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Impacts of alien polychaete species in marine ecosystems: a systematic review

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Abstract

This systematic review analysed scientific publications to identify relevant research about the impact of alien polychaete species around the world, using the PRISMA (Preferred Reporting Items for Systematic reviews and Meta-Analysis) guide. The criterion for inclusion was studies published in English, with the key terms (e.g. 'impact', 'alien species', 'polychaetes') in the title, abstract and keywords. The literature search was conducted in Scopus and Web of Science from April to December 2020. The search resulted in 150 papers that included information about impact of alien polychaete species. Of these studies, 98% were published in the last 25 years, reporting on the impact of 40 species in 18 regions of the world. Sixty-one per cent of the research was conducted in the Baltic Sea, South-west Atlantic and Mediterranean Sea. The most frequent type of study was field surveys (46%) and the most studied system was open coast areas (36%). The species with the highest number of publications about their impacts were *Ficopomatus enigmaticus*, *Marenzelleria viridis*, *Sabella spallanzanii* and *Boccardia proboscidea*. Based on evidence of their most severe documented impacts in their introduced ranges, the impact mechanisms (IMos) of the alien polychaete species were strongly related to their biology and lifestyles. We found that species that build conspicuous reefs and tube-dwellers mainly showed physical and structural impact on ecosystems; shell-borers, mainly parasitism and infauna species, showed mainly chemical, physical and structural impacts on ecosystems. Some recommendations for the study of alien polychaete species are discussed.

Introduction

Although it is technically more appropriate to refer to polychaetes as marine annelids (Hutchings & Kupriyanova, 2018) we still use the term polychaetes due to its wide use in the historical literature. Polychaetes form one of the most important components of benthic communities, representing between 30 and 50% (but up to 70%) of the total abundance of the benthos (Rosenberg *et al.*, 1996; Witte *et al.*, 2003; Murugesan *et al.*, 2011; Kuk-Dzul *et al.*, 2012). Polychaetes also comprise around half of the diversity of annelids with about 100 families and around 12,000 valid species (Appeltans *et al.*, 2012; Weigert & Bleidorn, 2016; Magalhães *et al.*, 2021). The majority of these families occur worldwide and are found in nearly every marine habitat where they often dominate macrofaunal assemblages (Hutchings, 1998).

Polychaetes display a diverse range of life histories and feeding guilds (Fauchald & Jumars, 1979; Jumars *et al.*, 2015) allowing them to occupy almost all trophic levels and, coupled with their distribution and abundance, they generally provide a whole suite of ecological functions and ecosystem services where they occur in their native ranges (Cyrino *et al.*, 2018). As such, they are often regarded as ecosystem engineers (Fadhullah & Syakir, 2016), altering their surrounding environments through their ability to act as bioturbators, sediment stabilizers or refuge/substrate providers. Furthermore, some polychaetes are of practical use to humans as bioindicators of a range of pollutants (Mauri *et al.*, 2003; Giangrande *et al.*, 2005; Catalano *et al.*, 2012; Maranho *et al.*, 2014; Pires *et al.*, 2016) as well as ecosystem health (Cardoso *et al.*, 2007).

The economic contributions of polychaetes are also substantial; in a global review of bait worm fisheries, Watson *et al.* (2017) estimated that the ~121,000 tons of polychaetes collected globally were valued at £5.9 billion. They found that the five most expensive marine species sold on the global fisheries market (price kg^{-1}) are all polychaetes. Further economic impacts are experienced when polychaetes act as pests, such as shell-boring spionids (*Dipolydora* spp., *Polydora* spp., *Boccardia* spp.) that have a long history of impacting shellfish aquaculture industries worldwide by devaluing products destined for the half-shell market and requiring burdensome treatments and interventions to manage infestations (Spencer *et al.*, 2020).

Globally, opportunities have increased for the transport of polychaetes beyond their native ranges to become aliens (synonyms: adventive, exotic, foreign, introduced, non-indigenous, non-native or neocosmopolitan) (Richardson *et al.*, 2011; Blackburn *et al.*, 2014; Robinson *et al.*, 2016; Darling & Carlton, 2018). It has been estimated that there may be as many as 300 alien polychaete species in various regions of the world (Çinar, 2013). However, this number needs to be revised, as some species previously considered to be 'cosmopolitan' are confirmed as aliens (e.g. Bergamo *et al.*, 2019), as cryptic invasions are uncovered (e.g. Elgetany *et al.*, 2020), or as species previously thought to be alien resolve into multiple indigenous species (Simon *et al.*, 2019). The deliberate distribution of polychaetes via the trade of bait worms can inadvertently lead to their dispersal and establishment when live unused bait is discarded, as occurred in Portugal with the importation of *Perinereis aibuhitensis* from Korea (Fidalgo E Costa *et al.*, 2006). Furthermore, Mito & Uesugi (2004) showed that out of the 620 million live animals imported into Japan in 2003, 90% were classified as worms for fishing bait, suggesting a great scope for spread of worms via this vector. The global trade of molluscs such as oysters, mussels and abalone is considered one of the most important vectors of alien species (Ruesink *et al.*, 2005) including shell-boring worms such as *Boccardia proboscidea* (Simon *et al.*, 2009; Simon & Sato-Okoshi, 2015). Worms may also be spread unintentionally when fouling polychaetes such as *Ficopomatus enigmaticus*, *Hydroides elegans* and *Sabella spallanzanii* travel the world on ship hulls (Vitousek *et al.*, 1997; Kocak *et al.*, 1999; Hayes *et al.*, 2005). Furthermore, with the increased speed of shipping, trans-oceanic shipping can now take place in less time than the duration of larval stages of most marine invertebrates. Thus, the huge volumes of ballast water carried by these ships and dumped in or near ports have also led to the establishment of invasive species (Carlton & Geller, 1993; Çinar, 2013).

Once established in recipient regions, alien species may cause significant changes to local species richness and abundance, population genetic composition, behaviour patterns, trophic networks, ecosystem productivity or habitat structure through competition, displacement or predation (Brooks *et al.*, 2004; Hendrix *et al.*, 2008; Shine, 2010; Pyšek *et al.*, 2012; Ricciardi *et al.*, 2013). There has therefore been significant interest in evaluating the impacts of alien species in different components of recipient ecosystems (Blackburn *et al.*, 2014; Bacher *et al.*, 2018; Pyšek *et al.*, 2020). Unfortunately, marine invasion science can be biased towards certain taxonomic groups, study types, marine systems and invasion stages. For example, South African marine invasion science is biased towards conducting field surveys on established species, especially *Mytilus galloprovincialis*, in the rocky intertidal (Alexander *et al.*, 2016), while impacts of the movement of oysters have also been reviewed extensively (e.g. Haupt *et al.*, 2010).

Few studies have been conducted on the impacts of alien polychaetes in their recipient regions (Schwindt *et al.*, 2001; Holloway & Keough, 2002*a*; Delefosse *et al.*, 2012; Elías *et al.*, 2015). However, because many polychaetes provide ecosystem functions in their natural distribution ranges, it is likely that they may have significant impacts should the worms become established as aliens. An ecological function such as bioturbation comprises a series of processes that affects the physical and chemical properties of the sediment that may strongly influence bacterial communities involved in nutrient cycling (Biles *et al.*, 2002), ultimately modifying the benthic community structure. For example, bioturbators, such as the deposit-feeding lugworm family Arenicolidae, have been known to exclude sympatric species such as the tube-building polychaetes *Polydora cornuta* and *Lanice conchilega* (Volkenborn *et al.*, 2009). Tube-building polychaetes, conversely, are sediment stabilizers which can aid in protecting the environment against erosion (Frey & Wheatcroft, 1989), and facilitate the establishment of many other species not only by providing attachment points for plants and bivalves but also by providing refugia for smaller infaunal organisms, leading to higher species diversities in areas where they are found (Bell & Coen, 1982; Ban & Nelson, 1987). Finally, abundant soft-bottom polychaetes have also been known to play a major role in the diets of demersal fish (Yeung *et al.*, 2013) and birds (Kalejta & Hockey, 1991).

Understanding the impacts of alien polychaetes at species level is crucial due to the great variations in morphology, feeding modes and reproductive cycles of polychaetes as well as the services that they provide and their abundance.

A review of the impacts that alien polychaetes are having worldwide could help predict future alien establishments and thereby facilitate management of new alien species. However, impacts at species level are context dependent and impacts ascertained for one species may not be indicative of the expected impacts of closely related species or sometimes even for the same species in a different ecosystem. Indeed, some species behave differently outside their native distribution range as in the case of *B. proboscidea*, a non-reef forming species native to California that builds massive intertidal reefs in sewage-impacted areas in the South-west Atlantic, causing a reduction in the diversity of native species (Jaubet *et al.*, 2011; Elías *et al.*, 2015). Furthermore, this species is a pest on abalone farms in South Africa (Simon *et al.*, 2010) but not in its native distribution. A review of species impacts can therefore help alert managers to unpredictable species such as *B. proboscidea* and even help point to local gaps in knowledge by highlighting overlooked study types or marine systems.

Information about the impact of alien polychaete species is sparse or restricted to some geographic areas and species (Çinar, 2013; Katsanevakis *et al.*, 2014), and to date there has been no integrative and systematic review of the status and gaps of knowledge on this topic. The present systematic review analysed the advances in the research on the impacts of alien polychaetes in marine ecosystems and identifies gaps in the present knowledge that can be used to inform future research. This review aims to answer the following specific questions:

(1) How many and which alien polychaete species have been investigated globally to measure their impact?
(2) What are the trends in research into the impacts of alien polychaetes in marine ecosystems?
(3) What kinds of impacts do alien polychaetes have?
(4) What are the different management strategies that have been proposed or executed to manage different scenarios of impacts in the environment?

Materials and methods

This systematic review was performed using the main principles of the PRISMA (Preferred Reporting Items for Systematic reviews and Meta-Analyses) approach, which recommends a series of procedures for systematic reviews and meta-analyses to make them repeatable and prevent low-quality or methodologically biased studies (Moher *et al.*, 2009; Sierra-Correa & Cantera Kintz, 2015). The approach consists of four phases: (1) Identification of publications through the systematic use of search engines; (2) Screening publications based on titles, abstracts and keywords; (3) Judging eligibility after a full review of remaining publications; and (4) Inclusion of all publications remaining in the final subset to extract the information (Figure 1).

Data collection and eligibility criteria

The bibliographic search focused on peer-reviewed publications in English from reputable journals with research conducted in marine environments. We followed the recommendations of Koricheva *et al.* (2013) and the search was conducted using both the advanced systematic search engine in Elsevier's Scopus database (www.scopus.com) and ISI Web of Science (www.webofknowledge.com).

