

Alien polychaete species worldwide: current status and their impacts

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This paper reviews the alien polychaete species in the world's oceans and their impacts on the marine ecosystems and humans. A total of 292 polychaete species belonging to 164 genera and 39 families have been transported around the world's oceans with human-mediated assistance. Almost 15% of total number of known polychaete genera and 3.4% of total number of species are included in this phenomenon. A total of 180 species have become established in the world's oceans and 31 species (casual species) have a potential to establish viable populations in a new location. The most speciose genera are Hydroides (16 species) and Polydora (16 species), both accounting for 10% of the total number of alien species. The families Spionidae (53 species) and Serpulidae (46 species) have the highest number of alien species. The Mediterranean Sea (134 species), and the coasts of the Hawaii Islands (47 species) and the USA Pacific (34 species) have been intensively invaded by alien polychaetes. The origins of alien species vary among regions. Alien polychaete species in the Mediterranean Sea mostly originated from the Red Sea and Indo-Pacific areas. Benthic habitats of the areas between 40°N and 40°S were colonized by polychaetes mostly originating from other tropical and subtropical regions. The Suez Canal and shipping are the major vectors for species introductions. Some species imported and exported as fishing baits have become established at non-native localities. The invasive polychaete species have greatly altered habitat structures in some areas, restructured the food webs, and created important economic problems.

Keywords: biological invasions, alien species, invasive species, Polychaeta, worldwide

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INTRODUCTION

The anthropogenic translocation of marine species between disjunct biogeographical regions is one of the most serious and gradually increasing threats to marine ecosystems. This human-mediated process has created significant, unpredictable and irreversible changes to abiotic and biotic environments in a large variety of water bodies worldwide and may cause severe economic damage (Carlton, 1996; Ruiz *et al.*, 1997). When alien species proliferate populations in an area they are capable of re-structuring the food web, introducing new disease agents or parasites, altering habitat structures and changing gene pools (Holland, 2000; Occhipinti Ambrogi, 2001; Schwindt *et al.*, 2001; Occhipinti Ambrogi *et al.*, 2011). Some invasions may trigger a set of changes in the ecosystem such as energy flow between trophic groups, primary production, relative extent of organic material decomposition and benthic–pelagic coupling (Vitousek *et al.*, 1997). Alien species cause a total annual economic loss of \$120 billion in the United States (Pimentel *et al.*, 2005) and \$15 billion in China (Xu *et al.*, 2006). In the US, almost 42% of the threatened or endangered species are at risk due to impacts of alien species (Pimentel *et al.*, 2005). Impacts of alien species are largely exacerbated by on-going climatic change and pollution in the sea (Stachowicz *et al.*, 2002; Çinar *et al.*, 2006). Walther *et al.* (2009) emphasized

that global warming has enabled alien species to expand into regions where previously they could not survive and reproduce.

Three main vectors for species introductions are recognized: building canals (e.g. Suez and Panama), ship transport (hull fouling or ballast water), and deliberate introductions (i.e. mariculture, including associated species with cultured species) (Elton, 1958; Carlton, 1985; Taylor *et al.*, 2001). The number of introduced species has increased since transoceanic shipping crossings have increased in speed and time which is less than the larval stages of most marine invertebrates (Jensen & Knudsen, 2005). Huge volumes of ballast water (~12 billion t annually) are being discharged into or near ports (Netwig, 2007), leading to the establishment of some alien species. Fouling species that are attached to underwater surfaces of ships can become invasive in some areas. Sabellids and serpulid polychaetes are known to travel around the world on ships' hulls. For example, *Ficopomatus enigmaticus*, *Hydroides elegans* and *Sabella spallanzanii* have become a fouling problem as they have the ability to change the prevailing ecosystem drastically (Vitousek *et al.*, 1997; Koçak *et al.*, 1999; Hayes *et al.*, 2005). Except for the areas close to man-made canals, such as the eastern Mediterranean, the main vectors for species introductions were hull fouling (33% of all marine alien species worldwide) and ballast water (27%) (Gollasch, 2007).

Successful settlement of alien species largely depends on the coincidence between delivery of the species to the new location and suitable conditions for establishment, including the absence of predators and the availability of resources (Hayden *et al.*, 2009). Species-poor communities such as

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brackish-water environments and polluted waters are known to be more vulnerable to introductions (Elton, 1958; Koçak *et al.*, 1999; Nehring, 2006). Stachowicz *et al.* (1999) postulated that more diverse communities were less easily invaded as the amount of open space available for invasion decreased. Such spaces (niches) are also available in estuarine and polluted areas. For example, Baltic Sea estuaries are known to serve as stepping stones for the establishment of alien species (Leppäkoski & Olenin, 2000b). Crooks *et al.* (2011) also demonstrated that alien species were less affected by pollutants (e.g. copper) than native species. A seasonal analysis of soft-bottom benthic communities in the eastern Mediterranean showed a positive, significant correlation between the density of *Streblospio gynobranchia*, and ammonium and silicate concentrations (Çinar *et al.*, 2006).

Polychaete species showing a great variety of feeding and reproductive strategies have been introduced from one area to another via ballast water, hull fouling (Carlton, 1985; Godwin, 2003) and canals (Çinar, 2009). Some polychaete species such as *Terebrasabella heterouncinata* and *Polydora uncinata* are known to bore into commercially important bivalve species and were transferred to different regions with their host species (Fitzhugh & Rouse, 1999; Moreno *et al.*, 2006). Polychaetes comprise 33% and 12% of the total number of alien species observed off the coasts of California (Foss *et al.*, 2007) and the Mediterranean Sea (Zenetos *et al.*, 2010), respectively. Alien polychaete species have become a subject of interest regionally: i.e. the Mediterranean Sea (Zenetos *et al.*, 2010); Chile (Moreno *et al.*, 2006); Brazil (Neves & Rocha, 2008); the North Sea (Reise *et al.*, 1999); South Africa (Mead *et al.*, 2011); the Black Sea (Kurt Sahin & Çinar, 2012); and Japan (Iwasaki, 2006). Nishi & Kato (2004) analysed alien polychaete species worldwide and reported 74 species belonging to 15 families. This estimate is below the diversity of alien polychaetes. For example, only in the Mediterranean basins, a total of 134 alien polychaetes have been reported so far (Zenetos *et al.*, 2010).

The aims of this review are to present the worldwide status of marine and brackish-water alien polychaete species, and also to emphasize the importance of these species in the ecosystem and economy.

MATERIALS AND METHODS

A list of alien polychaete species was prepared based on species records updated in January 2012. The species data were mainly extracted from the regional reviews on alien species and check-lists of polychaete species. Alien species are investigated within all regions in terms of their establishment success, their area of origin and their mode of introduction.

Alien species were grouped into 4 main categories, namely established, casual, questionable and cryptogenic. The definition of the terms can be found in Zenetos *et al.* (2010). Briefly, established species are the alien species with self-maintaining populations; casual species are the species which were reported only once in the region; questionable species are the species which were reported without sufficient information and their taxonomic status is uncertain; cryptogenic species are the species with no definite evidence of their native or introduced status according to the categories proposed by Carlton (1996). Invasive species are the

established aliens that have overcome biotic and abiotic barriers and are able to expand their geographical range through the production of fertile offspring with noticeable impact on the invaded habitats.

RESULTS AND DISCUSSION

How many alien polychaete species?

A compilation of the literature revealed that 292 polychaete species belonging to 164 genera were reported as alien species in at least one locality in the world's oceans (Table 1). According to Beesley *et al.* (2000), almost 8348 polychaete species belonging to 1099 genera have been described worldwide. Based on this finding, it was estimated that almost 15% of total number of polychaete genera and 3.4% of total number of species have been reported as alien species throughout the world. The most speciose genera are *Hydroides* (16 species) and *Polydora* (16 species), both accounting for 11% of total number of alien species, followed by *Boccardia* (9 species) and *Syllis* (8 species) (Figure 1). Many genera are represented by a single species.

Thirty-nine polychaete families (almost half of the known families) include alien species. Spionidae ranked highest in terms of number of alien species (53 species, 18% of the total number of species). Other families represented by a high number of alien species worldwide are Serpulidae (46 species, 15% of the total number of species), Nereididae (26 species, 9% of the total number of species) and Sabellidae (23 species, 7% of the total number of species) (Figure 2). Thirteen families had only a single record of an alien species.

The number of alien polychaete species greatly varied according to regions. The highest number of alien species (134 species) were reported from the Mediterranean Sea (Figure 3). This region has been greatly influenced by the influx of lessepsian migrants (i.e. species migration from the Red Sea to the Mediterranean via the Suez Canal) after the opening of the Suez Canal in November 1869, and was relatively well studied in this respect (Ben-Eliahu, 1991; Çinar, 2009). The other regions with high number of alien polychaetes are the coasts of the Hawaii Islands (47 species) and the USA Pacific (34 species). The coasts of Australia (20 species), the Red Sea (20 species), New Zealand (17 species), the North Sea (16 species) and Argentina (16 species) were also affected by dense invasions by polychaete species. In some areas, such as the coasts of Pakistan (*Hydroides elegans*) (Ishaq & Mustaqim, 1996), Singapore (*Hydroides sanctaerucis*) (Lewis *et al.*, 2006) and the Philippines (*Boccardia berkeleyorum*) (Williams, 2001), only a single alien polychaete species has been reported so far. The main difference in the number of alien polychaete species among regions is related to a number of factors. This includes sampling area, scientific effort, resistance of native marine populations to invasion, frequency of inoculation by invading populations, and difficulties in resolving the species-level taxonomy of alien organisms.

Alien polychaetes are grouped into four broad categories namely established, casual, questionable and cryptogenic. Of the total number of alien species (292 species), 211 species were classified as established or casual alien species in a given area. A total of 180 species have become established in

Table 1. The list of alien polychaete species reported from the world's ocean. MI, probable means of introduction (Sh, ship (ballast water or fouling); Su, Suez Canal; D, deliberate stocking; A, aquaculture); Succ, establishment success (E, established; C, casual; Cr, cryptogenic; Q, questionable).

