolfi*, *S. edentatus,* and *E. belizensis*, appear in these documents. The six aforementioned species have been excluded from our list.

Conclusions

This study is the first exhaustive compilation of new records for Spain of polychaete species that are native from different biogeographical areas and updates the previous compilations made for Portugal. According to the current literature, Spain is the third European country in terms of the number of polychaete NIS, with 21 established and another nine casual ones, whereas Portuguese mainland accounts for five established and five casual species. Considering the Iberian distribution of these species, the Mediterranean coast was the area where more NIS have been found, with 14 established and seven casual species, whereas the figure was slightly lower in the Atlantic coast, numbering 20 NIS (11 established and nine casual). The translocation pathway was unknown for a third of the species, but in those for which a vector has been proposed, shipping was the most frequent way of transport, accounting for 14 introductions of established species and for the presence of another casual one (10 in ballast water and five as a part of the fouling fauna). Other known recorded introduction pathways were aquaculture (three established and two casual species) and bait importation (one established species). Approximately 25% of the reported NIS originated in the the Warm Western Atlantic region and nearly 18 and 12% in Tropical Indo-West Pacific and Warm Eastern Atlantic regions, respectively. However, the situation is different if the two sides of the Iberian Peninsula are compared; the species from warm regions constitute the bulk of the Mediterranean NIS, whereas they are approximately half of the taxa reported from the Atlantic coast. It indicates the existence of clearly distinct biogeographical patterns of colonization. The effects of these introductions in native marine fauna are largely unknown, and the displacement of native species in heavily disturbed environments or at least slight economic damages are suspected. Nevertheless, more severe environmental impacts were recorded in SE Spain for *Ficopomatus enigmaticus*, which causes flow alteration in tidal creeks of brackish marshes.

Abbreviations

NIS: non-indigenous species; PhD: *Philosophiæ doctor*; NOR: North-Atlantic Spanish Demarcation (*Demarcación Marina Noratlántica*); PT: Portuguese mainland coast; SUD: South-Atlantic Spanish Demarcation (*Demarcación Marina Sudatlántica*); ESAL: Gibraltar and Alborán Sea Spanish Demarcation (*Demarcación Marina del Estrecho y Alborán*); LEBA: Levantine and Balearic Spanish Demarcation (*Demarcación Marina Levantino-balear*); cf.: Confer (doubtful species level identification); BOE: Official Bulletin of the State (*Boletín Oficial del Estado*); NW: north-western; SW: south-western; SE: south-eastern; Aq: aquaculture; Bt: bait commerce; BW: ship ballast water; HF: ship hull fouling; Ls: Lessepsian migrant; Uk: unknown; Cr: cryptogenic species; DW: deep-water species; Mi: misidentification; Qu: questionable identification.

Authors' contributions

EL conducted the main literature review on Polychaeta, compiled the data, and led writing of the paper. AR initiated the study, reviewed the general literature on biological invasions, and co-wrote the paper. Both authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Consent for publication

In this study, human participants whose consent for publication was needed were not involved.

Ethics approval and consent to participate

Since neither live animals were used for experimentation nor biological material (be it genetically modified or not) were used for the current study, approval from the "Cómite de Ética en la Investigación" (Ethics Committee for Research) of the Universidad Autónoma de Madrid was not required, as established in the University, regional and national normatives. In no case human participants whose consent to participate was needed were involved.

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