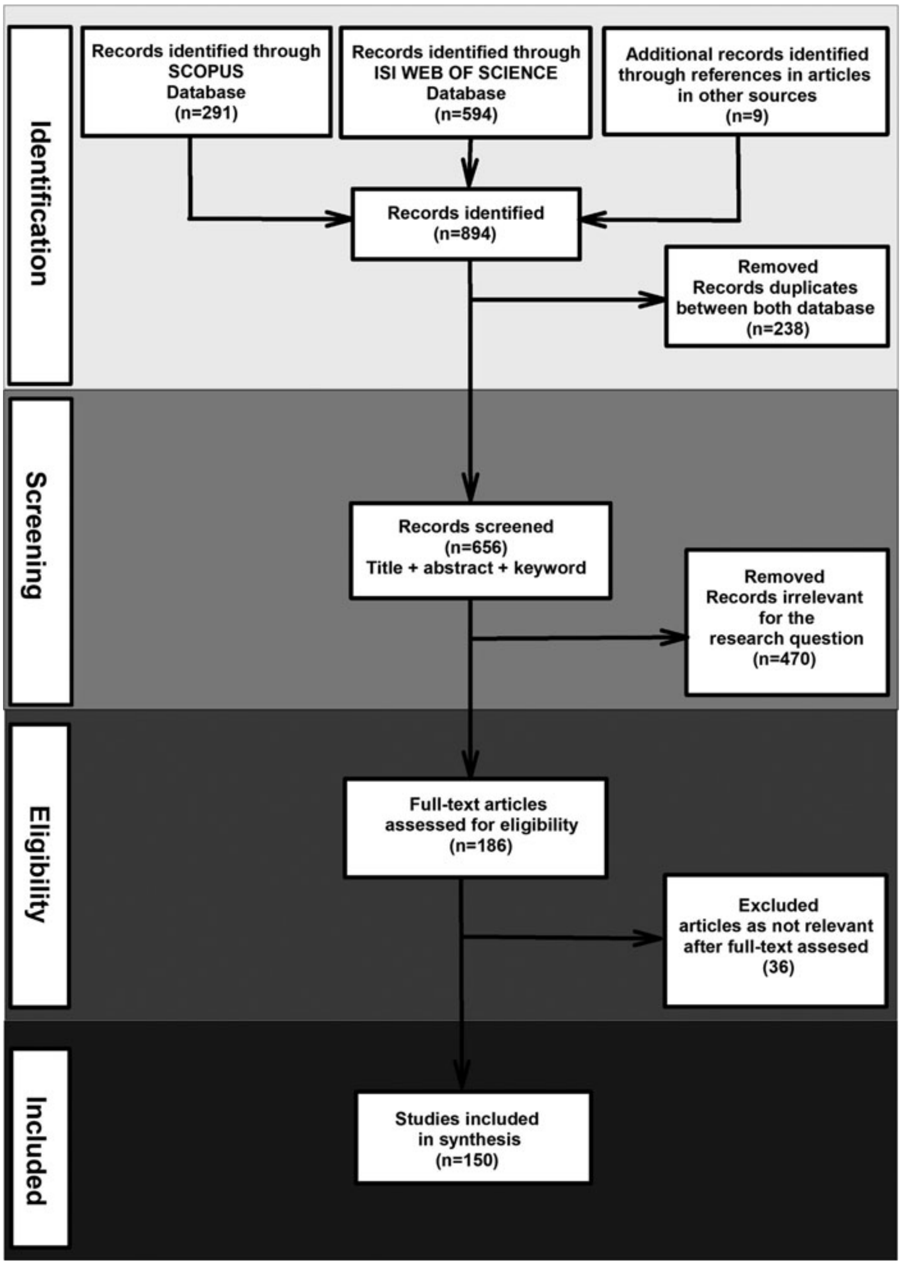

Fig. 1. Flow diagram depicting the phases and actions taken during the literature review where '*n*' is the number of studies relating to action.

The criteria for selection included any article, review or book chapter published between 1950 and 31 December 2020, with the following search terms in the title, abstract or keywords:

(1) 'impact', OR 'impacts' OR 'effect' OR 'effects'
AND
(2) 'alien species', OR 'invasive species', OR 'allochthonous species', OR 'introduced species' OR 'non-indigenous species' OR 'non-native species' OR 'invasion' OR 'exotic' OR 'adventive' OR 'foreign'
AND
(3) 'polychaetes' OR 'polychaeta' OR 'marine worm' OR 'marine worms'.

The following information was extracted from each selected article:

(1) Year of publication.
(2) Marine system: aquaculture facility, coastal lagoon, estuary, harbour, marina, open coast, or multiple if the study included more than one type of marine system.
(3) Study type: Field survey, experiment *in situ*, field and laboratory experiment, laboratory experiment, review, theoretical model and meta-analysis.
(4) Family of polychaetes.
(5) Species of polychaetes.
(6) Impact of alien species, according to the classification of Blackburn *et al.* (2014).

A field survey refers to research conducted during a sampling survey followed by analysis of samples in the laboratory; an experiment *in situ* was conducted in the field followed by analysis of samples in the laboratory; field and laboratory experiment is a combination of these two study types in the same research; theoretical model refers to studies that analysed data to design a mathematical model; meta-analyses is any research that applied statistical analysis that combined the results of multiple scientific studies; a review is any research based on the revision of the literature of invasive taxa that included one or more species of marine annelids.

All species names and authorities were verified and updated according to the online World Polychaeta Database (Read & Fauchald, 2021).

The impacts of alien polychaete species were evaluated according to the classification of alien species proposed by Blackburn *et al.* (2014). This classification system is based on the magnitude of the environmental impacts with regards to the impact mechanism (IMo) used to code species in the International Union for Conservation of Nature (IUCN) Global Invasive Database (Table 1). This system uses five semi-quantitative scenarios for each IMo, so impact values range from one to five, where one is minimal impact and five the highest impact that could be documented in 13 impact mechanisms (Table 1). Thus, the classification considers consequences not likelihoods, so species are classified on the basis of the evidence of all their most severe documented impacts in regions to which they have been introduced (Blackburn *et al.*, 2014).

Results

Papers included

The Identification phase produced 885 papers (Figure 1). Nine additional papers relevant to the topic, which were independently identified by the authors during the review process, were added to bring the total to 894 papers. Duplicates accounted for 238 of these records and after removal left 656 papers. During the Screening phase, based on the revision of the title, abstract and keywords, we removed a further 470 records which did not include information relevant to the impact of alien marine polychaetes, resulting in 186 papers remaining. Finally, in the Eligibility phase, the full texts were evaluated, and 36 papers were excluded for not including relevant information about any impacts of alien polychaete species (Figure 1). Thus, 150 papers remained to be included in this study. The bibliographic details of all papers are available in Supplementary Material (Supplementary Table S1).

Annual trend of papers published

The final subset of papers spanned the period from 1980 to 31 December 2020. Only six papers were published on the impacts of alien polychaetes in the 17 years from 1980 to 1997. Thereafter, research on the topic increased until averaging almost six papers annually between 1998 and 2020, reaching a maximum of 12 papers published in both 2018 and 2020 (Figure 2).

As time went by, there was a change in both the systems investigated and the types of studies conducted. In the initial period between 1980 and 1997, the marine systems studied were limited to coastal lagoons, estuaries and marinas, after which aquaculture facilities, open coasts and marine harbour systems also featured (Figure 3). Only from 2002 onwards were papers focusing on multiple marine systems within a single paper published (Figure 3). Over the complete timespan, 54 papers (36%) reported on research conducted on open coasts (Figure 4) followed by 27 (18%) studies in coastal lagoons, 19 (13%) in estuaries, 18 (12%) in harbours and 16 (10%) in multiple systems (Figure 4). The fewest studies were conducted in aquaculture facilities and marinas which accounted for 9 (6%) and 7 (5%) studies, respectively.

Study types in the period 1980–1997 were mainly field surveys with results of only one field and laboratory experiment published in that period (Davies *et al.*, 1989) (Figure 5). From 1998 onwards, field surveys remained popular but several other study types also rose in popularity (Figure 5). The breakdown of study types over the complete period shows field surveys as the most popular with 70 papers (46%), followed by *in situ* experiments with 25 papers (17%), 23 review papers (15%), 18 laboratory experiments (12%) and 10 theoretical studies (7%) (Figure 6). Only three studies included both field and laboratory experiments (2%) and only one meta-analysis (<1%) has been conducted.

Geographic distribution

Six papers were excluded (Rodriguez, 2006; Levin & Crooks, 2011; Olenin & Minchin, 2011; Çinar, 2013; Anton *et al.*, 2019; Bruschetti, 2019) from the analysis of geographic distribution of research. These papers were global reviews and one meta-analysis not investigating any specific geographic region. The remaining 144 papers were spread among 18 regions around the world (Figure 7). Half the papers were based on research conducted in two regions: the Baltic (33%) and South-west Atlantic (17%). Other well-studied geographic regions included the Mediterranean, the US Pacific coast and Australia, contributing just under 30% more of the papers. In contrast, less well-studied regions included the Wadden Sea (7 papers, 5%), South Africa (5 papers, 3%), New Zealand (4 papers, 3%) and the English Channel (3 papers, 2%). The remaining geographic regions represented were the Arabian Sea, Black Sea, Caspian Sea, Pacific coast of Canada, Sea of Azov, South-eastern Pacific, Tropical Eastern Pacific, U.S. Atlantic coast and Yellow Sea, each with a single publication.

In 11 of the 18 geographic regions studied around the world, more than one type of marine system has been studied (Figure 8). In the Baltic Sea most of the systems were studied (6 systems), except aquaculture facilities, followed by Australia and U.S. Pacific (5 each); Mediterranean and South Africa (4 each); South-west Atlantic, English Channel and Wadden Sea (3 each) and U.S. Atlantic coast, South-eastern Pacific and New Zealand (2 each) (Figure 8). In the South-west Atlantic, the main marine system studied was the coastal lagoon, followed by open coast and multiple systems, respectively. In the Mediterranean Sea, the papers focused mainly on harbours and open coasts, and fewer on aquaculture facilities and multiple systems. Studies from the Pacific coast of the USA mainly focused on aquaculture facilities and estuaries and in lower number harbours, marinas and open coast. In Australia, all marine systems were studied except aquaculture facilities and coastal lagoons.

The most common type of study was the field survey (conducted in all regions), followed by experiments *in situ* (7 regions), reviews (6 regions) and theoretical models (5 regions), whereas laboratory experiments and studies that included field and laboratory experiments were conducted in the fewest regions (Figure 9). The regions where all or most study types classified in the present review were conducted were the Baltic Sea, South-west Atlantic and the Pacific coast of the USA (Figure 9).

Number of species

The publications considered here provided information on impacts of 40 alien polychaete species, belonging to 11 families and 25 genera (Table 2, see Supplementary Table S1). In the present review 9 species were labelled as cryptogenic [CG] (see below) because their alien statuses are in question.

The families with most species are Spionidae, Serpulidae, Sabellidae and Nereididae, together representing 83% of the total number of alien species investigated (Figure 10). The remaining 17% were represented by the families Capitellidae, Ampharetidae, Cirratulidae, Glyceridae, Maldanidae, Sternaspidae and Terebellidae.