	Possible origin of introduction	Area of introduction	MI	Succ	Reference
POLYNOIDAE					
<i>Harmothoe imbricata</i> (Linnaeus, 1767)	?	USA Atlantic	?Sh	E/Cr	Ruiz <i>et al.</i> (2000)
<i>Lepidonotus carinulatus</i> (Grube, 1870)	Indo-Pacific/Red Sea	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
	Indo-Pacific/Red Sea	Sea of Marmara	?	Q	Çinar (2010)
<i>Lepidonotus tenuisetosus</i> (Gravier, 1902)	Indo-Pacific/Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Paradyte crinoidicola</i> (Potts, 1910)	Indo-Pacific	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
<i>Paralepidonotus ampulliferus</i> (Grube, 1878)	Indo-Pacific	New Zealand	Sh	E	Read (2006)
<i>Subadyte pellucida</i> (Ehlers, 1864)	Mediterranean	Red Sea	Su	E	Por (1978)
ACOETIDAE					
<i>Eupanthalis kinbergi</i> McIntosh, 1876	Atlantic/Mediterranean	India	?Sh	E	Subba Rao (2005)
AMPHINOMIDAE					
<i>Eurythoe complanata</i> (Pallas, 1766)	Atlantic/Pacific	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
<i>Hermodice nigrolineata</i> Baird, 1868	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Linopherus canariensis</i> Langerhans, 1881	Atlantic	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Notopygos crinita</i> Grube, 1855	W Atlantic	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
PARALACYDONIIDAE					
<i>Paralacydonia paradoxa</i> Fauvel, 1913	Mediterranean	Red Sea	Su	E	Por (1978)
PISIONIDAE					
<i>Pisione guanche</i> San Martín, López & Núñez, 1999	E Atlantic	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Pisione oerstedii</i> Grube, 1857	South Africa	India	Sh	E	Subba Rao (2005)
SPINTHERIDAE					
<i>Spinther japonicus</i> Imajima & Hartman, 1964	?Japan	?Hawaii	?	Cr	Carlton & Eldredge (2009)
<i>Spinther miniaceus</i> Grube, 1860	Mediterranean	Red Sea	Su	E	Por (1978)
PHYLLODOCIDAE					
<i>Eumida sanguinea</i> (Örsted, 1843)	?NE Atlantic	Hawaii	?Sh	E	Carlton & Eldredge (2009)
<i>Hesionura serrata</i> (Hartmann-Schroder, 1960)	Red Sea	Mediterranean	Su	C	Zenetos <i>et al.</i> (2010)
<i>Phyllodoce longifrons</i> Ben-Eliahu, 1972	Red Sea	Mediterranean	Suez	E	Ben-Eliahu (1976)
<i>Pterocirrus macroceros</i> (Grube, 1860)	Mediterranean	India	Sh	E	Subba Rao (2005)
HESIONIDAE					
<i>Gyptis arenicola</i> (La Greca, 1946)	Mediterranean	India	Sh	E	Subba Rao (2005)
<i>Hesionides arenaria</i> Friedrich, 1937	?Atlantic	Black Sea	Sh	E	Zaitsev & Öztürk (2001)
<i>Leocrates chinensis</i> Kinberg, 1866	Pacific	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Podarkeopsis capensis</i> (Day, 1963)	Indo-Pacific	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
<i>Microphthalmus similis</i> Bobretzky, 1870	?	North Sea	?	E	Gollasch & Nehring (2006)
PILARGIDAE					
<i>Sigambra constricta</i> (Southern, 1921)	Indo-Pacific/Red Sea	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
	Indo-Pacific/ Red Sea	Sea of Marmara	?	Q	Çinar (2010)
<i>Sigambra parva</i> (Day, 1963)	Indian	Mediterranean	Sh	Q	
<i>Sigambra tentaculata</i> (Treadwell, 1941)	?Atlantic	India	Sh	E	Subba Rao (2005)
<i>Syllidia armata</i> (Quatrefages 1865)	W Atlantic	Argentina	Sh	Cr	Orensanz <i>et al.</i> (2002)
<i>Synelmis rigida</i> (Fauvel, 1919)	Indo-Pacific	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
	Indo-Pacific	Sea of Marmara	Sh	Q	Çinar (2010)
SYLLIDAE					
<i>Amblyosyllis speciosa</i> Izuka, 1912	Japan	USA Pacific	Sh	C	Cohen <i>et al.</i> (2005)
<i>Branchiosyllis exilis</i> (Gravier, 1900)	Indo-Pacific/Red Sea	USA Pacific	Sh	C	Cohen <i>et al.</i> (2005)
	Indo-Pacific/Red Sea	Mexico Pacific	?Sh	Q	Salazar-Vallejo & Londoño-Mesa (2004)
	Indo-Pacific/Red Sea	Panama	?Sh	Q	Salazar-Vallejo & Londoño-Mesa (2004)
<i>Erinaceosyllis serratosetosa</i> (Hartmann-Schröder, 1982)	Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Eusyllis kupfferi</i> Langerhans, 1879	Atlantic	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Exogone africana</i> Hartmann-Schröder, 1974	Indo-Pacific	Mediterranean	Su	C	Zenetos <i>et al.</i> (2010)
<i>Exogone breviantennata</i> Hartmann-Schröder, 1959	?Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Exogone lourei</i> Berkeley & Berkeley, 1938	?	USA Pacific	?Sh	Cr	Wasson <i>et al.</i> (2005)
<i>Myrianida pachycera</i> (Augener, 1913)	W Pacific	USA Pacific	Sh	C	Cohen <i>et al.</i> (2005)
	W Pacific	Hawaii	Sh	E	Carlton & Eldredge (2009)
<i>Paraehlersia weissmaniodes</i> (Augener, 1913)	Indo-Pacific	Mediterranean	Su	C	Zenetos <i>et al.</i> (2010)
<i>Perkinsyllis augeneri</i> (Hartmann-Schröder, 1979)	Indo-Pacific	Mediterranean	Sh	C	Faulwetter <i>et al.</i> (2011)

Continued

Table 1. Continued

	Possible origin of introduction	Area of introduction	MI	Succ	Reference
<i>Prosphaerosyllis longipapillata</i> (Hartmann-Schröder, 1979)	SW Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Streptosyllis varians</i> Webster & Benedict, 1887	W Atlantic	Black Sea	Sh	Q	Gomoiu <i>et al.</i> (2002)
<i>Syllis alosae</i> San Martin, 1992	W Atlantic	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Syllis bella</i> (Chamberlin, 1919)	Pacific	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
<i>Syllis gracilis</i> (Grube 1840)	?Mediterranean	Argentina	?Sh	Cr	Orensanz <i>et al.</i> (2002)
<i>Syllis hyllebergi</i> (Licher, 1999)	Red Sea	Mediterranean	Su	C	Zenetos <i>et al.</i> (2010)
<i>Syllis mayeri</i> Musco & Giangrande, 2005	W Atlantic	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Syllis nipponica</i> (Imajima, 1966)	Japan	USA Pacific	Sh	E	Cohen <i>et al.</i> (2005)
<i>Syllis pectinans</i> Haswell, 1920	Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Syllis schulzi</i> (Hartmann-Schröder, 1962)	Red Sea	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
NEREIDIDAE					
<i>Alitta succinea</i> (Frey & Leuckart, 1847)	?NW Atlantic	USA Pacific	?Sh	E	Nichols & Thompson (1985)
	?NW Atlantic	Hawaii	Sh	E	Carlton & Eldredge (2009)
	?NW Atlantic	Japan	?Sh	E	Imajima (1972)
	?NW Atlantic	Australia	?Sh	E	Hayes <i>et al.</i> (2005)
	?NW Atlantic	Brazil	?Sh	Cr	Neves & Rocha (2008)
	?NW Atlantic	Argentina	?Sh	Cr	Orensanz <i>et al.</i> (2002)
	?NW Atlantic	South Africa	?Sh	E	Mead <i>et al.</i> (2011)
<i>Alitta virens</i> (M. Sars, 1835)	?	North Sea	?Sh	E	Gollasch & Nehring (2006)
	?	Baltic Sea	?Sh	E	Gollasch & Nehring (2006)
<i>Ceratonereis mirabilis</i> Kinberg, 1866	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Hediste diversicolor</i> (O.F. Müller, 1776)	?Black Sea	Caspian Sea	D	E	Grigorovich <i>et al.</i> (2003)
	Sea of Azov	Aral Lake	D	E	Leppäkoski & Olenin (2000a)
<i>Leonnates decipiens</i> Fauvel, 1929	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Leonnates indicus</i> Kinberg, 1966	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Leonnates persicus</i> Wesenberg-Lund, 1949	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Namalycastis abiuma</i> (Grube, 1871)	Indo-Pacific	USA Pacific	Bait	Q	Cohen & Carlton (1995)
	Indo-Pacific	Hawaii	?	Cr	Carlton & Eldredge (2009)
<i>Namalycastis brevicornis</i> (Audouin & M. Edwards, 1833)	Atlantic	Hawaii	Sh	Q	Carlton & Eldredge (2009)
<i>Namalycastis hawaiiensis</i> (Johnson, 1903)	?	Hawaii	?Sh	Cr	Carlton & Eldredge (2009)
<i>Namalycastis senegalensis</i> (Saint-Joseph, 1900)	Atlantic	Hawaii	Sh	Q	Carlton & Eldredge (2009)
<i>Namanereis amboinensis</i> (Plugfelder, 1933)	?	Hawaii	?	Cr	Carlton & Eldredge (2009)
<i>Namanereis littoralis</i> Grube, 1872	?	USA Atlantic	?	E	Ruiz <i>et al.</i> (2000)
	?	Hawaii	?	Cr	Carlton & Eldredge (2009)
<i>Neanthes acuminata</i> Ehlers, 1868	W Atlantic	USA Pacific	Sh	C	Ranasinghe <i>et al.</i> (2005)
<i>Neanthes agulhana</i> (Day, 1963)	South Africa	Mediterranean	?Sh	E	Zenetos <i>et al.</i> (2010)
<i>Neanthes arenaceodentata</i> (Moore, 1903)	W Atlantic	Hawaii	?Sh	E	Carlton & Eldredge (2009)
<i>Neanthes willeyi</i> (Day, 1934)	Indo-Pacific	Mediterranean	Su	C	Zenetos <i>et al.</i> (2010)
<i>Nereis aibuhitensis</i> (Grube, 1878)	?Korea	Japan	Bait	?E	Nishi & Kato (2004)
	Indo-Pacific	Portugal	Bait	E	Fidalgo e Costa <i>et al.</i> (2006)
<i>Nereis gilchristi</i> Day, 1960	Red Sea	Mediterranean	Su	C	Zenetos <i>et al.</i> (2010)
<i>Nereis jacksoni</i> Kinberg, 1866	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Nereis persica</i> Fauvel, 1911	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
	Indo-Pacific	Sea of Marmara	?Sh	Q	Çinar (2010)
<i>Perinereis nuntia</i> (Savigny, 1818)	Indian	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
<i>Platynereis abnormis</i> (Horst, 1924)	Indo-Pacific	Hawaii	Sh	Cr	Carlton & Eldredge (2009)
<i>Platynereis australis</i> (Schmarda, 1861)	Pacific	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Platynereis dumerilii</i> (Audouin & Milne-Edwards, 1834)	?	Brazil	?Sh	Cr	Neves & Rocha (2008)
<i>Pseudonereis anomala</i> (Gravier, 1900)	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
NEPHTYIDAE					
<i>Inermonephtys inermis</i> (Ehlers, 1887)	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Nephtys ciliata</i> (O.F. Müller, 1776)	E Atlantic	Black Sea	Sh	Q	Gomoiu <i>et al.</i> (2002)
<i>Nephtys simoni</i> Perkins, 1980	W Atlantic	USA Pacific	?Sh	C	Ranasinghe <i>et al.</i> (2005)
GLYCERIDAE					
<i>Glycera capitata</i> Örsted, 1843	E Atlantic	Black Sea	Ship	Q	Gomoiu <i>et al.</i> (2002)
GONIADIDAE					
<i>Glycinde bonhourei</i> Gravier, 1904	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Goniadella gracilis</i> (Verrill, 1873)	W Atlantic	Britain	Sh	E	Eno <i>et al.</i> (1997)
EUNICIDAE					

Continued

Table 1. Continued

	Possible origin of introduction	Area of introduction	MI	Succ	Reference
<i>Eunice antennata</i> (Savigny, 1820)	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Eunice cariboea</i> Grube, 1856	W Atlantic	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Eunice floridana</i> (Portuales, 1867)	W Atlantic	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Eunice indica</i> Kinberg, 1865	Indo-Pacific	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
<i>Eunice pennata</i> (O.F. Müller, 1776)	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Eunice torquata</i> Quatrefages, 1866	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Euniphysa tubifex</i> (Crossland, 1904)	Indian Ocean	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
<i>Lysidice collaris</i> Grube, 1870	Pacific/Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Lysidice natalensis</i> (Kinberg, 1865)	Indo-Pacific	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
<i>Lysidice ninetta</i> Audouin & M.-Edwards, 1833	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Marphysa sanguinea</i> (Montagu, 1815)	?	USA Pacific	Sh/A	E	Nichols & Thompson (1985)
	Middle Atlantic	North Sea	A	E	Wijnhoven & Dekker (2010)
<i>Marphysa disjuncta</i> Hartman, 1961	Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Palola valida</i> (Gravier, 1900)	Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
LUMBRINERIDAE					
<i>Lumbrinerides neogaeae</i> Miura, 1980	South Africa	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
<i>Lumbrineris acutifrons</i> (Gallardo, 1967)	Pacific	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Lumbrineris coccinea</i> (Renier, 1804)	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Lumbrineris perkinsi</i> Carrera-Parra, 2001	Indo-Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Lumbrineris sphaerocephala</i> (Schmarda, 1861)	Indo-Pacific	Hawaii	Sh	Cr	Carlton & Eldredge (2009)
<i>Scoletoma debilis</i> (Grube, 1878)	Indo-Pacific	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
	Indo-Pacific	Sea of Marmara	?Sh	Q	Çinar (2010)
DORVILLEIDAE					
<i>Dorvillea similis</i> (Crossland, 1924)	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Protodorvillea egena</i> (Ehlers, 1913)	Indian Ocean/Red Sea	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
<i>Protodorvillea biarticulata</i> Day, 1963	Indian Ocean	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Ophryotrocha adherens</i> Paavo, Bailey-Brock & Åkesson, 2000	?Mediterranean	Hawaii	Sh	E	Carlton & Eldredge (2009)
<i>Ophryotrocha diadema</i> Åkesson, 1976	Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Ophryotrocha japonica</i> Claparède & Mecznirow 1968	Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Ophryotrocha labronica</i> Bacci & La Greca, 1962	Mediterranean	USA Pacific	Sh	E	Carlton (1985)
<i>Schistomeringos rudolphi</i> (Delle Chiaje 1828)	?Mediterranean	Argentina	?Sh	Cr	Orensanz <i>et al.</i> (2002)
OENONIDAE					
<i>Drilonereis monroi</i> Day, 1960	South Africa	India	Sh	E	Subba Rao (2005)
<i>Oenone fulgida</i> (Savigny, 1818)	Indo Pacific/Red Sea	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
	Indo Pacific/Red Sea	Guam	?Sh	E	Bailey-Brock (2003)
ONUPHIDAE					
<i>Epidiopatra hupferiana hupferina</i> Augener, 1918	Tropical Atlantic	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
<i>Epidiopatra hupferiana monroi</i> Day, 1957	Indian Ocean	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
<i>Longibranchium atlanticum</i> (Day, 1973)	Atlantic	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
<i>Onuphis eremita oculata</i> Hartman 1951	W Atlantic	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
ORBINIIDAE					
<i>Naineris quadriceps</i> Day, 1965	Red Sea	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
<i>Naineris setosa</i> (Verrill, 1900)	W Atlantic	Mediterranean	A	E	Blake & Giangrande (2011)
<i>Haploscoloplos kerguelensis</i> McIntosh, 1885	Antarctic	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Scolaricia capensis</i> Day, 1961	South Africa	India	Sh	E	Subba Rao (2005)
SPIONIDAE					
<i>Apoprionospio pygmaea</i> (Hartman, 1955)	Pacific	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
<i>Boccardia berkeleyorum</i> Blake & Woodwick, 1971	E Pacific	Phillipines	A	E	Williams (2001)
<i>Boccardia knoxi</i> (Rainer, 1973)	?	Australia	A	E	Sato-Okoshi <i>et al.</i> (2008)
<i>Boccardia polybranchia</i> (Haswell, 1885)	Indo-Pacific	Argentina	?Sh	Cr	Orensanz <i>et al.</i> (2002)
<i>Boccardia proboscidea</i> Hartman, 1940	Japan	Australia	Sh	E	Polland & Hutchings (1990)
	Japan	New Zealand	Sh	E	Glasby <i>et al.</i> (2009)
	W Atlantic	Hawaii	A	E	Bailey-Brock (2000)
	?Japan	Argentina	Sh	E	Jaubet <i>et al.</i> (2011)
	?Japan	South Africa	A	E	Simon <i>et al.</i> (2010)
	?Japan	Spain Atlantic	A	E	Martinez <i>et al.</i> (2006)
<i>Boccardia pseudonatrix</i> (Day, 1961)	South Africa	New Zealand	?Sh	C	Glasby <i>et al.</i> (2009)
<i>Boccardia redeki</i> (Horst, 1920)	North Sea	Baltic Sea	Sh	E	Leppäkoski & Olenin (2000b)
<i>Boccardia semibranchiata</i> Guerin, 1990	Mediterranean	France Atlantic	A	E	Gouilletquer <i>et al.</i> (2002)
<i>Boccardia tricuspa</i> (Hartman, 1939)	Pacific	Chile	?	E	Moreno <i>et al.</i> (2006)
<i>Boccardiella hamata</i> (Webster, 1879)	W Atlantic	USA Pacific	Sh	C	Foss <i>et al.</i> (2007)