The species investigated most intensely was the serpulid *Ficopomatus enigmaticus* with studies conducted in the South-west Atlantic, Atlantic and Pacific coast of the USA, South Africa, Black Sea and English Channel (Table 2). The second most studied species was the spionid *Marenzelleria viridis*, with its impacts analysed in the Baltic and Wadden Seas. A

Table 1. Impact criteria for assigning alien species to different categories, according to the five semi-quantitative scenarios proposed by Blackburn *et al.* (2014)

Impact class	Massive (MA) 5	Major (MR) 4	Moderate (MO) 3	Minor (MI) 2	Minimal (ML) 1
Categories should adhere to the following general meaning	Causes at least local extinction of species, and irreversible changes in community composition; even if the alien species is removed the system does not recover its original state.	Causes changes in community composition, which are reversible if the alien species is removed.	Causes declines in population densities, but no changes in community composition.	Causes reductions in individual fitness, but no declines in native population densities.	No effect on fitness of individuals of native species.
Competition (1)	Competition resulting in replacement or local extinction of one or several native species; changes in community composition are irreversible.	Competition resulting in local or population extinction of at least one native species, leading to changes in community composition, but changes are reversible when the alien species is removed.	Competition resulting in a decline of population size of at least one native species, but no changes in community composition.	Competition affects fitness (e.g. growth, reproduction, defence, immunocompetence) of native individuals without decline of their populations.	Negligible level of competition with native species; reduction of fitness of native individuals is not detectable.
Predation (2)	Predators directly or indirectly (e.g. via mesopredator release) resulting in replacement or local extinction of one or several native species (i.e. species vanish from communities at sites where they occurred before the alien arrived); changes in community composition are irreversible.	Predators directly or indirectly (e.g. via mesopredator release) resulting in local or population extinction of at least one native species, leading to changes in community composition, but changes are reversible when the alien species is removed.	Predators directly or indirectly (e.g. via mesopredator release) resulting in a decline of population size of at least one native species but no changes in community composition.	Predators directly or indirectly (e.g. via mesopredator release) affecting fitness (e.g. growth, reproduction) of native individuals without decline of their populations.	Negligible level of predation on native species.
Hybridization (3)	Hybridization between the alien species and native species is common in the wild; hybrids are fully vigorous and fertile; pure native species cannot be recovered by removing the alien, resulting in replacement or local extinction of native species by introgressive hybridization (genomic extinction).	Hybridization between alien species and native species is common in the wild; F1 hybrids are vigorous and fertile, however offspring of F1 hybrids are weak and sterile (hybrid breakdown) thus limited gene flow between alien and natives; individuals of alien species and hybrids discernible from pure natives, pure native populations can be recovered by removing the alien and hybrids.	Hybridization between alien species and native species and native species is regularly observed in the wild; hybrids are vigorous, but sterile (reduced hybrid fertility), limited gene flow between alien and natives, local decline of populations of pure native species, but pure native species, but pure native species persists.	Hybridization between alien and native species is observed in the wild, but rare; hybrids are weak and never reach maturity (reduced hybrid viability), no decline of pure native populations.	No hybridization between alien species and native species observed in the wild (prezygotic barriers), hybridization with a native species might be possible in captivity.
Transmission of diseases to native species (4)	Transmission of diseases to native species resulting in replacement or local extinction of native species (i.e. species vanish from communities at sites where they occurred before the alien arrived); changes in community composition are irreversible.	Transmission of diseases to native species resulting in local or population extinction of at least one native species, leading to changes in community composition, but changes are reversible when the alien species is removed.	Transmission of diseases to native species resulting in a decline of population size of at least one native species, but no changes in community composition.	Transmission of diseases to native species affects fitness (e.g. growth, reproduction, defence, immunocompetence) of native individuals without decline of their populations.	The alien species is not a host of diseases transmissible to native species or very low level of transmission of diseases to native species; reduction of fitness of native individuals is not detectable.
Parasitism (5)	Parasites or pathogens directly or indirectly (e.g. apparent competition) resulting	Parasites or pathogens directly or indirectly (e.g. apparent competition) resulting	Parasites or pathogens directly or indirectly (e.g. apparent competition) resulting	Parasites or pathogens directly or indirectly (e.g. apparent competition) affecting fitness (e.g. growth,	Negligible level of parasitism or disease incidence (pathogens) on native species,

(*Continued*)

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Table 1. (*Continued.*)

Impact class	Massive (MA) 5	Major (MR) 4	Moderate (MO) 3	Minor (MI) 2	Minimal (ML) 1
	in replacement or local extinction of one or several native species (i.e. species vanish from communities at sites where they occurred before the alien arrived); changes in community composition are irreversible.	in local or population extinction of at least one native species, leading to changes in community composition, but changes are reversible when the alien species is removed.	in a decline of population size of at least one native species but no changes in community composition.	reproduction, defence, immunocompetence) of native individuals without decline of their populations.	reduction of fitness of native individuals is not detectable.
Poisoning/ toxicity (6)	The alien species is toxic/allergenic by ingestion, inhalation, or contact to wildlife or allelopathic to plants, resulting in replacement or local extinction of native species; changes in community composition are irreversible.	The alien species is toxic/allergenic by ingestion, inhalation, or contact to wildlife or allelopathic to plants, resulting in local or population extinction of at least one native species (i.e. species vanish from communities at sites where they occurred before the alien arrived), leading to changes in community composition, but changes are reversible when the alien species is removed.	The alien species is toxic/allergenic by ingestion, inhalation, or contact to wildlife or allelopathic to plants, resulting in a decline of population size of at least one native species, but no changes in community composition (native species richness).	The alien species is toxic/ allergenic by ingestion, inhalation, or contact to wildlife or allelopathic to plants, affects fitness (e.g. growth, reproduction, defence, immunocompetence) of native individuals without decline of their populations.	The alien species is not toxic/allergenic/ allelopathic, or if it is, the level is very low, reduction of fitness of native individuals is not detectable
Bio-fouling (7)	Bio-fouling resulting in replacement or local extinction of one or several native species (i.e. species vanish from communities at sites where they occurred before the alien arrived); changes in community composition are irreversible.	Bio-fouling resulting in local or population extinction of at least one native species, leading to changes in community composition, but changes are reversible when the alien species is removed.	Bio-fouling resulting in a decline of population size of at least one native species, but no changes in community composition.	Bio-fouling affects fitness (e.g. growth, reproduction, defence, immunocompetence) of native individuals without decline of their populations.	Negligible level of bio-fouling on native species; reduction of fitness of native individuals is not detectable.
Grazing/ herbivory/ browsing (8)	Herbivory resulting in replacement or local extinction of one or several native plant species (i.e. species vanish from communities at sites where they occurred before the alien arrived); changes in community composition are irreversible.	Herbivory resulting in local or population extinction of at least one native plant species, leading to changes in community composition, but changes are reversible when the alien species is removed.	Herbivory resulting in a decline of population size of at least one native species, but no changes in community composition.	Herbivory affects fitness (e.g. growth, reproduction, defence, immunocompetence) of individual native plants without decline of their populations.	Negligible level of herbivory on native plant species, reduction of fitness on native plants is not detectable.
Chemical, physical, or structural impact on ecosystem (9,10,11)	Many changes in chemical, physical, and/or structural biotope characteristics; or changes in nutrient and water cycling; or disturbance regimes; or changes in natural succession, resulting in replacement or local extinction of native species (i.e. species vanish from communities at sites where they occurred before the alien arrived); changes (abiotic and biotic) are irreversible.	Changes in chemical, physical, and/or structural biotope characteristics; or changes in nutrient cycling; or disturbance regimes; or changes in natural succession, resulting in local extinction of at least one native species, leading to changes in community composition, but changes are reversible when the alien species is removed.	Changes in chemical, physical, and/or structural biotope characteristics; or changes in nutrient cycling; or disturbance regimes; or changes in natural succession, resulting in a decline of population size of at least one native species, but no changes in community composition.	Changes in chemical, physical, and/or structural biotope characteristics; or changes in nutrient cycling; or disturbance regimes; or changes in natural succession detectable, affecting fitness (e.g. growth, reproduction, defence, immunocompetence) of native individuals without decline of their populations.	No changes in chemical, physical, and/or structural biotope characteristics; or changes in nutrient cycling; or disturbance regimes; or changes in natural succession detectable, or changes are small with no reduction of fitness of native individuals detectable.

(*Continued*)

Table 1. (*Continued.*)

Impact class	Massive (MA) 5	Major (MR) 4	Moderate (MO) 3	Minor (MI) 2	Minimal (ML) 1
Interaction with other alien species (12)	Interaction of an alien species with other aliens (e.g. pollination, seed dispersal, habitat modification) facilities replacement or local extinction of one or several native species (i.e. species vanish from communities at sites where they occurred before the alien arrived), and produces irreversible changes in community composition that would not have occurred in the absence of the species. These interactions may be included in other impact classes (e.g. predation, apparent composition) but would not have resulted in the particular level of impact without an interaction with other alien species.	Interaction of an alien species with other aliens (e.g. pollination, seed dispersal habitat modification) facilitates local or population extinction of at least one native species, and produces changes in community composition that are reversible but would not have occurred in the absence of the species. These interactions may be included in other impact classes (e.g. predation, apparent competition) but would not have resulted in the particular level of impact without an interaction with other alien species.	Interaction of an alien species with other aliens (e.g. pollination, seed dispersal, habitat modification) facilitates a decline of population size of at least one native species, but no changes in community composition; changes would not have occurred in the absence of the species. These interactions may be included in other impact classes (e.g. predation, apparent competition) but would not have resulted in the particular level of impact without an interaction with other alien species.	Interaction of an alien species with other aliens (e.g. pollination, seed dispersal) affects fitness (e.g. growth, reproduction, defense, immunocompetence) of native species, individuals without decline of their populations; changes would not have occurred in the absence of the species. These interactions may be included in other impact classes (e.g. predation, apparent competition) but would not have resulted in the particular level of impact without an interaction with other alien species.	Interaction of an alien species with other aliens (e.g. pollination, seed dispersal) but with minimal effects on native species; reduction of fitness of native individuals is not detectable.

The impact classes are according to the impact mechanisms (IMos) in the GISD (Global Invasive Species Database).

smaller number of papers also analysed the impact of *Marenzelleria arctia* and *Marenzelleria neglecta* in the Baltic Sea. Furthermore, several papers report the impact of *Marenzelleria* as a complex of these three species (*Marenzelleria* spp.) and additional studies referred to *M.* cf. *arctia* and *M.* cf. *viridis*. Thus, if studies of impact are considered at genus level, *Marenzelleria* would be the most studied genus in the world. However, it is important to note that almost all studies on this genus are concentrated in the Baltic Sea region while *F. enigmaticus* was studied in several geographic areas worldwide.

The species with the third highest number of publications was the Mediterranean sabellid *Sabella spallanzanii*, for which all studies were conducted in Australia and New Zealand. The spionid *Boccardia proboscidea* was the fourth species with most of the studies conducted in South-west Atlantic and South Africa.

Approximately 50% of the remaining 34 species studied globally have been investigated in at least one locality in the Mediterranean Sea, while investigations of the rest were conducted at various locations around the world, with only one paper each.

Impact of alien polychaete species

Reviews and meta-analyses were excluded from the analysis of impacts of alien polychaete species to avoid duplicating information. Following the Blackburn *et al.* (2014) classification, we applied the precautionary principle that cryptogenic species are evaluated as if they are aliens, but their impact categorization is modified by the [CG] label. This indicates that it is unclear if the species registered at a location is native or alien, or if the identification is questionable, as is the case for *F. enigmaticus*, *Hydroides dianthus*, *Hydroides operculata*, *Branchiomma boholense*, *Branchiomma bairdi*, *Spirobranchus kraussii*, *Pseudopolydora paucibranchiata* and *Allita succinea*. Although there is no doubt about the presence of *Polydora websteri* in the studies analysed in the present review (Martinelli *et al.*, 2020; Spencer *et al.*, 2020; Waser *et al.*, 2020), its presence must be corroborated in other regions. The species studied in the publications analysed in this review could be assigned to 8 of the 12 impact mechanisms (IMo) defined by Blackburn *et al.* (2014) (Table 1; Figure 11): competition (1), transmission of diseases to native species (4), parasitism (5), biofouling (7), chemical (9), physical (10), structural (11) and interaction with other alien species (12). In general, most of the species studied in the publications analysed here were classified as having chemical, physical or structural impacts (IMo 11,10 and 9) in the ecosystem in the recipient region (Figure 11). Furthermore, 74% of the impacts could be classified as major or massive.