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Table 1. Continued

	Possible origin of introduction	Area of introduction	MI	Succ	Reference
<i>Boccardiella ligerica</i> (Ferrognière, 1898)	Japan	USA Atlantic	Sh	E	Baker <i>et al.</i> (2004)
	E Atlantic	USA Pacific	Sh	E	Ruiz <i>et al.</i> (2000)
	E Atlantic	USA Atlantic	Sh	Cr	Ruiz <i>et al.</i> (2000)
	?	Germany/inland	?Sh	E	Gollasch & Nehring (2006)
<i>Dipolydora armata</i> Langerhans, 1880	E Atlantic	Australia	Sh /A	Cr	Hayes <i>et al.</i> (2005)
	E Atlantic	New Zealand	Sh /A	Cr	Glasby <i>et al.</i> (2009)
<i>Dipolydora flava</i> Claparède, 1870	Mediterranean	Australia	Sh /A	Cr	Hayes <i>et al.</i> (2005)
	Mediterranean	New Zealand	Sh /A	Cr	Glasby <i>et al.</i> (2009)
<i>Dipolydora giardi</i> (Mesnil, 1896)	?E Atlantic	Chile	A	E	Moreno <i>et al.</i> (2006)
	?E Atlantic	New Zealand	?	E	Glasby <i>et al.</i> (2009)
<i>Dipolydora socialis</i> (Schmarda, 1861)	NW Atlantic	Australia	Sh /A	Cr	Hayes <i>et al.</i> (2005)
	NW Atlantic	USA Pacific	Sh	Cr	Boyd <i>et al.</i> (2002)
<i>Dispio magnus</i> (Day, 1955)	Indian Ocean	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Dispio uncinata</i> Hartman, 1951	W Atlantic	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
	W Atlantic	Chile	Sh	E	Castilla <i>et al.</i> (2005)
<i>Laonice norgensis</i> Sikorski, 2003	E Atlantic	Mediterranean	Ship	E	Dagli <i>et al.</i> (2011)
<i>Marenzelleria neglecta</i> Sikorski & Bick, 2004	Atlantic	North Sea	Sh	Q	Nehring (2006)
	W Atlantic	Baltic Sea	Sh	E	Leppäkoski & Olenin (2000b)
	W Atlantic	Norway	Sh	?Cr	Hopkins (2002)
<i>Marenzelleria viridis</i> (Verrill, 1873)	W Atlantic	North Sea	Sh	C	Reise <i>et al.</i> (1999)
	W Atlantic	USA Pacific	Sh	E	Cohen & Carlton (1995)
	W Atlantic	Britain	Sh	E	Eno <i>et al.</i> (1997)
	W Atlantic	Norway	Sh	?Cr	Hopkins, (2002)
	?Pacific	Mediterranean	Sh	Cr	Zenetos <i>et al.</i> (2010)
<i>Paraprionospio coora</i> Wilson, 1990	?Pacific	Sea of Marmara	Sh	Cr	Çinar (2010)
<i>Polydora agassizi</i> Claparede, 1869	Mediterranean	Taiwan	?Sh	Q	Radashevsky & Hsieh (2000a)
<i>Polydora biocipitalis</i> Blake & Woodwick, 1971	?Pacific	Chile	?	E	Moreno <i>et al.</i> (2006)
<i>Polydora ciliata</i> (Johnston, 1838)	E Atlantic	Australia	Sh	E	Polland & Hutchings (1990)
	E Atlantic	Argentina	Sh	Cr	Orensanz <i>et al.</i> (2002)
<i>Polydora colonia</i> Moore 1907	W Atlantic	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
	?	Brazil	Sh	Cr	Neves & Rocha (2008)
<i>Polydora cornuta</i> Bosc, 1802	?NW Atlantic	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	?NW Atlantic	USA Pacific	Sh	E	Nichols & Thompson (1985)
	?NW Atlantic	Australia	Sh	E	Hayes <i>et al.</i> (2005)
	?NW Atlantic	New Zealand	Sh	E	Glasby <i>et al.</i> (2009)
	?NW Atlantic	Sea of Marmara	Sh	E	Çinar (2010)
	?NW Atlantic	Black Sea	Sh	E	Boltachova & Lisitskaya (2007)
	?NW Atlantic	Brazil	Sh	E	Neves & Rocha (2008)
	?NW Atlantic	Argentina	Sh	E	Orensanz <i>et al.</i> (2002)
	?NW Atlantic	Taiwan	Sh	E	Paxton & Chou (2000)
	?	Mexico Atlantic	Sh	E	Perkins & Savage 1975
	?NW Atlantic	Mexico Pacific	Sh	E	Salazar-Vallejo & Londoño-Mesa (2004)
	?NW Atlantic	Costa Rica Pacific	Sh	E	Salazar-Vallejo & Londoño-Mesa (2004)
	?NW Atlantic	China	Sh	E	Radashevsky & Hsieh (2000a)
	?NW Atlantic	Portugal	Sh	E	Carvalho <i>et al.</i> (2011)
<i>Polydora ecuadoriana</i> Blake, 1983	?Ecuador	Brazil	A	E	Radashevsky <i>et al.</i> (2006)
<i>Polydora flava</i> (Claparède 1870)	?E Atlantic	Argentina	?Sh	Cr	Orensanz <i>et al.</i> (2002)
<i>Polydora haswelli</i> Blake & Kudenov, 1978	Australia	Brazil	A	Q	Radashevsky <i>et al.</i> (2006)
	?	New Zealand	A	Cr	Read (2010)
<i>Polydora hoplura</i> Claparède, 1869	?Mediterranean	New Zealand	?A	E	Handley (2000)
	?Mediterranean	North Sea	?A	E	Kerckhof <i>et al.</i> (2007)
	?Mediterranean	South Africa	?A	E	Mead <i>et al.</i> (2011)
<i>Polydora limicola</i> Annenkova, 1934	?Barents Sea	Russia Pacific	Sh	E	Zvyagintsev (2002)
<i>Polydora nuchalis</i> Woodwick, 1953	E Pacific	Hawaii	A	E	Bailey-Brock (1990)
<i>Polydora rickettsi</i> Woodwick, 1961	E Pacific	Chile	A	E	Moreno <i>et al.</i> (2006)
	E Pacific	Brazil	A	Q	Radashevsky <i>et al.</i> (2006)
<i>Polydora socialis</i> (Schmarda 1861)	Pacific	Argentina	?Sh	Cr	Orensanz <i>et al.</i> (2002)
<i>Polydora spongicola</i> Berkeley & Berkeley, 1950	Pacific	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Polydora uncinata</i> Sato-Okoshi, 1998	Japan	Chile	A	E	Moreno <i>et al.</i> (2006)
	Japan	Australia	A	E	Sato-Okoshi <i>et al.</i> (2008)
<i>Polydora websteri</i> Hartman, 1943	USA Pacific	Hawaii	A	E	Bailey-Brock & Ringwood (1982)

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Table 1. Continued

	Possible origin of introduction	Area of introduction	MI	Succ	Reference
	USA Pacific	Australia	A	E	Hayes <i>et al.</i> (2005)
	USA Pacific	New Zealand	A	E	Handley (2000)
<i>Prionospio krusadensis</i> Fauvel 1929	Indo-Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Prionospio sexoculata</i> Augener, 1918	Atlantic/Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Prionospio depauperata</i> Imajima, 1990	NE Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Prionospio saccifera</i> Mackie & Hartley, 1990	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Prionospio paucipinnulata</i> Blake & Kudenov, 1978	Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Prionospio ehlersi</i> Fauvel, 1928	?Atlantic	New Zealand	Sh	E	Glasby <i>et al.</i> (2009)
<i>Prionospio pulchra</i> Imajima, 1990	Atlantic/Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	Atlantic/Pacific	Black Sea	Sh	E	Dagli & Çinar, (2011)
	Atlantic/Pacific	Sea of Marmara	Sh	E	Çinar <i>et al.</i> (2011)
<i>Pseudopolydora kempfi</i> (Southern, 1921)	Japan	USA Pacific	Sh	E	Nichols & Thompson (1985)
<i>Pseudopolydora paucibranchiata</i> Okuda 1937	Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	Pacific	Sea of Marmara	Sh	E	Çinar <i>et al.</i> (2011)
	Japan	Australia	Sh	E	Polland & Hutchings (1990)
	Japan	USA Pacific	Sh/A	E	Cohen & Carlton (1995)
	Pacific	Taiwan	Sh	E	Radashevsky & Hsieh (2000b)
<i>Pygospio elegans</i> Claparède, 1863	E Atlantic	USA Atlantic	?Sh	Cr	Ruiz <i>et al.</i> (2000)
	E Atlantic	USA Pacific	?Sh	Cr	Boyd <i>et al.</i> (2002)
<i>Scolecopsis bonnieri</i> (Mesnil, 1896)	?	Norway	Sh	Q	Hopkins (2002)
<i>Spiophanes algidus</i> Meißner, 2005	Indian	Mediterranean	Ship	E	Dagli <i>et al.</i> (2011)
<i>Spiophanes 'bombyx'</i> (Claparède, 1870)	?	USA Atlantic	?Sh	Cr	Ruiz <i>et al.</i> (2000)
	?	Chile	?Sh	E	Castilla <i>et al.</i> (2005)
	?	USA Pacific	?Sh	E	Boyd <i>et al.</i> (2002)
<i>Streblospio benedicti</i> Webster, 1879	NE Atlantic	USA Pacific	Sh	E	Nichols & Thompson (1985)
	NE Atlantic	Hawaii	Sh	E	Carlton & Eldredge (2009)
	NE Atlantic	France Atlantic	Sh	E	Gouilletquer <i>et al.</i> (2002)
<i>Streblospio gynobranchiata</i> Rice & Levin, 1998	W Atlantic	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	W Atlantic	Sea of Marmara	Sh	E	Çinar (2010)
	W Atlantic	Black Sea	Sh	E	Boltachova (2008)
	Mediterranean	Caspian Sea	Sh	E	Taheri <i>et al.</i> (2009)
HETEROSPIONIDAE					
<i>Heterospio longissima</i> Ehlers, 1874	NW Atlantic	India	Sh	E	Subba Rao (2005)
SCALIBREGMIDAE					
<i>Hyboscolex longiseta</i> Schmarda, 1861	?Pacific	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
FLABELLIGERIDAE					
<i>Pherusa parmata</i> (Grube, 1878)	Indo-Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Stylarioides grubei</i> Salazar-Vallejo, 2011	Red Sea	Mediterranean	Su	E	Salazar-Vallejo (2011)
CHAETOPTERIDAE					
<i>Chaetopterus</i> sp.	?	Hawaii	Sh	E	Carlton & Eldredge (2009)
POECILOCHAETIDAE					
<i>Poecilochaetus serpens</i> Allen, 1904	Mediterranean	Red Sea	Su	E	Por (1978)
OPHELIIDAE					
<i>Armandia intermedia</i> Fauvel, 1902	?Atlantic	Hawaii	Sh	Cr	Carlton & Eldredge (2009)
CAPITELLIDAE					
<i>Capitellethus dispar</i> (Ehlers, 1907)	Indo-Pacific/Red Sea	Mediterranean	?Su	Q	Zenetos <i>et al.</i> (2010)
	Indo-Pacific/Red Sea	Sea of Marmara	?Sh	Q	Çinar (2010)
	Indo-Pacific/Red Sea	Black Sea	?Sh	Q	Gomoiu <i>et al.</i> (2002)
<i>Dasybranchus carneus</i> Grube, 1870	Red Sea	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
	Red Sea	Sea of Marmara	?Sh	Q	Çinar (2010)
<i>Heteromastus filiformis</i> (Claparède, 1864)	?Mediterranean	USA Pacific	Sh	E	Nichols & Thompson (1985)
<i>Leiochrides australis</i> Augener, 1914	Pacific	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
<i>Mediomastus californiensis</i> Hartman, 1944	USA Pacific	USA Atlantic	Sh	Cr	Baker <i>et al.</i> (2004)
<i>Mediomastus capensis</i> Day, 1961	Indian Ocean	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Neopseudocapitella brasiliensis</i> Rullier & Amoureux, 1979	W Atlantic/Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Notomastus aberans</i> Day, 1957	Indian/Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Notomastus mossambicus</i> (Thomassin, 1970)	Indian	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Notomastus profundus</i> (Eisig, 1887)	Mediterranean	Red Sea	Su	E	Por (1978)
CIRRATULIDAE					
<i>Aphelochaeta marioni</i> (Saint-Joseph, 1894)	?	North Sea	?	E	Gollasch & Nehring (2006)
<i>Caulleriella killariensis</i> (Southern, 1914)	?	North Sea	?A	?E	Gollasch & Nehring (2006)