In the case of the spionid species that typically are part of the infauna (*Marenzelleria* species, *Streblospio gynobranchiata*, *Streblospio benedicti*, *P. paucibranchiata*, *Polydora cornuta* and *Boccardia tricuspa*) it was found that they mainly registered IMos in chemical, physical and structural categories with some cases of competition. Species that are shell borers (*P. websteri*, *Polydora rickettsi*, *Polydora hoplura* and *Boccardia pseudonatrix*) were classified with IMos of competition, parasitism and interaction with other alien species. The only species that registered a score in competition and parasitism as well in physical and structural impact in the ecosystem was *B. proboscidea* (Figure 11). In the case of Serpulidae species (reef builders), these registered mainly IMos in physical and structural impact on the ecosystem, additionally *F. enigmaticus* registered impact in transmission of diseases and interaction with other alien species, being the serpulid with most IMos. The IMo of biofouling was only registered in *Hydroides elegans*, *Hydroides dirampha* and *Neodexiospira brasiliensis*.

For the species of Sabellidae (tube dwellers) *S. spallanzanii* registered the most IMos: biofouling, chemical, physical and structural impact; *Desdemona ornata* and *B. bairdi* displayed

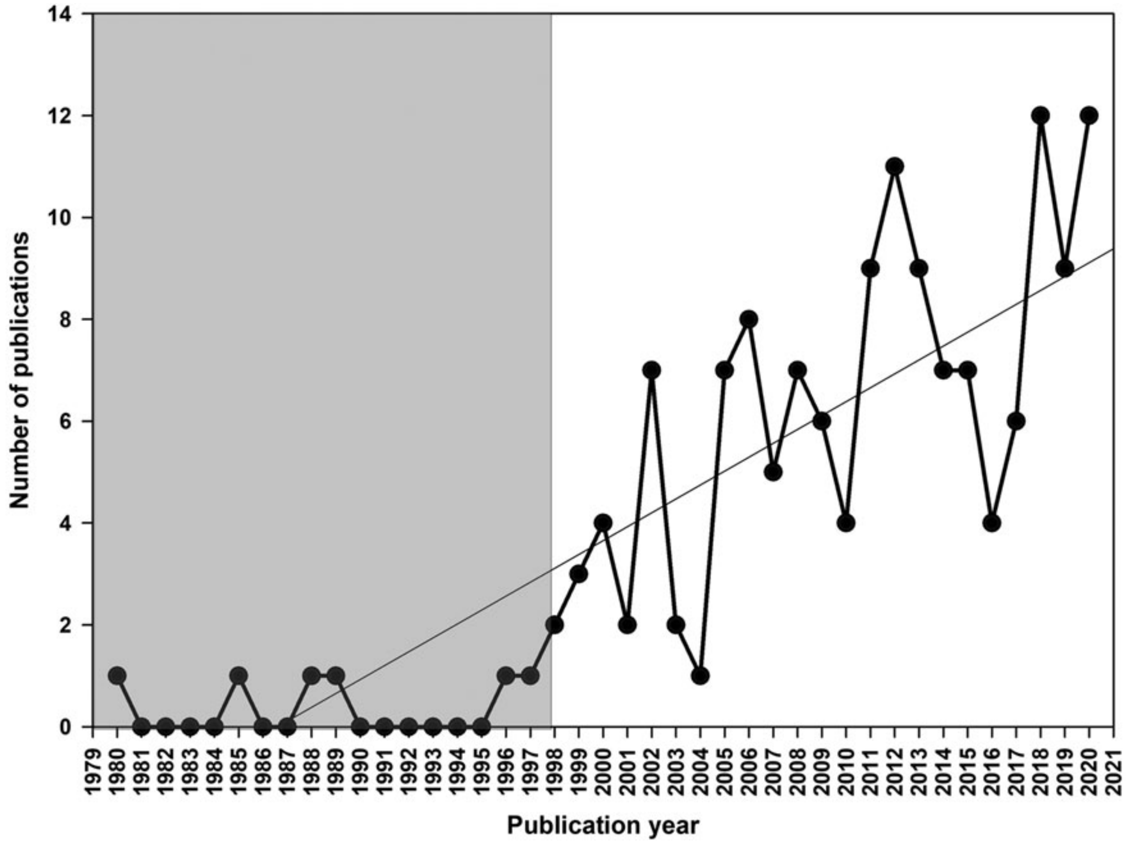

Fig. 2. Yearly number of worldwide published studies concerning impacts of alien marine polychaetes from 1980 to 2020. The grey area indicates the period with lowest rate of publications.

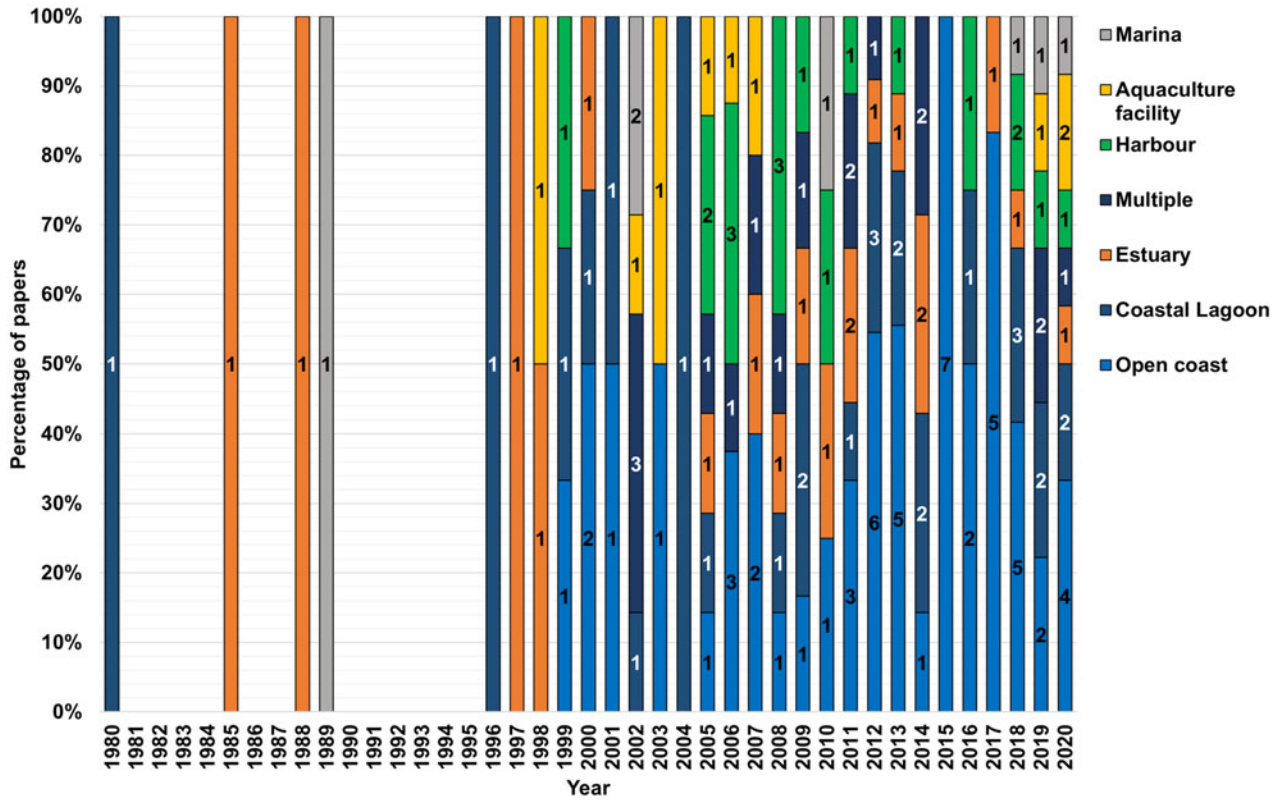

Fig. 3. Yearly number of worldwide studies investigating the impacts of alien marine polychaetes according to the marine system studied. The number of papers is indicated in the bars.

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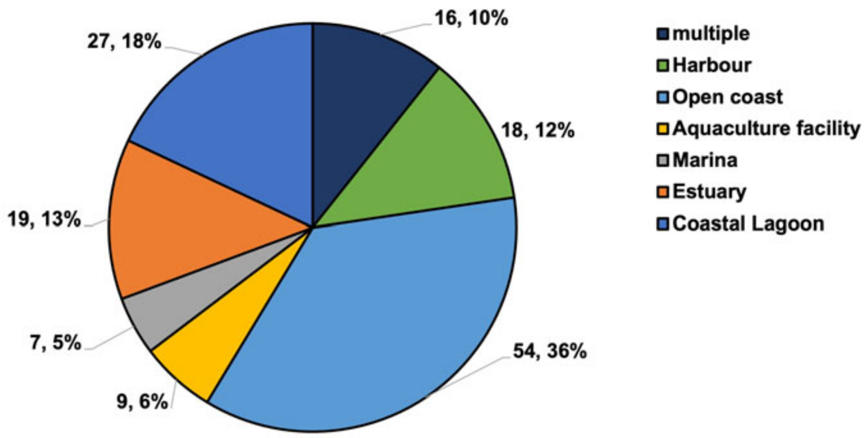

Fig. 4. Total worldwide number of studies investigating impacts of alien marine polychaetes between 1980 and 2020 according to the marine system studied. The first number indicates the number of studies and the second is the percentage of the total number of studies it represents.

physical and/or structural impacts; *B. boholense* registered a competitive impact mechanism and *Terebrasabella heterouncinata* was the only sabellid registering a parasitism IMo.

The remaining species (representatives of infauna) were assigned to Imos of structural impact on ecosystem, except for *Perinereis linea* assigned to IMo of transmission of diseases to native species and *Clymenella torquata* to IMo of interaction with other alien species.

Discussion

Before the 1980s, many researchers accepted that globally widespread species, or cosmopolitanism, was common among polychaetes (Hutchings & Kupriyanova, 2018). However, recent taxonomic revisions have shown that most species that are truly widespread, including polychaetes, have been spread by anthropogenic means (Darling & Carlton, 2018). It is therefore not surprising that the appearance and gradual increase in investigations into the impact of alien species coincided with this change in mind-set regarding 'cosmopolitan' vs alien species. Consequently, for this review, only papers published from 1980 onwards could be found that investigated impacts of alien polychaete species. Nevertheless, studies investigating the impacts of alien polychaete are scarce.

Development of alien impact research

When we analysed the development of research in the three most studied alien polychaete species, the first records of impacts were documented in the 1980s for the serpulid *Ficopomatus enigmaticus* on the Atlantic coast of the USA (Hoagland & Turner, 1980) and the spionid *Marenzelleria viridis* (Essink & Kleef, 1988) in the Wadden Sea, while the first record for the sabellid *Sabella spallanzanii* was in the 1990s (Cohen *et al.*, 2000) in Australia.

The detection of *F. enigmaticus* on the Atlantic coast of the USA was possible due to the implementation of an extended study that monitored marine boring and fouling organisms in the vicinity of Barnegat Bay, New Jersey since 1971 (Hoagland & Turner, 1980). Although the impact of this species has been assessed in several regions of the world, approximately a third of these studies (mainly experiments *in situ* and field surveys) have been conducted in the Mar Chiquita coastal lagoon of the South-west Atlantic (Supplementary Table S1). It is important to indicate that in this lagoon, *F. enigmaticus* was first reported in the early 1970s (Orensanz & Estivariz, 1971), but papers investigating its impact only started being published 30 years later.

Studies on the impacts of *M. viridis* began with more field surveys and reviews, although publications of laboratory experiments, to evaluate the impact of this species mainly in the Baltic Sea region, started in 2003 (Kotta & Ólafsson, 2003).

With regards to *S. spallanzanii*, there is evidence that this species has been present in Australia since at least 1965 (Hutchings, 1999), however, we only found papers on the impact of this species in Australia (mainly experiments *in situ*) starting in the late 1990s (Cohen *et al.*, 2000). Meanwhile, in New Zealand, *S. spallanzanii* was detected by a national surveillance programme in 2008 (Read *et al.*, 2011) but papers related to the impact of this species included a theoretical model, two experiments *in situ* and one field survey, in the period 2018–2020 (Supplementary Table S1).