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Table 1. Continued

	Possible origin of introduction	Area of introduction	MI	Succ	Reference
<i>Chaetozone corona</i> Berkeley & Berkeley, 1941	W Atlantic	Mediterranean	Ship	Cr	Zenetos <i>et al.</i> (2010)
	W Atlantic	Sea of Marmara	Ship	Cr	Çinar <i>et al.</i> (2011)
<i>Cirriiformia semicineta</i> (Ehlers, 1905)	Red Sea	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
<i>Dodecaceria capensis</i> Day, 1961	Indian	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
<i>Dodecaceria fewkesi</i> Berkeley & Berkeley, 1954	E Pacific	South Africa	Ship	E	Mead <i>et al.</i> (2011)
<i>Timarete anchylochaeta</i> (Schmarda, 1861)	Pacific	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
	Pacific	Sea of Marmara	?Sh	Q	Çinar (2010)
<i>Timarete caribous</i> (Grube, 1859)	W Atlantic	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	W Atlantic	Guam	Sh	E	Bailey-Brock (2003)
<i>Timarete dasylophius</i> (Marenzeller, 1879)	Indo Pacific	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
	Indo Pacific	Sea of Marmara	?Sh	Q	Çinar (2010)
<i>Timarete punctata</i> (Grube, 1859)	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
CTENODRILIDAE					
<i>Ctenodrilus serratus</i> (Schmidt, 1857)	?Atlantic	USA Pacific	Sh	Cr	Wasson <i>et al.</i> (2005)
MALDANIDAE					
<i>Clymenella torquata</i> (Leidy, 1855)	W Atlantic	North Sea	A	C	Reise <i>et al.</i> (1999)
	W Atlantic	Ireland	A	E	Minchin (2007)
	W Atlantic	Britain	A	E	Eno <i>et al.</i> (1997)
<i>Euclymene collaris</i> (Claparède, 1869)	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Euclymene lumbricoides</i> (Quatrefages, 1865)	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Metasychis gotoi</i> (Izuka, 1902)	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
	Indo-Pacific	Sea of Marmara	Su	E	Çinar <i>et al.</i> (2011)
<i>Petaloproctus terricolus</i> Quatrefages, 1866	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Sabaco elongatus</i> (Verrill, 1873)	W Atlantic	USA Pacific	Sh	E	Ruiz <i>et al.</i> (2000)
COSSURIDAE					
<i>Cossura coasta</i> Kitamori, 1960	Pacific	Mediterranean	Sh	Q	Zenetos <i>et al.</i> (2010)
SABELLARIIDAE					
<i>Sabellaria nanella</i> Chamberlin 1919	?USA Pacific	?Brazil	Sh	Cr	Kirtley (1994)
STERNASPIDAE					
<i>Sternaspis scutata</i> Ranzani, 1817	?Mediterranean	Britain	?Sh	E	Shelley <i>et al.</i> (2008)
AMPHARETIDAE					
<i>Alkmaria romijni</i> Horst, 1919	?	North Sea	Sh	Cr	Streftaris <i>et al.</i> (2005)
	?	Norway	?	?Cr	Hopkins (2002)
<i>Hobsonia florida</i> (Hartman, 1951)	Atlantic	USA Pacific	?A	E	Wonham & Carlton (2005)
<i>Hypania invalida</i> (Grube, 1860)	Black Sea/Caspian	European rivers	Canals	E	Van Der Velde <i>et al.</i> (2002)
<i>Isolda pulchella</i> Muller 1858	W Atlantic	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
TEREBELLIDAE					
<i>Lanicola carus</i> (Young & Kritzler, 1987)	Caribbean	Panama Pacific	Sh	E	Londoño-Mesa (2009)
<i>Loimia medusa</i> (Savigny, 1818)	Red Sea	Mediterranean	?Su	Q	Zenetos <i>et al.</i> (2010)
<i>Pista cristata</i> (Müller, 1776)	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Pista unibranchia</i> Day, 1963	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Polycirrus twisti</i> Potts, 1928	Suez Canal	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Streblosoma comatus</i> (Grube, 1856)	Indo-Pacific	Mediterranean	?Su	E	Zenetos <i>et al.</i> (2010)
<i>Terebella ehrenbergi</i> Grube, 1870	Red Sea	Mediterranean	Su	Q	Zenetos <i>et al.</i> (2010)
<i>Terebella lapidaria</i> (Linnaeus, 1767)	Europe	Ireland	A	Q	Minchin (2007)
	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Thelepus setosus</i> (Quatrefages, 1865)	?Atlantic	Guam	Sh	E	Bailey-Brock (2003)
SABELLIDAE					
<i>Amphicorina pectinata</i> (Banse, 1957)	Pacific	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
<i>Branchiomma bairdi</i> (McIntosh, 1885)	Atlantic/Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	W Atlantic	Mexico Pacific	Sh	E	Tovar-Hernández <i>et al.</i> (2009)
<i>Branchiomma bohollensis</i> (Grube, 1878)	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Branchiomma curtum</i> (Ehlers, 1901)	E Pacific	Mexico Atlantic	Sh	E	Tovar-Hernández & Knight-Jones (2006)
	E Pacific	New Zealand	Sh	E	Tovar-Hernández & Knight-Jones (2006)
<i>Branchiomma lucullanum</i> (Delle Chiaje, 1828)	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Branchiomma luctuosum</i> (Grube, 1869)	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Branchiomma japonica</i> (McIntosh, 1883)	Pacific	Hawaii	Sh	E	Carlton & Eldredge (2009)
<i>Desdemonia ornata</i> Banse, 1957	Indo-Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	Indo-Pacific	Sea of Marmara	Sh	E	Çinar (2010)
	Indo-Pacific	Britain	Sh	E	Smith <i>et al.</i> (1999)
	Indo-Pacific	Portugal	Sh	E	Carvalho <i>et al.</i> (2011)

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Table 1. Continued

	Possible origin of introduction	Area of introduction	MI	Succ	Reference
<i>Euchone limnicola</i> Reish, 1959	?E Pacific	Australia	?Sh	E	Hewitt <i>et al.</i> (2004)
<i>Fabricia sabella</i> (Ehrenberg, 1836)	Atlantic	USA Pacific	Sh	E	Foss <i>et al.</i> (2007)
<i>Fabriciola qhardaqa</i> Banse 1959	Red Sea	Mediterranean	Su	C	Zenetos <i>et al.</i> (2010)
<i>Hypsicomus stichophthalmos</i> (Grube, 1863)	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Laonome elegans</i> Gravier, 1906	Red Sea	Mediterranean	Su	C	Zenetos <i>et al.</i> (2010)
<i>Laonome triangularis</i> Hutchings & Murray, 1984	SW Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Manayunkia speciosa</i> Leidy, 1858	?USA Atlantic	USA Pacific	?Sh	?E	Ruiz <i>et al.</i> (2000)
	USA Atlantic	Argentina	Sh	E	Armendáriz <i>et al.</i> (2011)
<i>Megalomma claparedei</i> Gravier, 1908	Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Myxicola infundibulum</i> (Renier, 1804)	Mediterranean	Australia	Sh	E	Hewitt <i>et al.</i> (2004)
	?Mediterranean	USA Pacific	Sh	E	Boyd <i>et al.</i> (2002)
<i>Novafabricia infratorquata</i> Fitzhugh, 1983	W Atlantic	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Parasabella leucaspis</i> (Kinberg, 1867)	?Peru	Australia	?Sh	E	Ruiz <i>et al.</i> (2000)
<i>Pseudopotamilla ocellata</i> Moore, 1905	NE Pacific	Russia Pacific	Sh	E	Zvyagintsev (2002)
<i>Sabella spallanzanii</i> (Gmelin, 1791)	Mediterranean	Australia	Sh	E	Currie <i>et al.</i> (2000)
	Mediterranean	Azores	Sh	E	Cardigos <i>et al.</i> (2006)
<i>Sabellastarte spectabilis</i> (Grube, 1878)	Red Sea/Indo-Pacific	Hawaii	Sh	E	DeFelice <i>et al.</i> (2001)
	Red Sea/Indo-Pacific	Guam	Sh	E	Bailey-Brock (2003)
<i>Terebrasabella heterouncinata</i> Fitzhugh & Rouse 1999	South Africa	USA Pacific	A	C	Fitzhugh & Rouse (1999)
	South Africa	Chile	A	E	Moreno <i>et al.</i> (2006)
SERPULIDAE					
<i>Circeis armoricana</i> Saint-Joseph, 1894	E Atlantic	Hawaii	Sh	C	Godwin <i>et al.</i> 2004
	?Atlantic	USA Pacific	Sh	Cr	Wasson <i>et al.</i> (2005)
<i>Eulaeospira orientalis</i> Pillai, 1960	Indo-Pacific	Hawaii	Sh	Cr	Godwin <i>et al.</i> 2004
<i>Ficopomatus enigmaticus</i> (Fauvel, 1923)	Australia	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	Australia	USA Atlantic	Sh	E	Ruiz <i>et al.</i> (2000)
	Australia	USA Pacific	Sh	E	Cohen <i>et al.</i> (2005)
	Australia	Argentina	Sh	E	Schwindt <i>et al.</i> (2001)
	Australia	Hawaii	Sh	E	Carlton & Eldredge (2009)
	Australia	Baltic Sea	Sh	E	Leppäkoski & Olenin (2000b)
	Australia	Japan	Sh	E	Nishi & Kato (2004)
	Australia	North Sea	Sh	E	Wolff (1999)
	Black Sea	Caspian Sea	Sh	E	Grigorovich <i>et al.</i> (2003)
	Australia	Ireland	Sh	E	Minchin (2007)
	Australia	Britain	Sh	E	Eno <i>et al.</i> 1997
	Australia	France Atlantic	Sh	E	Gouletquer <i>et al.</i> (2002)
	Australia	Sea of Marmara	Sh	E	Çinar (2010)
	Australia	Black Sea	Sh	E	Zaitsev & Mamaev (1997)
	Australia	Panama	Sh	E	Salazar-Vallejo (1996)
	Australia	India	Sh	E	Subba Rao (2005)
	Australia	South Africa	Sh	E	Day (1967)
	Australia	Nigeria	Sh	E	Hill (1967)
	Australia	Spain Atlantic	Sh	E	Campoy (1982)
<i>Ficopomatus miamiensis</i> (Treadwell, 1934)	W Atlantic	Panama	?Sh	E	Bastida-Zavala (2008)
	W Atlantic	Mexico Pacific	?Sh	E	Bastida-Zavala (2008)
<i>Ficopomatus uschakovi</i> (Pillai, 1960)	W Pacific	Brazil	Sh	E	Assis <i>et al.</i> (2008)
	W Pacific	USA Pacific	Sh	E	Assis <i>et al.</i> (2008)
<i>Hydroides alatalateralis</i> (Jones, 1962)	W Atlantic	Colombia Pacific	Sh	E	Bastida-Zavala & ten Hove (2003)
<i>Hydroides albiceps</i> Grube, 1870	Red Sea	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
	Red Sea	New Zealand	Sh	C	Piola & Conwell (2010)
<i>Hydroides branchyacanthus</i> Rioja, 1941	Indo-Pacific	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
	Indo-Pacific	Hawaii	Sh	E	Carlton & Eldredge (2009)
<i>Hydroides crucigera</i> (Mörch, 1863)	?Atlantic	Hawaii	Sh	E	Godwin <i>et al.</i> 2004
<i>Hydroides dianthus</i> (Verrill, 1873)	NW Atlantic	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	NW Atlantic	North Sea	Sh /A	E	Simon <i>et al.</i> (2010)
	NW Atlantic	France Atlantic	Sh /A	E	Gouletquer <i>et al.</i> (2002)
	NW Atlantic	Britain	Sh /A	E	Eno <i>et al.</i> 1997
	NW Atlantic	Argentina	Sh	E	Orensanz <i>et al.</i> (2002)
	NW Atlantic	Mexico Pacific	Sh	Q	Salazar-Vallejo & Londoño-Mesa 2004
	NW Atlantic	Japan	Sh	E	Link <i>et al.</i> (2009)
	NW Atlantic	Nigeria	Sh	E	Hill (1967)