The number of publications, types of research and timing of the research seem to be related to the implementation of monitoring programmes of estuaries and coastal areas and groups of research in some regions of the world. For example, the National Danish Aquatic Monitoring and Assessment Programme has been operating since the late 1980s in areas of the Wadden Sea, North Sea and Baltic Sea (Svendsen *et al.*, 2005). The Baltic Sea, in particular, has an over 50-year-long tradition of monitoring soft-bottom macrofaunal communities, providing a unique time series to study changes over time (Nygård *et al.*, 2020). This tradition was reinforced with the Helsinki Commission (HELCOM) Baltic Sea Action Plan, adopted in 2007 by the coastal countries of the Baltic Sea (Denmark, Estonia, Finland, Germany, Latvia, Lithuania, Poland, Russia, Sweden as well as the European Community) which is structured around a set of ecological objectives used to define indicators and targets that include a regional monitoring implementation (Backer *et al.*, 2010). In the South-west Atlantic, the presence and continuous activity of research groups has focused on benthic communities in institutions such as Universidad Nacional de Mar del Plata in Argentina. Here, researchers Rodolfo Elias, Maria Cielo Bazterrica, Maria L. Jaubet, Griselda V. Garaffo and Carlos Martin Bruschetti determined that in the last 50 years, changes in the community structure were induced by sewage discharge and introduction of non-indigenous species (Llanos *et al.*, 2019; Martinez *et al.*, 2020). In Australia research groups lead by the polychaete taxonomists Pat Hutchings, Elena Kupriyanova and Christopher J. Glasby are active at national museums of the country, while in New Zealand the research by Geoffrey Read at the National Institute of Water and Atmospheric Research is active in the taxonomy of polychaetes. In these last two countries the polychaete taxonomists collaborate with institutions and are involved in programmes in biosecurity such as the Center for Introduced Marine Pests (CRIMP) established by Australia in the early 1990s and the Biosecurity Act of 1993 in New Zealand which provides for targeted surveillance in harbours,

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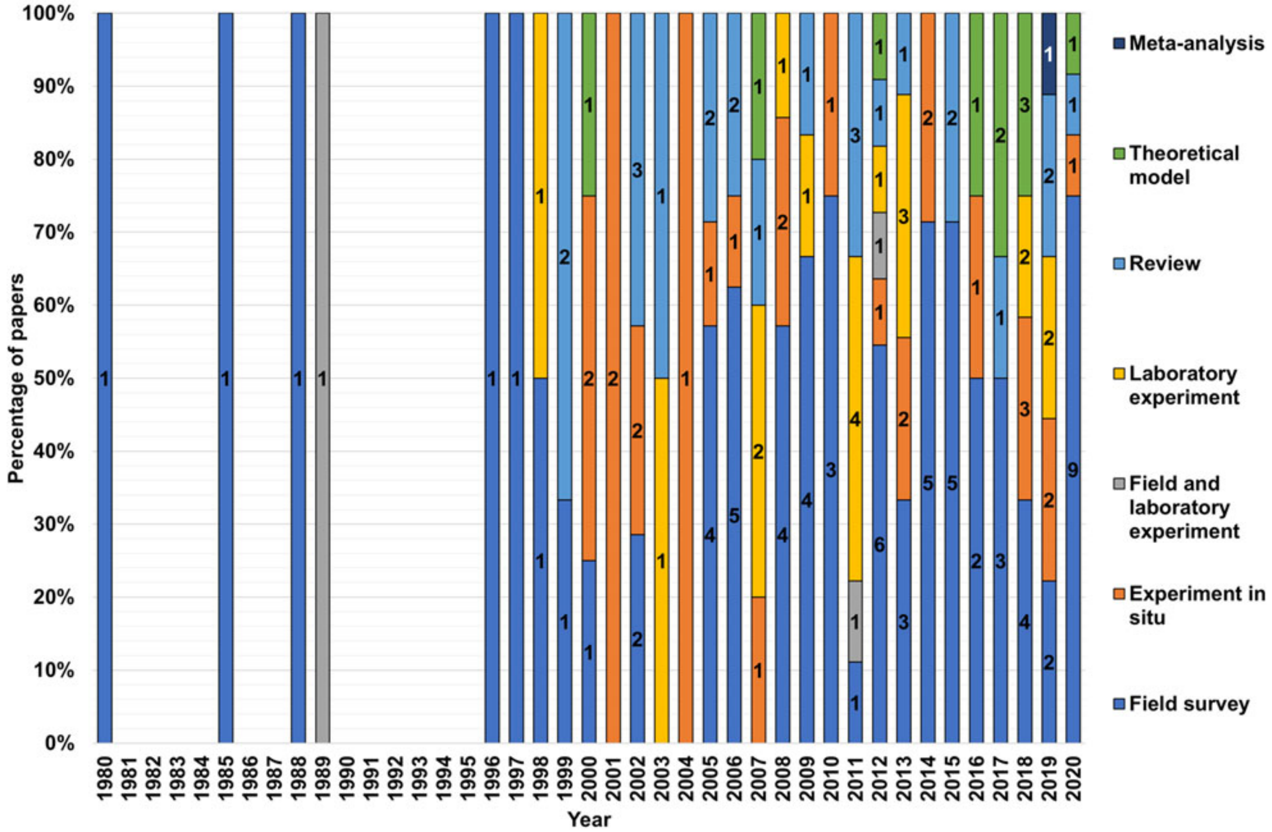

Fig. 5. Yearly number of worldwide studies investigating the impacts of alien marine polychaetes according to the study type. The number of papers is indicated in the bars.

ports, marinas and high-value natural environments (Atalah *et al.*, 2019).

Contrastingly, we found little information about the impact of alien polychaete species in the rest of coastal Europe except for the Mediterranean and Baltic Sea. This could be because the European Water Framework Directive (WFD) did not refer explicitly to alien species; this omission was rectified for the marine environment in the enactment of the Marine Strategy Framework Directive (MSFD). Unfortunately, countries in Europe are inconsistent in their use of historical dates to determine when a species is considered alien and few countries monitor alien species specifically for the WFD (Lehtiniemi *et al.*, 2015; Boon *et al.*, 2020). However, there are efforts to create lists of alien marine species which include polychaetes in Europe (Katsanevakis *et al.*, 2014) and specifically in the Mediterranean (Streftaris & Zenetos, 2006; Zenetos, 2010; Gerovasileiou *et al.*, 2016; Zenetos *et al.*, 2017), where the alien status of several species is questionable. With respect to the creation of lists of alien marine species, Marchini *et al.* (2015) point out the importance of 'best practices' to standardize lists of marine alien species to avoid uncertainty in the species' taxonomic identification or the occurrence of the species in a specific area that will consequently determine its status as an alien. The implementation of monitoring programmes and 'best practices' in the development and elaboration of lists of marine alien species in different regions of the world will undoubtedly help in the development of the study field regarding impacts of alien polychaete species.

In general, except for papers that focus on *F. enigmaticus*, *M. viridis* and *S. spallanzanii*, most of the remaining papers about the impact of alien polychaete species have been field

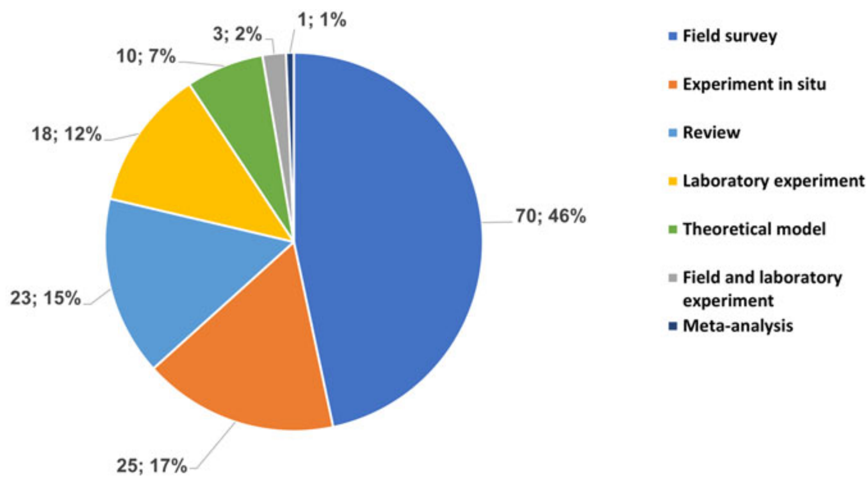

Fig. 6. Total worldwide number of studies investigating impacts of alien marine polychaetes between 1980 and 2020 according to the study type. The first number indicates the number of studies and the second is the percentage of the total number of studies it represents.

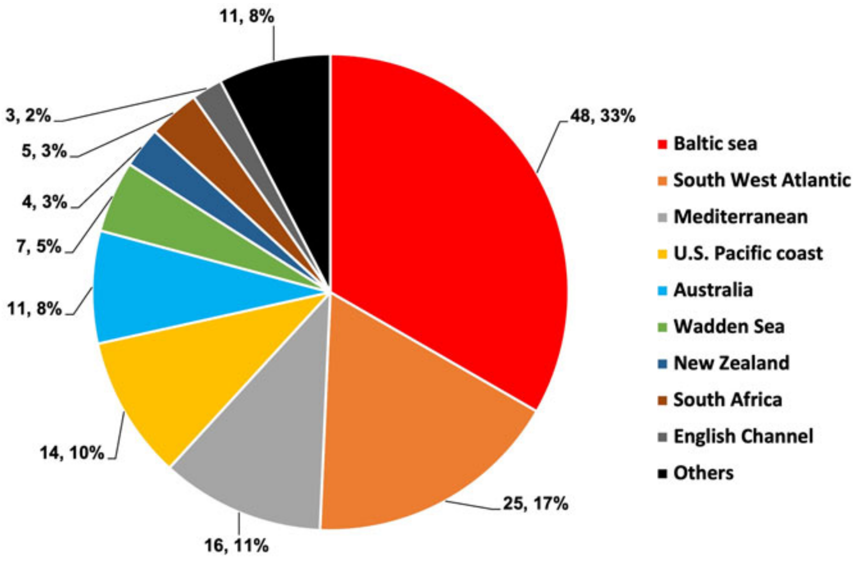

Fig. 7. Total worldwide number of studies investigating impacts of alien marine polychaetes between 1980 and 2020 according to the region of origin. The first number indicates the number of studies and the second is the percentage of the total number of studies it represents.

surveys. The least frequently conducted study types were field and laboratory experiments and meta-analyses, probably because conducting the former is logistically complicated, while too few data about impacts are available to conduct meaningful meta-analyses. However, the paucity of these study types are linked, because experiments are key in the generation of quantitative data to determine whether or not alien species are causing statistically significant alterations in an environment (Olenin & Minchin, 2011).

The least studied systems are marinas and aquaculture facilities, even though they are focal points of entry for alien species (Peters *et al.*, 2014; Simon & Sato-Okoshi, 2015). But as artificial environments, evaluating impact there is likely more complex. Furthermore, although the presence of shell-boring polychaete species on mariculture farms has been well documented (Sato-Okoshi *et al.*, 2008; Simon & Sato-Okoshi, 2015; Spencer *et al.*, 2020), problems with regards to the reliable identification of these species (if they are even identified to species level) has hindered the process of associating these impacts to alien or indigenous species (as discussed in more detail below). This, in turn, could have led many such studies from aquaculture facilities being overlooked by this review due to our search terms focusing on alien-orientated keywords. However, mariculture studies have rarely investigated the impacts of focal species outside studied mariculture farms (e.g. Culver & Kuris, 2000; Kuris, 2002) or have only identified to genus (Stenton-Dozey *et al.*, 1999), probably including indigenous and alien species.

Impact of alien species

As mentioned previously, there is a lag between first detection of alien species and the first studies on impact. According to Blackburn *et al.* (2015) the process whereby a species becomes an alien can be divided into the sequential stages of transport, introduction, establishment and spread. In the species analysed in this review, most of the IMos were classified as 'massive', which seems to reflect that alien polychaete species are probably only studied once significant impacts in the ecosystem have been noticed during establishment and spread stages in the ecosystem. The impacts of species reviewed here are strongly related to their biology and lifestyles and depends on whether the species build conspicuous reefs, are tube-dwellers, shell-borers or are part of the infauna.

Tube/reef building species

The serpulid *F. enigmaticus* is a calcareous tube builder that is 6–12 mm long (Fauvel, 1923), and is considered an ecosystem engineer, as it may directly or indirectly control the availability of resources to other organisms by changing the physical state of biotic or abiotic materials (Jones *et al.*, 1994). This species, particularly in Mar Chiquita Lagoon in Argentina, builds intertidal calcareous reefs that grow up to 7 m in diameter and 0.5 m in height (Obenat & Pezzani, 1994) that have been expanding along this lagoon since 1975 until it covered 80% of this ecosystem (Schwindt & Iribarne, 2000). These reefs have influenced many physical effects including the transport of sediments and flow of water (Schwindt *et al.*, 2004). The ongoing investigation of these reefs has made it possible to determine the cascading effects of this species and its influence in several ecological aspects such as changes in the community structure of native benthic communities (Schwindt *et al.*, 2001) and the effects of suspension feeding and biodeposition (Bruschetti *et al.*, 2011). The suspension feeding activity of *F. enigmaticus* affects the composition of phytoplankton (Pan & Marcoval, 2014) and zooplankton (Bruschetti *et al.*, 2016) and could be seen as a positive impact in some areas where it is introduced, because it contributes to maintaining water quality in polluted systems (Davies *et al.*, 1989). Other positive aspects observed have been the increase of feeding and resting areas for migratory and local birds (Bruschetti *et al.*, 2009), and the interaction with native macroalgae (*Polysiphonia subtilissima*) in a mutually beneficial relationship in the establishment of both species (Bazterrica *et al.*, 2014).

However, other aspects that are considered as negatives is that *F. enigmaticus* could be an intermediary in the transmission of parasites (Etchegoin *et al.*, 2012), and facilitates the spread of other alien species (Bazterrica *et al.*, 2020). Another negative aspect of serpulid alien species *F. enigmaticus* is the dense encrustations on artificial substrates such as concrete marine facilities, buoys and shipping hulls that potentially complicate maritime navigation and marine recreational activities (Davies *et al.*, 1989; Bezuidenhout & Robinson, 2020).

Importantly, this species is not always an extensive reef builder in all introduced sites. For example, in South Africa, it only forms small aggregations in some localities (Davies *et al.*, 1989; McQuaid & Griffiths, 2014; Bezuidenhout & Robinson, 2020), likely due to the low temperatures (<20°C) in winter (Miranda *et al.*, 2016). Furthermore, *F. enigmaticus* is most successful in higher temperatures usually associated with low oxygen

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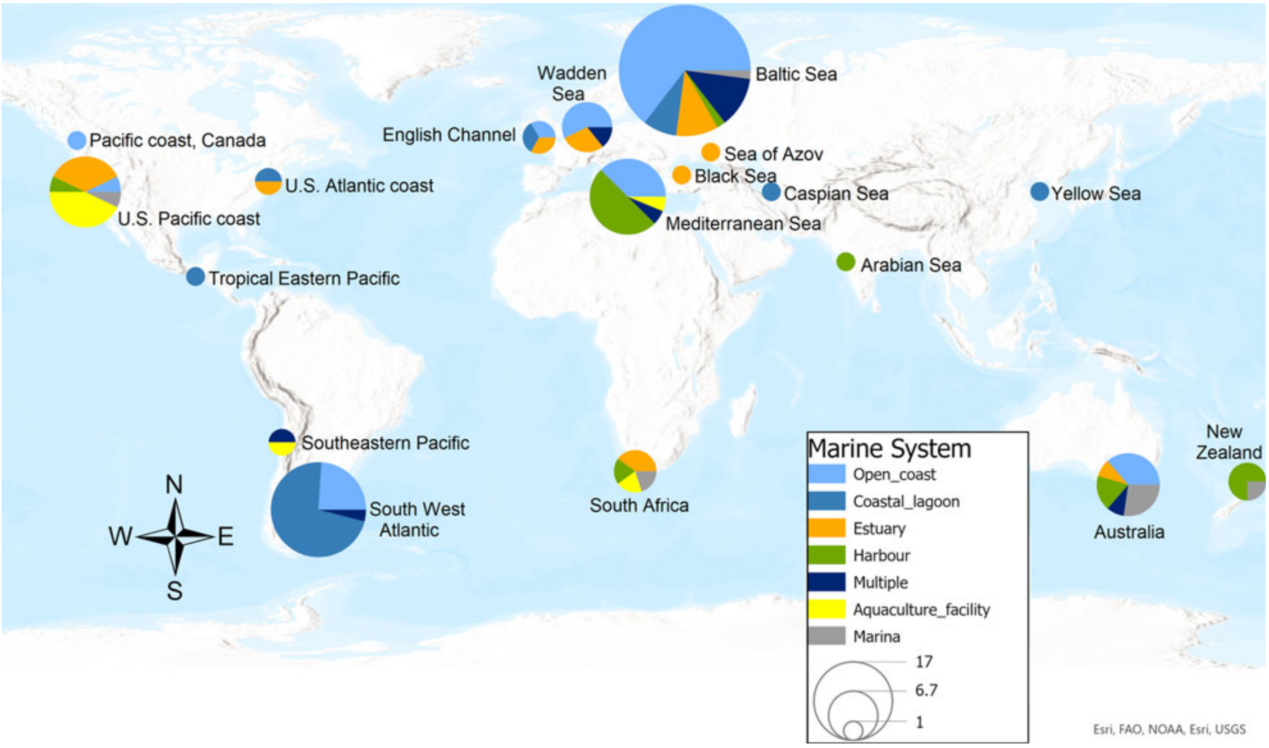

Fig. 8. Total number of regional studies investigating impacts of alien marine polychaetes between 1980 and 2020 according to the studied marine system. Circle size indicates number of studies.

conditions in which it may have an advantage over native species that are less tolerant of such conditions (Jewett *et al.*, 2005). In New Jersey *F. enigmaticus* overcame the low winter temperatures by settling in thermal effluent from a nuclear plant (Hoagland & Turner, 1980). This is an important consideration for climate change conditions because this species could become more widespread in areas where previously environmental conditions were not suitable for tropical and subtropical species.

The impact of alien serpulid species that have the potential to form extensive reefs may also depend on the availability of artificial structures. For example, the impact of *Ficopomatus uschakovi* introduced in the Tropical Pacific (Mexico) is considered

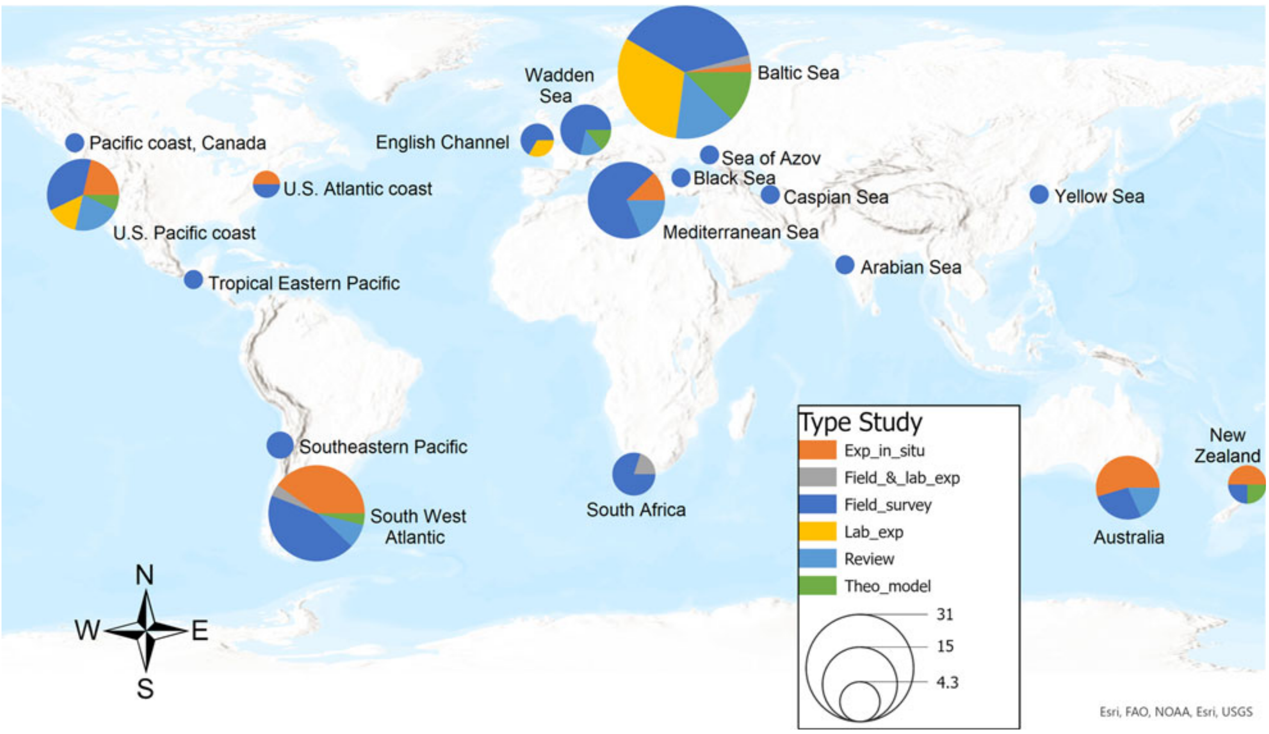

Fig. 9. Total number of regional studies investigating impacts of alien marine polychaetes between 1980 and 2020 according to the types of studies conducted. Circle size indicates number of studies.