Continued

Table 1. Continued

	Possible origin of introduction	Area of introduction	MI	Succ	Reference
<i>Hydroides diramphus</i> Mörch, 1863	NW Atlantic	Spain Atlantic	Sh	E	Campoy (1982)
	W Tropical Atlantic	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	W Tropical Atlantic	Hawaii	Sh	E	Carlton & Eldredge (2009)
	W Tropical Atlantic	USA Pacific	Sh	E	Cohen <i>et al.</i> (2005)
	W Tropical Atlantic	Sea of Marmara	Sh	E	Çinar (2010)
	W Tropical Atlantic	USA Atlantic	Sh	E	Power <i>et al.</i> (2006)
	W Tropical Atlantic	Colombia Atlantic	Sh	E	Salazar-Vallejo (1996)
	W Tropical Atlantic	China	Sh	E	Paxton & Chou (2000)
	W Tropical Atlantic	Mexico Pacific	Sh	E	Salazar-Vallejo & Londoño-Mesa (2004)
	W Tropical Atlantic	Brazil	Sh	E	Bastida-Zavala (2008)
	W Tropical Atlantic	Mexico Atlantic	Sh	E	Bastida-Zavala (2008)
	W Tropical Atlantic	South Africa	Sh	E	Bastida-Zavala (2008)
	W Tropical Atlantic	New Zealand	Sh	E	Bastida-Zavala (2008)
	W Tropical Atlantic	Venezuela	Sh	E	Bastida-Zavala (2008)
<i>Hydroides elegans</i> (Haswell, 1883)	W Tropical Atlantic	Australia	Sh	E	Hewitt (2002)
	W Tropical Atlantic	Red Sea	Sh	E	Wehe & Fiege (2002)
	W Tropical Atlantic	Spain Atlantic	Sh	E	Campoy (1982)
	Indo-Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	Indo-Pacific	USA Pacific	Sh	E	Cohen <i>et al.</i> (2005)
	Indo-Pacific	USA Atlantic	Sh	E	Baker <i>et al.</i> (2004)
	Indo-Pacific	Hawaii	Sh	E	Carlton & Eldredge (2009)
	Indo-Pacific	Britain	Sh	E	Zibrowius & Thorp (1989)
	Indo-Pacific	Australia	Sh	Cr	Hewitt (2002)
	Indo-Pacific	North Sea	Sh	E	Simon <i>et al.</i> (2010)
	Indo-Pacific	Japan	Sh	E	Nishi & Kato (2004)
	Indo-Pacific	Argentina	Sh	E	Orensanz <i>et al.</i> (2002)
	Indo-Pacific	China	Sh	E	Paxton & Chou (2000)
	Indo-Pacific	Mexico Atlantic	Sh	E	Perkins & Savage (1975)
<i>Hydroides ezoensis</i> Okuda, 1934	Indo-Pacific	Canary Islands	Sh	E	Brito <i>et al.</i> (2005)
	Indo-Pacific	Brazil	Sh	E	Bastida-Zavala (2008)
	Indo-Pacific	South Africa	Sh	E	Bastida-Zavala (2008)
	Indo-Pacific	Mexico Pacific	Sh	E	Bastida-Zavala (2008)
	Indo-Pacific	Venezuela	Sh	E	Díaz & Liñero-Arana (2001)
	Indo-Pacific	Pakistan	Sh	E	Ishaq & Mustaqim (1996)
	Indo-Pacific	Russia Pacific	Sh	E	Zvyagintsev (2002)
	Indo-Pacific	Azores	Sh	E	Cardigos <i>et al.</i> (2006)
	Indo-Pacific	Red Sea	Sh	E	Wehe & Fiege (2002)
	Indo-Pacific	New Zealand	Sh	E	Piola & Conwell (2010)
	Indo-Pacific	Spain Atlantic	Sh	E	Campoy (1982)
	N Pacific	North Sea	Sh / A	C	Simon <i>et al.</i> (2010)
	N Pacific	Australia	Sh	E	Hewitt (2002)
	N Pacific	Britain	Sh / A	E	Eno <i>et al.</i> (1997)
<i>Hydroides gairacensis</i> Augener, 1934	N Pacific	France Atlantic	A	E	Wolff & Reise (2002)
	W Atlantic	Panama Pacific	Sh	E	Bastida-Zavala & ten Hove (2003)
<i>Hydroides heterocerus</i> (Grube, 1868)	Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Hydroides homocerus</i> Pixell, 1913	Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Hydroides minax</i> Grube, 1878)	Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Hydroides norvegicus</i> Gunnerus, 1768	?Mediterranean	Australia	Sh	E	Polland & Hutchings (1990)
<i>Hydroides operculatus</i> (Treadwell, 1929)	Indian Ocean	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
<i>Hydroides sanctaerucis</i> Krøyer in Mörch, 1863	W Atlantic	Australia	Sh	E	Lewis <i>et al.</i> (2006)
	W Atlantic	Mexico Pacific	Sh	E	Bastida-Zavala (2008)
	W Atlantic	Panama Pacific	Sh	E	Bastida-Zavala (2008)
	W Atlantic	Singapore	Sh	E	Lewis <i>et al.</i> (2006)
	W Atlantic	Hawaii	Sh	C	Carlton & Eldredge (2009)
<i>Hydroides steinitzi</i> Ben-Eliahu, 1972	Red Sea	Mediterranean	Sh	C	Zenetos <i>et al.</i> (2010)
<i>Janua (Dexiospira) pagenstecheri</i> (Quatrefages, 1865)	?E Atlantic	Hawaii	?Sh	E	Carlton & Eldredge (2009)
	?E Atlantic	South Africa	Sh	E	Mead <i>et al.</i> (2011)
	?E Atlantic	Galapagos	Sh	E	Carlton (2009)
<i>Leodora knightjonesi</i> (de Silva, 1965)	Indo-Pacific	Hawaii	Sh	Cr	Carlton & Eldredge (2009)
<i>Neodexiospira brasiliensis</i> (Grube, 1872)	W Atlantic	North Sea	Sh	C	Simon <i>et al.</i> (2010)
	Japan	Britain	A	C	Knight-Jones <i>et al.</i> (1975)

Continued

Table 1. Continued

	Possible origin of introduction	Area of introduction	MI	Succ	Reference
<i>Neodexiospira foraminosa</i> Moore & Bush, 1904	Pacific	South Africa	Sh	E	Mead <i>et al.</i> (2011)
<i>Neodexiospira mannarensis</i> Pillai, 1970	Japan	Hawaii	Sh	Cr	Godwin <i>et al.</i> (2004)
<i>Neodexiospira nipponica</i> (Okuda, 1934)	Indo Pacific	Argentina	Sh	Cr	Orensanz <i>et al.</i> (2002)
<i>Neodexiospira preacuta</i> Vine, 1972	Japan	Hawaii	Sh	Cr	Carlton & Eldredge (2009)
<i>Neodexiospira pseudocorrugata</i> (Bush, 1905)	?Red Sea	Hawaii	Sh	Cr	Godwin <i>et al.</i> (2004)
<i>Neodexiospira steueri</i> (Sterzinger, 1909)	Europe	Hawaii	Sh	Cr	Carlton & Eldredge (2009)
<i>Paralaeospira maldardi</i> (Caullery & Mesnil, 1897)	Indo-Pacific	Mediterranean	Su	C	Zenetos <i>et al.</i> (2010)
	Southern Seas	Britain	Sh	E	Knight-Jones & Knight-Jones (1977)
	Southern Seas	France Atlantic	Sh	E	Knight-Jones & Knight-Jones (1977)
<i>Pileolaria berkeleyana</i> (Rioja, 1942)	E Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	Pacific	North Sea	Sh	E	Simon <i>et al.</i> (2010)
	Pacific	Britain	Sh/A	E	Eno <i>et al.</i> (1997)
	Pacific	Canary Islands	Sh	E	Knight-Jones & Knight-Jones (1980)
<i>Pileolaria militaris</i> Claparède, 1868	Atlantic	Hawaii	Sh	E	Godwin <i>et al.</i> (2004)
<i>Pileolaria pseudoclavus</i> Vine, 1972	Red Sea	Hawaii	Sh	Cr	Carlton & Eldredge (2009)
<i>Placostegus tridentatus</i> (Fabricius, 1779)	Mediterranean	Red Sea	Su	E	Por (1978)
<i>Pomatoscerus minutus</i> Rioja, 1941	Pacific	Hawaii	?Sh	Q	Godwin <i>et al.</i> (2004)
<i>Pomatoscerus triqueter</i> (Linnaeus, 1758)	Mediterranean	Red Sea	Su	E	Por (1978)
	Atlantic	Guam	Sh	E	Bailey-Brock (2003)
<i>Salmacina tribranchiata</i> (Moore, 1923)	E Pacific	Hawaii	Sh	E	Godwin <i>et al.</i> (2004)
<i>Serpula vermicularis</i> Linnaeus, 1767	?Atlantic	Hawaii	?Sh	Cr/Q	Godwin <i>et al.</i> (2004)
<i>Serpula watsoni</i> Willey, 1905	Indo-Pacific	Hawaii	?Sh	E	Godwin <i>et al.</i> (2004)
<i>Simplaria pseudomilitaris</i> (Thiriot-Quievreux, 1965)	?E Atlantic	Hawaii	Sh	Cr	Godwin <i>et al.</i> (2004)
	?E Atlantic	Argentina	Sh	Cr	Orensanz <i>et al.</i> (2002)
	?E Atlantic	South Africa	Sh	Cr	Mead <i>et al.</i> (2011)
	?E Atlantic	Galapagos	Sh	Cr	Carlton (2009)
<i>Spirobranchus kraussii</i> (Baird, 1865)	Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
	Indo-Pacific	Hawaii	?Sh	E	Carlton & Eldredge (2009)
<i>Spirobranchus polytrema</i> (Philippi, 1844)	?Mediterranean	New Zealand	?Sh	E	Glasby <i>et al.</i> (2009)
<i>Spirobranchus tetracerus</i> (Schmarda, 1861)	Indo-Pacific/Red Sea	Mediterranean	Su	E	Zenetos <i>et al.</i> (2010)
<i>Spirorbis marioni</i> Caullery & Mesnil, 1897	Atlantic/Pacific	Mediterranean	Sh	E	Zenetos <i>et al.</i> (2010)
	Atlantic/Pacific	Canary Islands	Sh	E	Knight-Jones & Knight-Jones (1980)
	Atlantic/Pacific	Hawaii	Sh	Cr	Carlton & Eldredge (2009)
<i>Vinaria koehlerii</i> (Caullery & Mesnil, 1897)	E Pacific	Azores	Sh	E	Cardigos <i>et al.</i> (2006)
	?Pacific	Hawaii	Sh	Cr	Carlton & Eldredge (2009)
NERILLIDAE					
<i>Mesonerilla fagei</i> Swedmark, 1959	NE Atlantic	Hawaii	Sh	C	Carlton & Eldredge (2009)

W Atlantic, western Atlantic; E Atlantic, eastern Atlantic; NE Atlantic, north-eastern Atlantic; W Pacific, western Pacific; SW Pacific, south-western Pacific; NW Atlantic, north-western Atlantic; NW Tropical Atlantic, north-western Tropical Atlantic; N Pacific, northern Pacific.

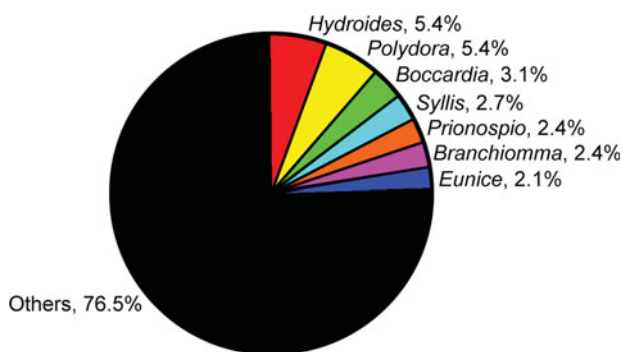


Fig. 1. Relative dominance of polychaete genera by the number of alien species.

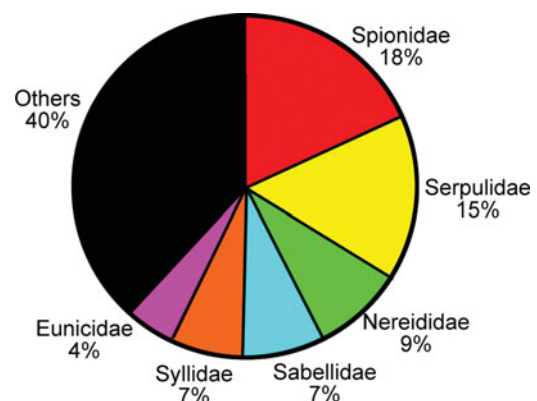


Fig. 2. Relative dominance of polychaete families by the number of alien species.

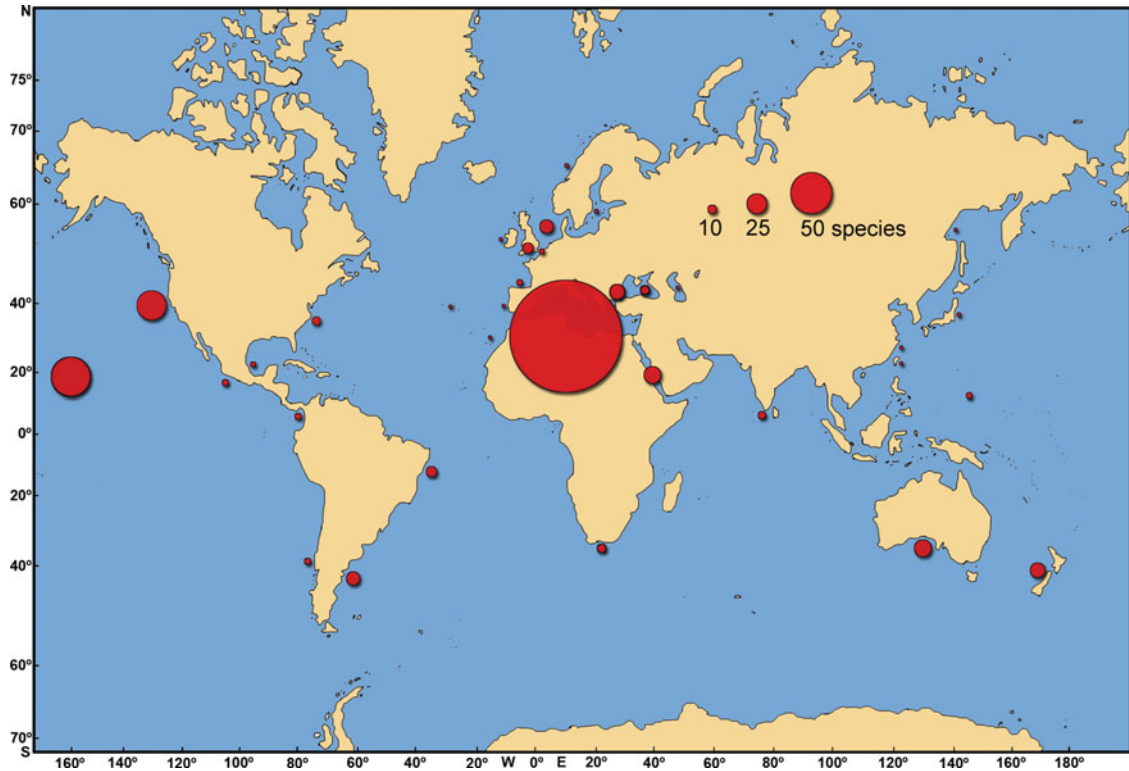


Fig. 3. The number of alien polychaete species worldwide.

the world's oceans and 31 species (casual species) have a potential to establish viable populations. The number of established and casual polychaete species vary among regions, with the highest score (94 species) in the Mediterranean Sea,

followed by the Hawaii Islands (25 species) and the USA Pacific coast (28 species) (Figure 4). The Red Sea (20 species), Australia (16 species) and New Zealand (13 species) had also high number of established alien species.

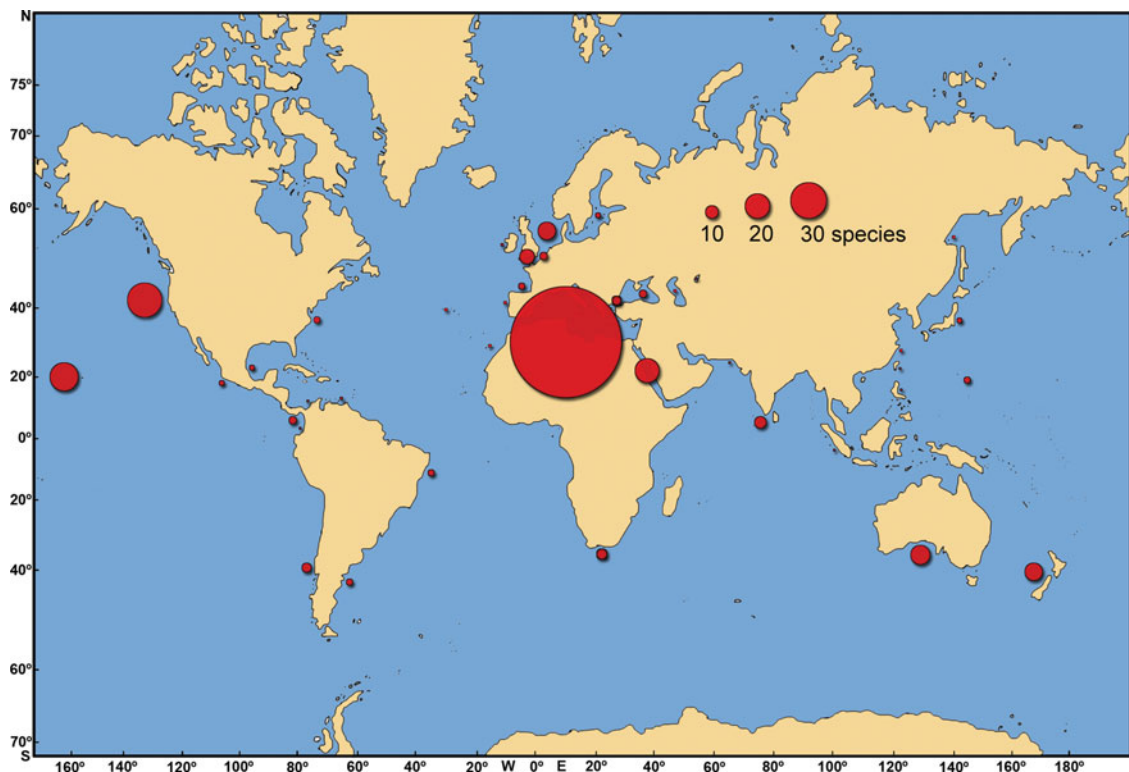


Fig. 4. The number of established and casual alien species worldwide.

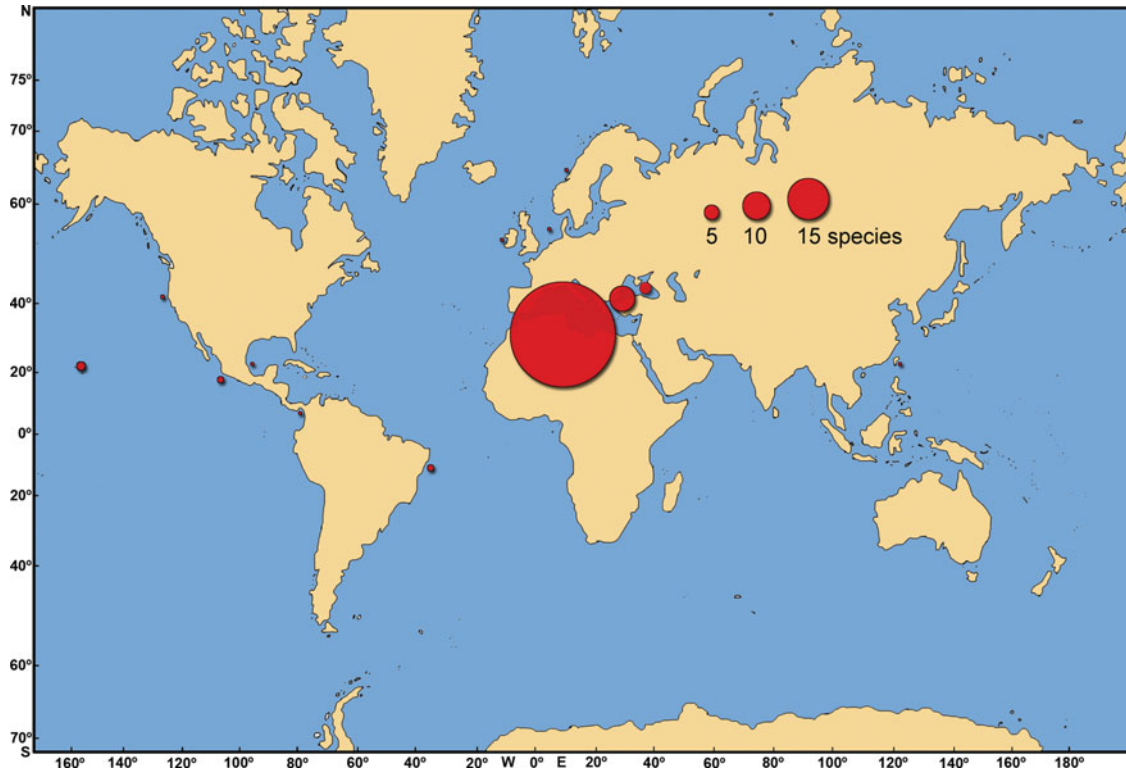


Fig. 5. The number of questionable alien species worldwide.

The Mediterranean (38 species) and Sea of Marmara (9 species) possessed a high number of questionable alien species (Figure 5). They are the species mostly reported from ecological or faunal studies in the region without detailed descriptions (i.e. Rullier, 1963). Species such as *Spiophanes bombyx* (parentheses in Table 1) cited as aliens require confirmation after the recent generic revisions (e.g. Meißner, 2005).

The highest number of cryptogenic species (19 species) were reported from the Hawaii Islands (Carlton & Eldredge, 2009) (Figure 6). The south-west coast of the Atlantic Ocean (Argentina and Brazil) also had a high number of cryptogenic species (Figure 6). Ten cryptogenic species were reported on the coast of Argentina by Orensanz *et al.* (2002). Regions such as the USA Pacific coast (Boyd *et al.*, 2002; Wasson *et al.*, 2005), the USA Atlantic coast (Ruiz *et al.*, 2000) and Norway (Hopkins, 2002) also had a relatively high number of cryptogenic species. In the Mediterranean Sea, only *Paraprionospio coora* and *Chaetozone corona* were known to be cryptogenic species (Zenetos *et al.*, 2010).

After re-evaluating the distribution patterns and taxonomic positions of the species, 16 polychaete species were excluded from the alien list of the Mediterranean Sea (see Zenetos *et al.*, 2005). Alien species lists of some regions have been prepared by non-polychaete taxonomists so these lists should be used with some reservations. After further examination the species currently identified as aliens could be re-identified as new or different taxa. In Table 1, some species from the alien list have been eliminated as there is more information about their distribution pattern. For example, *Ficopomatus enigmaticus* was considered as alien for the coasts of Australia (Hewitt, 2002), but Pillai (2008)

indicated that it could be a species native to Australia and might have been spread to other tropical and subtropical regions by shipping.