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Table 2. List of alien polychaetes species studied in the 150 published studies covered in this review

Family	Species	Possible origin of introduction	Area where the impact was documented	Possible vector of introduction	Reference
Ampharetidae	*Hobsonia florida* (Hartman, 1951)[1]	?	US Pacific coast	?	139
Capitellidae	*Notomastus aberans* Day, 1957[1]	?	Mediterranean Sea	Shipping	25
	Notomastus mossambicus (Thomassin, 1970)[1]	Lessepsian	Mediterranean Sea	Shipping	73
Cirratulidae	*Kirkegaardia dorsobranchialis* (Kirkegaard, 1959)[1]	?	Mediterranean Sea	Shipping	25
Glyceridae	*Glycinde bonhourei* Gravier, 1904[1]	Lessepsian	Mediterranean Sea	Shipping	73
Maldanidae	*Clymenella torquata* (Leidy, 1855)[1]	Atlantic and Gulf coasts of North America	Pacific coast, Canada	Aquaculture	70
Nereididae	[CG] *Alitta succinea* (Leuckart, 1847)[1]	?	Baltic Sea	?	92
	Leonnates indicus Kinberg, 1865[1]	?	Mediterranean Sea	?	14
	Perinereis linea (Treadwell, 1936)[1]	NW Pacific, South Korea	Mediterranean Sea	Live-fishing bait	62
	Pseudonereis anomala Gravier, 1899[4]	Indo-Pacific	Mediterranean Sea	Shipping	25, 66, 96, 99
Sabellidae	[CG] *Branchiomma bairdi* (McIntosh, 1885)[3]	Caribbean	Mediterranean Sea	?	55, 61
	[CG] *Branchiomma boholense* (Grube, 1878)[1]	?	Mediterranean Sea	?	27
	Desdemona ornata Banse, 1957[1]	?	Black Sea	?	93
	***Sabella spallanzanii* (Gmelin, 1791)[15]**	Mediterranean	Australia, New Zealand	Shipping, ballast water	7, 9, 13, 19, 24, 33, 59, 66, 104, 109, 115, 127, 128, 138, 141
	Terebrasabella heterouncinata Fitzhugh and Rouse, 1999[6]	South Africa	US Pacific coast	Aquaculture	66, 106, 126, 131, 137, 144
Serpulidae	**[CG] *Ficopomatus enigmaticus*** (Fauvel, 1923)**[35]**	Australia	South-west Atlantic, South Africa, US Atlantic and Pacific coast, Mediterranean Sea, Black Sea, English Channel, Baltic Sea,	Shipping, fouling	3, 6, 11, 19, 21, 22, 23, 40, 41, 51, 52, 53, 58, 66, 67, 74, 76, 78, 84, 85, 87, 89, 91, 93, 98, 101, 115, 117, 119, 123, 124, 130, 132, 135, 136, 147, 150
	Ficopomatus uschakovi (Pillai, 1960)[1]	Indo-West Pacific and Gulf of Guinea	Tropical Eastern Pacific	NA	71
	[CG] *Hydroides dianthus* (Verrill, 1873)[1]	?	Mediterranean	Aquaculture	21, 28, 84, 99
	Hydroides dirampha Mörch, 1863[1]	?	Mediterranean	Shipping	15
	Hydroides elegans (Haswell, 1883) [nomen protectum][5]	?	Mediterranean, Australia	Shipping, fouling	15, 66, 84, 97, 99
	[CG] *Hydroides operculata* (Treadwell, 1929)[3]	Indian Ocean	Mediterranean	Shipping	84, 113, 116
	Neodexiospira brasiliensis (Grube, 1872)[1]	?	English Channel	?	145
	Protula tubularia (Montagu, 1803)[1]	Sri Lanka	Arabian Sea	Shipping, ballast water	88
	[CG] *Spirobranchus kraussii* (Baird, 1864)[4]	Indian Ocean	Mediterranean	Shipping	66, 84, 113, 116

(*Continued*)

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Table 2. (*Continued.*)

Family	Species	Possible origin of introduction	Area where the impact was documented	Possible vector of introduction	Reference
Spionidae	*Boccardia pseudonatrix* Day, 1961 (as *B. knoxi*)[2]	Tasmania?	Australia	Aquaculture	66, 103
	Boccardia proboscidea **Hartman, 1940[11]**	West coast North America	Southwest Atlantic, South Africa	Shipping, ballast water, aquaculture	12, 19, 20, 21, 26, 42, 45, 47, 63, 75, 112
	Boccardia tricuspa (Hartman, 1939)[1]	?	Southeastern Pacific	?	8
	Marenzelleria arctia (Chamberlin, 1920)[10]	North America	Baltic Sea	Shipping, ballast water	18, 19, 29, 30, 44, 48, 56, 57, 60, 81
	Marenzelleria neglecta Sikorski & Bick, 2004[12]	North America	Baltic Sea, Sea of Azov	Shipping, ballast water	17, 29, 30, 36, 60, 76, 80, 90, 94, 108, 110, 111
	Marenzelleria viridis **(Verrill, 1873)[22]**	North America	Baltic Sea, Wadden Sea	Shipping, ballast water	5, 29, 30, 34, 54, 60, 65, 66, 72, 82, 83, 85, 92, 122, 125, 129, 132, 133, 140, 142, 143, 146, 148
	Polydora cornuta Bosc, 1802[7]	Atlantic Ocean	Black Sea, Mediterranean Sea	Shipping, ballast water	66, 84, 93, 99, 114, 116, 118
	Polydora hoplura Claparède, 1868[4]	Japan?	Australia, South Africa, South-eastern Pacific	Aquaculture	66, 103, 112, 120
	Polydora rickettsi Woodwick, 1961[1]	NA	South-eastern Pacific	NA	8
	[CG] *Polydora websteri* Hartman in Loosanoff & Engle, 1943[3]	Asia	Wadden Sea, US Pacific coast	Aquaculture	1, 2, 4
	Pseudopolydora kempi (Southern, 1921)[1]	NA	US Pacific coast	NA	139
	[CG] *Pseudopolydora paucibranchiata* (Okuda, 1937)[4]	Japan	Mediterranean, US Pacific coast	Shipping, ballast water	66, 84, 100, 121
	Streblospio benedicti Webster, 1879[2]	Australia	US Pacific coast	Shipping, fouling	87, 149
	Streblospio gynobranchiata Rice & Levin, 1998[8]	Atlantic Ocean	Black Sea, Caspian Sea, Mediterranean,	Shipping, ballast water	16, 66, 84, 93, 99, 114, 116, 118
	Polydora spp.[1]	?	Australia	?	107
	Marenzelleria **spp.[19]**	North America	Baltic Sea	Shipping, ballast water	10, 19, 31, 32, 35, 37, 38, 39, 43, 46, 49, 50, 64, 69, 77, 79, 86, 95, 105
	Marenzelleria cf. arctia[1]	?	Baltic Sea	?	68
	Marenzelleria cf. viridis[1]	North America	Baltic Sea	?	134
Sternaspidae	*Sternaspis scutata* (Ranzani, 1817)[1]	?	English Channel	?	102
Terebellidae	*Pista unibranchia* Day, 1963[1]	?	Mediterranean Sea	Shipping	25

[CG], Cryptogenic species.
The superscript number indicates the number of publications that included information about the impact of the species. Species with more than 10 papers are indicated in bold.
The references are indicated with the numbers that appear in the supplementary material, Table S1.

minimal, probably because of the absence of artificial hard substrates in the lagoon where it was introduced (Bastida-Zavala & García-Madrigal, 2012). By contrast, *Hydroides dianthus* formed reefs over hard artificial substrata in an artificial coastal lake in China; here the serpulid reefs provided a habitat for the settlement and proliferation of the native jellyfish *Aurelia coerulea* in the lake (Dong *et al*., 2018). The presence of serpulids over artificial substrates has been observed in structures of aquaculture facilities in the Mediterranean where *Hydroides elegans* and *Hydroides dirampha* were part of the community of hard substrata around a fish farm (Mangano *et al*., 2019). In hard artificial substrates in the Mumbai harbour in India, the serpulid *Protula tubularia* was reported as a dominant alien species (Gaonkar *et al*., 2010).

The use of natural hard substrates by alien serpulids has also been documented in the Mediterranean, where *H. elegans* and *H. dianthus* build mass calcareous structures associating with beds of *Mytilus galloprovincialis* providing new microenvironments (Çinar *et al*., 2008). In other cases, aggregations of *Hydroides operculata* and '*Spirobranchus kraussii*' (its taxonomic status is discussed below) have been observed both in natural and artificial hard substrates in the Mediterranean, where they cause changes in the benthic community structure and represent a potential additional impact for shipping activities (Çinar, 2006).

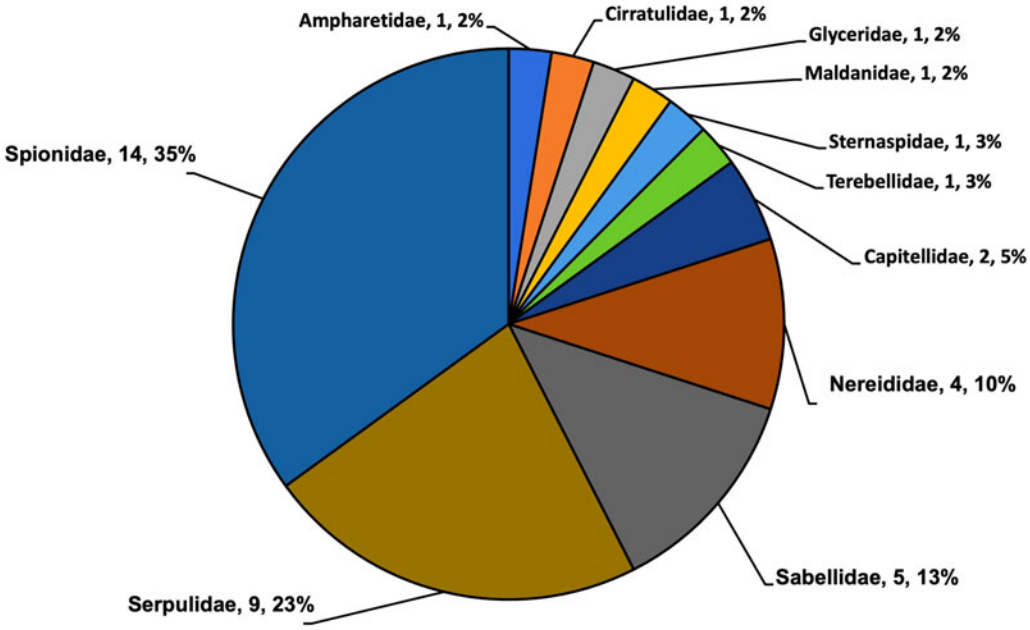

Fig. 10. Total number of alien marine polychaetes species, by family, for which impacts were reported in the reviewed studies published between 1980 to 2020.

Alien serpulids are also not limited to using hard substrates. In the English Channel *Neodexiospira brasiliensis* was reported as biofouling native eelgrass *Zostera marina* and the native algae *Fucus serratus* as well as the alien algae *Sargassum muticum* (Critchley *et al*., 1997).

Serpulids are not the only polychaetes that form reefs. Another important intertidal reef-building species is the spionid *Boccardia proboscidea* that clearly displays how context dependent environmental impacts can be. In its native range it occupies a wide ecological niche, burrowing into muddy and sandy sediments as well as into soft rock and crevices among encrusting algae (Hartman, 1940; Woodwick, 1963; Gibson *et al*., 1999). But as an alien, this tube-dweller builds reefs in intertidal areas previously enriched by organic matter coming from sewage discharges in Mar del Plata (Argentina) (Jaubet *et al*., 2011). This species differs from *F. enigmaticus* as the reefs, that may be 1 to 5 m^2 in diameter and up to 30 cm in height, are formed from sandy tubes and can take different forms that can evolve into a continuous platform, as is typical in impacted environments (Garaffo *et al*., 2012). However, unlike *F. enigmaticus*, these reefs cannot be seen as biodiversity hotspots, as the presence of this species demonstrates great environmental deterioration (Garaffo *et al*., 2012). Some of the negative impacts *of B. proboscidea* includes that its spread resulted in the eventual smothering of the native mussel *Brachiodontes rodriguezii* and a reduction in the diversity in the epilithic intertidal community in the sewage impacted sites in Mar del Plata (Jaubet *et al*., 2013; Elías *et al*., 2015).

The success of *B. proboscidea* is associated with its opportunistic and poecilogonous nature (r-strategy), which allows it to produce both planktotrophic and adelphophagic larvae (Simon & Sato-Okoshi, 2015). Furthermore, they thrive under conditions of organic enrichment either from sources of sewage effluent (Jaubet *et al*., 2018) or from high accumulation of nutrients coming from abalone farms where *B. proboscidea* is a secondary boring species that has infested cultured abalone shells (Simon *et al*., 2006). Due to these characteristics, this spionid has been classified as tolerant to moderate and high levels of organic contamination and could be used as an environmental indicator (Saracho Bottero *et al*., 2020).