Where do they come from?

The geographical origins of marine aliens are largely correlated with the predominant shipping routes in and out of a country (Hayden *et al.*, 2009). The majority of alien polychaete species (80% of the total number of species) in the Mediterranean Sea originated from the Red Sea and Indo-Pacific areas (Figure 7). The Suez Canal is the main vector for the species introductions in the region. The Atlantic species accounted for 18% of the total number of species and were introduced to the region mainly via ships. The Pacific coasts of America have been largely colonized by the species of Atlantic origin. For example, the Atlantic-originated species on the Pacific coast of USA, Mexico and Colombia accounted for 49%, 40% and 100% of total number of alien species, respectively. The shallow-water benthic habitats of the areas between 40°N and 40°S have alien polychaete species mostly originating from other tropical and subtropical regions. The Mediterranean species invade the Red Sea via the Suez Canal (anti-lessepsian migrants, 90% of total alien species in the Red Sea) (Por, 1978). The Mediterranean species were also transferred to the Indo-Pacific areas such as Taiwan (33% of total alien polychaete species) (Paxton & Chou, 2000; Radashevsky & Hsieh, 2000a, b), India (22%) (Subba Rao, 2005), Australia (21%) (Polland & Hutchings, 1990; Currie *et al.*, 2000; Hewitt *et al.*, 2004; Hayes *et al.*, 2005) and New Zealand (18%) (Handley, 2000; Glasby *et al.*, 2009) via ships. The coasts of Azores, France, Ireland and Britain were also largely colonized by the Mediterranean species. The alien

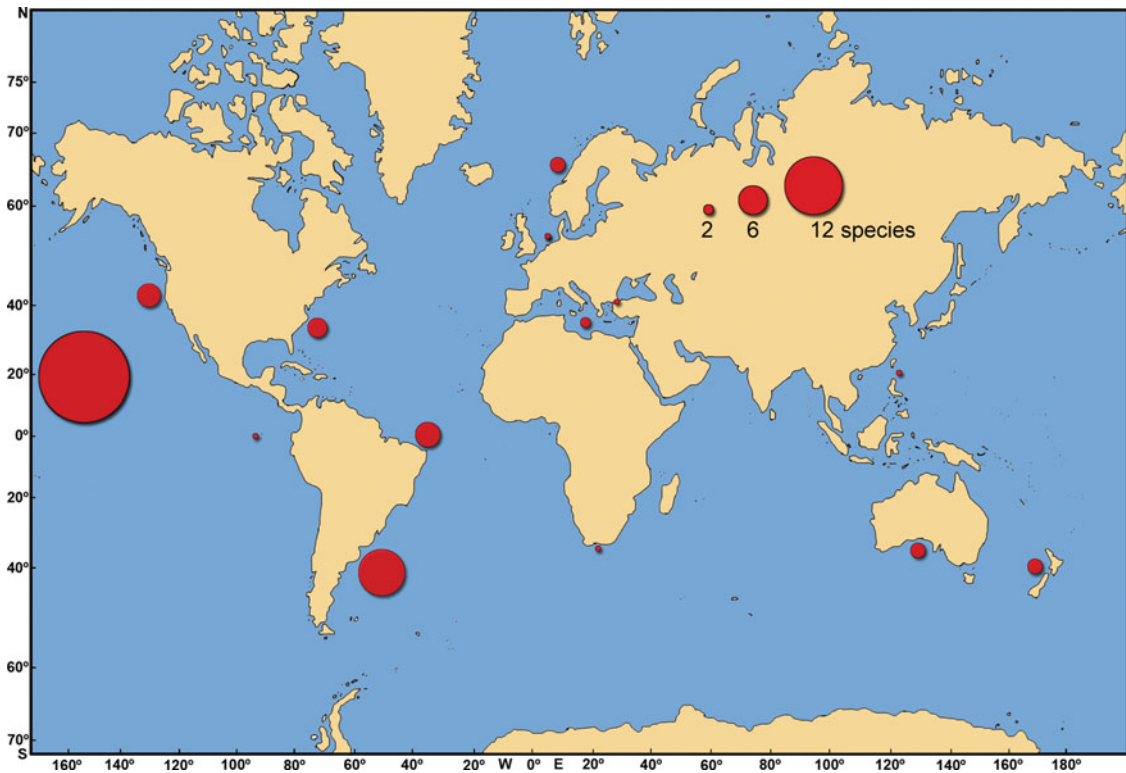


Fig. 6. The number of cryptogenic species worldwide.

polychaete species in the Caspian Sea and Aral Lake were mainly introduced from the Black Sea (Leppäkoski & Olenin, 2000a; Grigorovich *et al.*, 2003). The Indo-Malaysian region

can be identified as a centre of alien species originating from south-east Asia, China, Japan, the Philippines and Australian regions (Subba Rao, 2005).

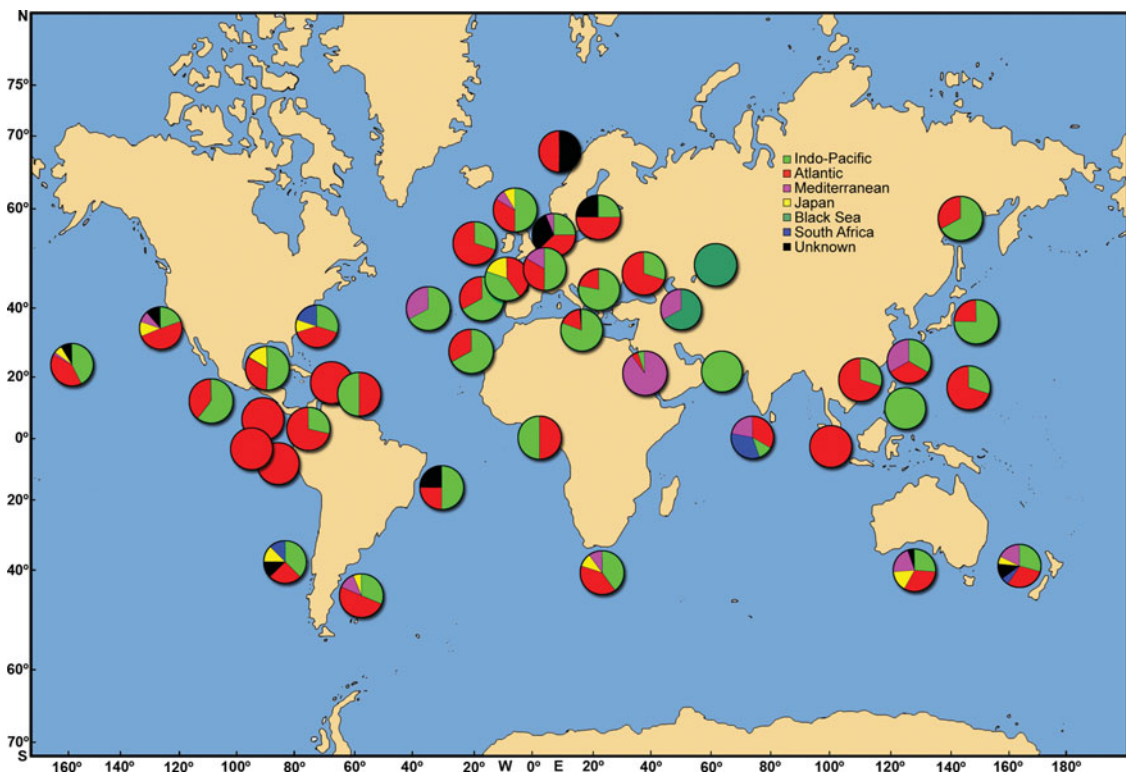


Fig. 7. The origins of alien polychaete species in regions.

What are the main vectors for species introductions?

Figure 8 indicates that shipping is a major vector for the introduction of polychaete species worldwide. Polychaetes can be transferred via ballast waters of ships or hull fouling. Almost 82% of serpulid species were introduced in a new region by ship fouling. Spionids, except for boring species, are translocated in ballast water (Carlton, 1985). The Suez Canal seems to have played an important role for the species exchange between the Mediterranean and Red Seas. Almost 48% of the alien polychaetes in the Mediterranean Sea are lessepsian migrants (Zenetos *et al.*, 2010). However, the importance of lessepsian migrants changes according to the basins of the Mediterranean. For example, lessepsian migrants comprised almost 51% of the alien polychaete species on the Levantine and Aegean coasts of Turkey, but only 6% on the Italian coast. The majority of alien polychaete species reported on the coasts of England (Eno *et al.*, 1997), Spain (Atlantic) (Martinez *et al.*, 2006), the Philippines (Williams, 2001) and Chile (Moreno *et al.*, 2006) were introduced to the areas in association with the aquaculture of some mollusc species such as *Crassostrea virginica* and *Haliotis rufescens*. Almost 30% of total alien species reported on the coasts of Australia (Hayes *et al.*, 2005; Sato-Okoshi *et al.*, 2008), New Zealand (Handley, 2000; Glasby *et al.*, 2009; Read, 2010) and Brazil (Radashevsky *et al.*, 2006) were introduced to the regions via aquaculture activities. Some large polychaete species are widely used as fish bait (Brown, 1993; Dagli *et al.*, 2005) and the bait trade has led to the introductions of some species. Two nereidid species are known to have been transferred by the worm bait trade. *Namalycastis abiuma* was exported from an Indo-Pacific area to the Pacific coast of the USA (Cohen & Carlton, 1995), and *Nereis aibuhitensis* from

Korea to Japan (Nishi & Kato, 2004) and Portugal (Fidalgo e Costa *et al.*, 2006). About 620 million live animals were brought into Japan in 2003 and more than 90% of these are classified as worms for fishing bait (Mito & Uesugi, 2003).

Three alien polychaete species, namely *Hediste diversicolor*, *Streblospio gynobranchiata* and *Ficopomatus enigmaticus*, were reported from the Caspian Sea (Grigorovich *et al.*, 2003; Taheri *et al.*, 2009). *Hediste diversicolor* was intentionally transferred from the Black Sea to the Caspian Sea for stocking, whereas the other species were introduced to the area via shipping. Only one alien species (*H. diversicolor*) was reported from Aral Lake (Leppäkoski & Olenin, 2000a) and was intentionally introduced to the area from the Black Sea.

Invasive species and their impacts

According to Williamson & Fitter (1996), 10% of the alien species could become established in the recipient area and 1% of them will eventually become invasive. This rule cannot be applied everywhere. In the Mediterranean, for example, 45% of the total number of alien species have become established and 18% of the total number have invasive characters (Zenetos *et al.*, 2010). These ratios also change according to the sub-areas of the Mediterranean. Established and invasive species accounted for up to 53% and 23% of the total number in the eastern Mediterranean; 50% and 8% of the total number in the western Mediterranean; and 43% and 29% of the total number in the Sea of Marmara, respectively.

Polluted or physically degraded environments are known to be more prone to invasion than pristine habitats (Çinar *et al.*, 2006; Galil, 2000). Native species might not be adapted to the changed environmental conditions, reducing their ability to exploit resources which provides opportunities

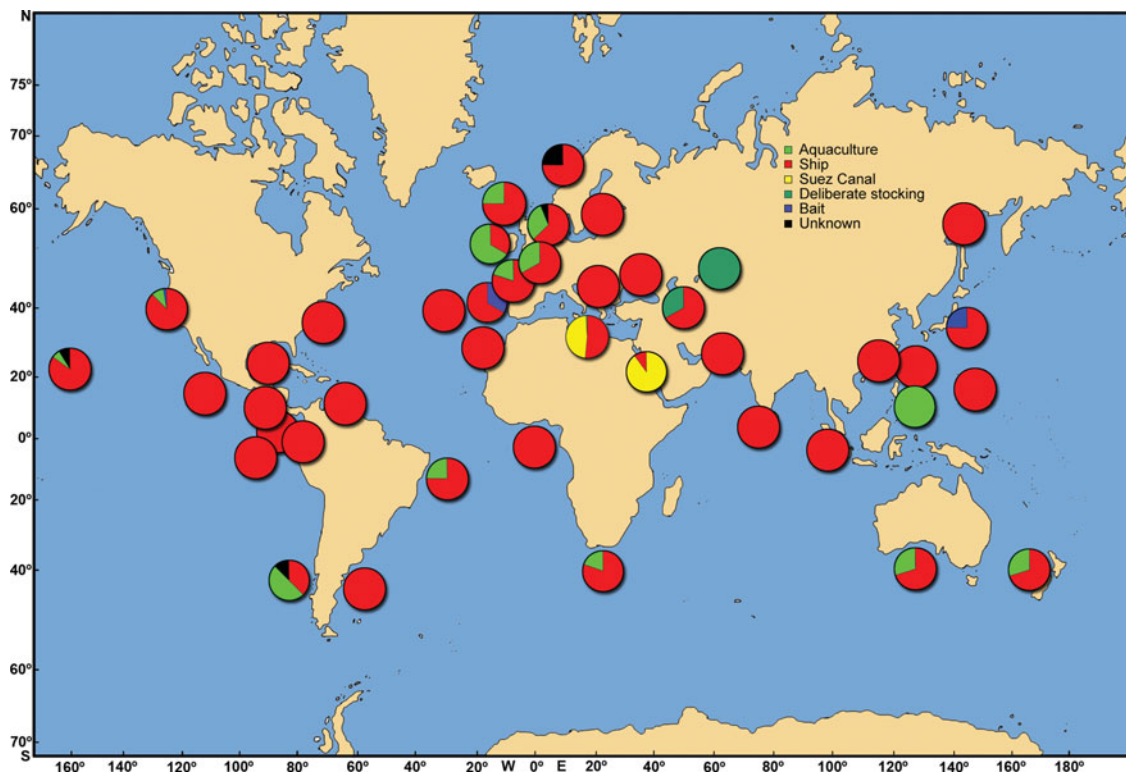


Fig. 8. The main vectors of species introductions worldwide.

for invaders (Shea & Chesson, 2002). Increased pollution exposure affects hard bottom assemblages dominated by natives to become either dominated by alien species or equally occupied by native and alien species (Piola & Johnston, 2008). The polluted soft-bottom benthic environments in Izmir Bay where a large international harbour is located have been densely invaded by the species originated from the north-west Atlantic Ocean (*Polydora cornuta* and *Streblospio gynobranchiata*) and the coast of Japan (*Pseudopolydora paucibranchiata*) (Çinar *et al.*, 2005; Dagli & Çinar, 2008). They constituted more than 95% of the total individuals and 70% of the total biomass at some stations. Çinar *et al.* (2005) indicated that these species had a great impact on the prevailing ecosystem and seemed to have replaced some opportunistic species previously known from the polluted Izmir Bay such as *Capitella capitata* and *Malacoceros fuliginosus*. Ranasinghe *et al.* (2005) found that *P. paucibranchiata* accounted for 52% of total zoobenthic populations in southern California embayments.

In the shallow-water benthic habitats of the eastern Mediterranean, some lessepsian migrants such as *Pseudonereis anomala* and *Eunice antennata* became dominant components of benthic communities and competed with some native species. Ben-Eliahu (1989) postulated that *Perinereis cultrifera*, a native nereidid species of the Mediterranean, was excluded from algal habitats along the Israeli coast, probably due to an efficient dispersal. *Perinereis cultrifera* has direct, non-pelagic development and its dispersal is consequently more restricted than that of the migrant species (*Pseudonereis anomala*), which has the pelagic *Heteronereis* stage. The changes that have occurred in benthic communities of the Levant coast of Turkey due to the dense populations of *E. antennata* (Kurt Sahin & Çinar, 2009) are unknown at this stage and require further investigation.

Some serpulid species such as *Hydroides elegans*, *H. ezoensis*, *H. sanctaecrucis* and *Ficopomatus enigmaticus* invade artificial substrates in polluted or brackish water environments in tropical and subtropical areas (i.e. Schwindt *et al.*, 2001; Hewitt, 2002; Zvyagintsev, 2002; Lewis *et al.*, 2006). The reef builder species, *F. enigmaticus*, was considered an important part of the ecosystem by providing a suitable habitat for other species and also by changing physical factors of the invaded environment (Schwindt *et al.*, 2001). This species may attain an annual production in dry weight of almost $21 \text{ kg.m}^{-2}.\text{yr}^{-1}$ (Fornós *et al.*, 1997) and a density of $150,000 \text{ ind.m}^{-2}$ (Bianchi & Morri, 2001) in the Mediterranean Sea. In harbours and estuarine areas it causes economic problems due to fouling (Read & Gordon, 1991). However, dense populations of *F. enigmaticus* in enclosed waters including harbours have very beneficial effects on water quality, reducing suspended particulate loads and improving both the oxygen and nutrient status (Davies *et al.*, 1989). This species also hosts other alien species such as *Polydora cornuta* and *Conopeum seurati* (Read & Gordon, 1991).

Hydroides elegans and *H. dianthus* can form dense populations in harbour environments. In the Mediterranean Sea, the population densities of *H. elegans* and *H. dianthus* may attain $110700 \text{ ind.m}^{-2}$ and 33050 ind.m^{-2} , respectively (Çinar *et al.*, 2008). In the lagoon of Orbetello (Italy), *H. dianthus* built a small (less than 1 m) reef (Bianchi & Morri, 2001). These species, with calcareous tubes, can become a nuisance when they attach to hard structures such as quays, mariculture equipment and ships' hulls (Relini, 1993). In

Hong Kong waters, mariculture cage nets were completely colonized by *H. elegans* after immersion for one month, the thickness and wet weight were reported to be 38 mm and 12.5 kg.m^{-2} , respectively (Jianjun & Zongguo, 1993). This species together with other fouling organisms can block the net mesh and greatly reduce water circulation (Zongguo *et al.*, 1999). They also add considerable weight to the nets which can cause the cages to sink, enabling the stock to escape. In the same area, the density and biomass of *H. elegans* on ferry docks and boats were estimated as $3.3 \times 10^5 \text{ ind.m}^{-2}$ and 20.5 kg.m^{-2} (Jianjun & Zongguo, 1993). *Hydroides elegans* is a mariculture pest in Japan, where it competes with oysters for food and oxygen. An outbreak of this serpulid polychaete in Hiroshima Bay has caused heavy economic loss of cultured oyster crops through fouling on their shells (Hirata & Akashige, 2004). In a study by Çinar (2006), alien serpulid species comprised more than 95% of the total serpulid specimens found in hard substrates such as rocks, molluscs and artificial substrates (i.e. docks' pilings, ropes and tires) in the eastern Mediterranean. *Spirobranchus kraussii* (previously known as *Pomatoleios kraussii*) formed a densely populated belt in shallow-water areas in Mersin Bay, providing a suitable habitat for small vagile fauna (Çinar, 2006). In the area, some man-made structures and also natural substrates such as stones were completely covered by *Hydroides operculatus*. The population density and biomass reached up to $384,000 \text{ ind.m}^{-2}$ and 246 g.m^{-2} , respectively (Çinar, 2006). In the United Kingdom, fouling of *H. ezoensis* (up to 30 cm thick) has caused navigation problems by reducing the flotation of navigation buoys (Eno *et al.*, 1997). Dense settlements of serpulid polychaetes may kill other native species such as young oysters and mussels by overgrowing (Eno *et al.*, 1997). The dense settlement of *Neodexiospira brasiliensis* on *Zostera* leaves resulted in decreasing the eel grass' photosynthetic efficiency (Critchley & Thorp, 1985).

Some sabellid species have become invasive in some regions. *Sabella spallanzani*, a native species of the Mediterranean Sea, forms dense populations on artificial substrates in Australian waters and competes with native suspension feeders (i.e. mussels) and interferes with their recruitment (Hayes *et al.*, 2005). The same impacts were also noted for *Branchiomma luctuosum* (Licciano *et al.*, 2002) and *B. bairdi* (Çinar, 2009) in the Mediterranean Sea. *Euchone limnicola* forms dense populations in soft substratum of Portland Harbour, Dorset, UK (mean density of 2127 ind.m^{-2}) and competes with native species for food and space (Wilson, 1999). The tubes retain sediment, thereby altering the habitat for other organisms (Wilson, 1999).

Marenzelleria viridis, a North American spionid, was first recorded in brackish waters of the Wadden Sea and Baltic Sea in the early 1980s (Kube *et al.*, 1996). It has spread rapidly and is now a dominant species of zoobenthos in estuaries and coastal lagoons. Leppäkoski & Olenin (2000b) calculated the mean rate of spread of *M. viridis* within the Baltic Sea as 480 km/year. *Marenzelleria viridis* managed to seasonally dominate soft bottom benthic habitats in the Baltic Sea, where the maximum density was estimated as $28,000 \text{ ind.m}^{-2}$ (Kube *et al.*, 1996; Gruszka, 1999). This species re-circulates organic matter deposited in deeper sediment, links benthic and pelagic subsystems, and provides new microhabitats for its associated fauna (Kube *et al.*, 1996; Gruszka, 1999). In the Ems estuary (North Sea), increasing

densities of *M. viridis* in a sandy habitat (maximum juvenile density 19300 ind.m⁻²) coincided with a reduced abundance of the polychaete *Hediste diversicolor* (Essink & Kleef, 1988).

Boring polychaetes belonging to the families Spionidae, Cirratulidae and Sabellidae commonly infest shells of cultured mollusc species (Blake, 1969; Evans, 1969; Moreno *et al.*, 2006). The intensive shellfish trade has been implicated in the introduction of several boring polychaetes to different parts of the world together with their hosts. Boring spionid polychaetes belonging to the genera *Boccardia*, *Dipolydora* and *Polydora*, and the sabellid *Terebrasabella heterouncinata* can cause severe damage to the mollusc shells, affecting the fitness of their hosts and often causing enormous financial loss to owners of aquacultures worldwide (Evans, 1969; Martín & Britayev, 1998; Fitzhugh & Rouse, 1999; Moreno *et al.*, 2006; Radashevsky *et al.*, 2006; Simon *et al.*, 2010).

Terebrasabella heterouncinata, a native species of the South African coast, densely infests several gastropods (Simon *et al.*, 2005) and has become a pest on cultured abalone in South Africa and California in the early 1990s (Fitzhugh & Rouse, 1999; Moore *et al.*, 2007). This species inhabits burrows that form when the larvae settle on the growing edge of shells of the abalone (*Haliotis midae*), and the host covers it with shell (Simon *et al.*, 2004). Farmed abalone with heavy infestations reduce or cease production of the prismatic layer of shell and develop brittle shells that are domed in shape with deformed or absent respiratory pores (Moore *et al.*, 2007). Consequently, dense settlement of the species results in deformation and weakening of the shell, a reduction in growth, or the death of the abalone (Simon *et al.*, 2004). The poor price obtained for abalone with deformed shells was directly responsible for the failure of several farms (Moore *et al.*, 2007).

Reports of the introductions of boring spionid polychaetes increased with the growth of the shellfish trade worldwide (Radashevsky & Olivares, 2005; Sato-Okoshi *et al.*, 2008). *Polydora websteri* is commonly associated with the shells of commercial oysters and other bivalves of estuaries and near-shore environments (Blake, 1996). The spread of *P. websteri* along the east coast of Australia (associated mortalities first recorded in 1880) forced Sydney oyster producers into an intertidal stick and tray culture system (Bower, 2001). Dense infestations of this species in cultured oysters caused the collapse of a highly intensive aquaculture industry in Hawaii (Bailey-Brock & Ringwood, 1982). In Chile, *Polydora rickettsi* was reported to have infested 24% of mature abalones *Haliotis rufescens* (Moreno *et al.*, 2006) while *P. uncinata* infested 99% of specimens of *Haliotis discus hannai* (up to 42 worms on one shell) (Radashevsky & Olivares, 2005). *Polydora uncinata* and *Boccardia knoxi* bore into the shells of cultured abalones as well as shells of native bivalve and gastropods (Sato-Okoshi *et al.*, 2008). Polydorid infestation can reduce the growth rates of shell and meat yield. Moreover, due to the stress caused by the boring spionids, the molluscs are more susceptible to adverse environmental changes leading to increased mortality (Bower, 2001).

CONCLUSIONS

The alien polychaete diversity greatly varies according to regions. Although there are many reasons for the difference in diversity the principal factor seems to be the magnitude of scientific efforts focusing on this aspect among regions.

The Mediterranean Sea accounted for 47% of the total number of alien species up to date recorded. As lessepsian migrants intensively invade benthic habitats of the eastern Mediterranean and have special attention in scientific and public media, the Mediterranean Sea has relatively been well studied. Although there are only a few data sets regarding alien polychaete species in western and eastern parts of Africa if intensive sampling is applied numbers will greatly increase. Expanding commercial trade between distinct regions via large ships accelerates the introduction of alien species. Large commercial harbours in various countries should be studied and monitored to record alien species distribution.

The alien polychaete species that have been reported in the literature from different parts of the world's oceans are amalgamated as a comprehensive list (Table 1). A list of alien polychaete species should be prepared and updated regularly to monitor their distribution and the adverse effects on the local ecosystem. These data will help to improve the management and regulation of invasive species.

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