All this background is important for environmental managers to consider, as the establishment, progression and outcome of an invasion may be dependent on what a specific species' reaction is to a novel environment.

Another group of tube-building polychaetes that are widely investigated are the sabellids. These polychaetes can form dense three-dimensional colonies, allowing them to function as ecosystem engineers. But unlike the serpulids, their tubes are made of hardened secreted mucus and are usually covered with algae debris and shell fragments and the colonies occur in the subtidal (Arias *et al*., 2013*a*, 2013*b*; Douglas *et al*., 2020).

The filter-feeding *S. spallanzanii* (80–400 mm in length) is one of the largest species in the family Sabellidae with a leathery tube and spiral feeding fan that can reach 10–15 cm in diameter which markedly modifies local water currents and rates of sediment deposition (Hutchings, 1999; O'Brien *et al*., 2006). However, the magnitude of the impact is not clear-cut. Cohen *et al*. (2000) suggested that in Australia, *S. spallanzanii* established in high numbers in subtidal habitats that were most likely unoccupied by native species, while Ross *et al*. (2007) suggested that the effects of the species on soft sediment assemblages could be negligible. However, experiments *in situ* showed that this sabellid strongly influences recruitment of other sessile taxa (e.g. barnacles, bryozoans and sponges) (Holloway & Keough, 2002*a*, 2002*b*) or the post-colonization process of other macrofauna (O'Brien *et al*., 2006). In fact, most of the studies conducted in Australia and New Zealand showed that this species causes changes in the composition of macrofauna and nutrient cycling with regards to the process of denitrification and bacterial communities (Ross *et al*., 2013; Atalah *et al*., 2019; Tait *et al*., 2020). It has even been suggested that the presence of *S. spallanzanii* increased the local biodiversity, although this increase probably also included other alien species (Douglas *et al*., 2020). Thus *S. spallanzanii* induces the same cascade effects observed for *F. enigmaticus*, but in a different ecological niche.

Similar impacts have been observed in the Mediterranean with other alien sabellids. *Branchiomma bairdi* is particularly abundant in degraded areas such as harbours and marinas, where their tubes influence and modify the habitat (Arias *et al*., 2013*a*,

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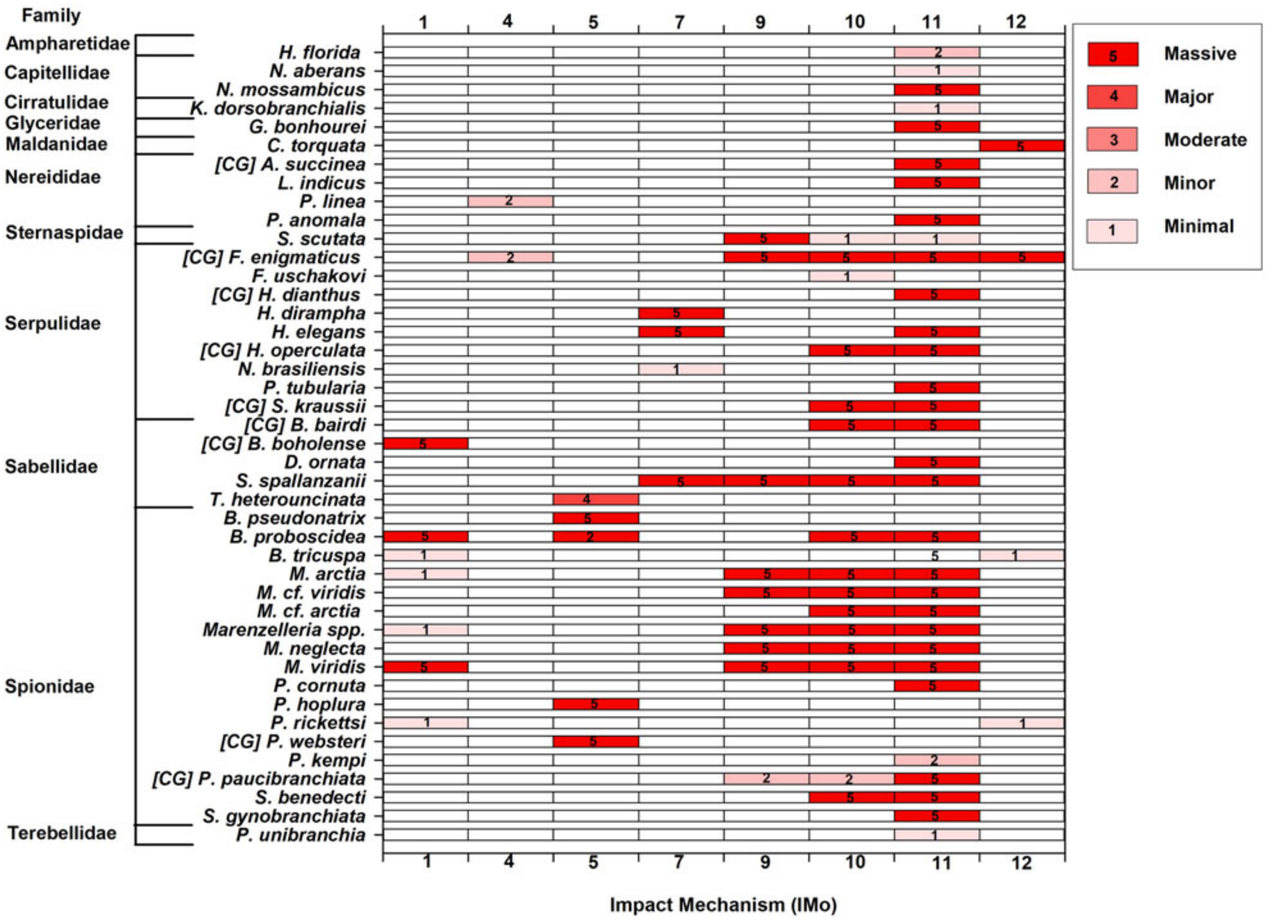

Fig. 11. Scores of the impact mechanism (IMo) of alien polychaete species studied worldwide between 1980 and 2020 according to the Blackburn *et al.* (2014) system of classification. IMos: 1 = Competition; 4 = Transmission of diseases to native species; 5 = Parasitism; 7 = Bio-fouling; 9 = Chemical impact on ecosystem; 10 = Physical impact on ecosystem; 11 = Structural impact on ecosystem; 12 Interaction with other alien species. Scale 5 = Massive; 4 = Major; 3 = Moderate; 2 = Minor; 1 = Minimal.

2013*b*). However, a positive aspect of this sabellid in the Mediterranean is its efficiency in removing bacteria which may counteract the effects of microbial pollution, thus playing a potential role for *in situ* bioremediation (Stabili *et al.*, 2014).

Tube dwellers have also been implicated in having a negative impact on economically important molluscs. For example, experiments conducted *in situ* in the Mediterranean suggest that the sabellid *Branchiomma boholense* dominate the use of substrates over the mussel *M. galloprovincialis* (Lezzi & Giangrande, 2018). Also, aggregations of the North-west Atlantic bamboo maldanid *Clymenella torquata*, an intertidal tube-dwelling ecosystem engineer widely distributed in British Columbia (Canada) and established in Samish Bay (Washington), create a spongy porous substrate that has proved detrimental to local commercial oyster farms (who typically grow oysters on the bottom of mudflats), causing the oysters to sink into the sediment and suffocate (Mach *et al.*, 2012).

Shell-boring species

As previously mentioned, impacts of shell borers in farmed molluscs are usually due to species of the Spionidae family that live in burrows within the shells of cultured molluscs, reducing the hosts' shell integrity, growth, survivorship and market value (Spencer *et al.*, 2020). Which species become problematic depend on their ability to reach mollusc farms and flourish under different culture conditions, enabling some species to become pests (Simon & Sato-Okoshi, 2015). Once established on farms, alien worms may spread even further when they escape from the farms and infest indigenous molluscs and disperse as larvae (Moreno *et al.*, 2006; Williams *et al.*, 2016). This release of alien boring species from mollusc farms to the natural ecosystem may have negative impacts on the native fauna (Radashevsky & Olivares, 2005). For example, in Australia it was found that the boring activity of the alien species *B. proboscidea*, *Boccardia pseudonatrix* and *Polydora hoplura* caused major damage in both cultivated and native molluscs especially when compared with the boring activity of native polydorid species in native mollusc species (Sato-Okoshi *et al.*, 2008). Furthermore, the alien boring species *Boccardia tricuspa* and *Polydora ricketsii* coexisted with native boring species (*Dipolyodra huelma* and *Dodecaceria opulens*) on both cultivated and natural mollusc populations in Chile (Neill *et al.*, 2020). Such alien species pose a great risk to commercial oyster farms. For example, in the Wadden Sea the alien *Polydora websteri* infested oyster reefs of the alien Pacific oysters *Crassostrea* (*Magallana*) *gigas* that are located close to commercial oyster farms, representing a potential economic problem to the oyster farms (Waser *et al.*, 2020), following what occurred in the Pacific west coast of the USA, where *P. websteri* was introduced recently and has considerably impacted commercial oyster farms of *C. gigas* (Martinelli *et al.*, 2020).

The eradication of an alien boring polychaete species in aquaculture facilities is a complex process. The only documented case of successful eradication of an alien polychaete species is of the shell-boring sabellid *Terebrasabella heterouncinata*, introduced to the coasts of California as an epizoic contaminant on South African abalone imported in the 1980s (Culver & Kuris, 2000).

This pest caused extensive shell deformities and greatly retarded body growth of abalone in mariculture farms in the introduced area (Leighton, 1998). The successful control of this species began with the correct taxonomic identification, conducted by Fitzhugh & Rouse (1999) as at the moment of the infestation neither genus nor species had been described. To mitigate the impact of this species during 2002–2006 all the native gastropods (potential hosts) were removed from close to the aquaculture facilities to avoid the dispersal of *T. heterouncinata*. This, together with thermal and fresh water treatments in the mariculture farms to eliminate the pest on the abalone, meant that *T. heterouncinata* was no longer detected in subsequent monitoring in the area (Leighton, 1998; Culver & Kuris, 2000; Moore *et al*., 2007). Thus, the control and management of alien polychaete shell-boring species begins with a correct taxonomic identification and continues with quick actions before the alien species reach the stage of establishment and spread.

Infaunal species

The impacts of alien spionids are not limited to reef-builders or shell-borers, but also includes infaunal species occupying soft-bottom sediments. In the Baltic Sea the alien *M. viridis* is not as conspicuous as the aforementioned species as it is part of the infauna where it is a burrowing deposit feeder, although it may also filter-feed (Dauer *et al*., 1981). The reason for the notoriety of this species was not its size (reach a length up to 10 cm), but its high abundance of 2600 to almost 20,000 individuals m^{-2} and the greater depth to which it burrows (20–40 cm) relative to native fauna (Essink & Kleef, 1988; Zmudziński, 1996). The bioturbation caused by the burrowing activity of *M. viridis* in the sediment could potentially affect redox conditions, modify diagenetic reaction pathways and change the microbial community structure (Kristensen *et al*., 2011; Quintana *et al*., 2011). Although some authors suggest that this species occupied an empty niche (Essink *et al*., 1998), a study conducted by Kotta & Ólafsson (2003) suggests that *M. viridis* could compete for food with the native amphipod *Monoporeia affinis*.

Although *M. viridis* is morphologically similar to its alien sibling species *Marenzelleria arctia* and *Marenzelleria neglecta* in the Baltic Sea, Renz & Forster (2013) observed in laboratory experiments that these three species have shown important ecological differences in their bioturbation of the sediment and therefore the authors did not recommend a functional grouping of these sibling species. This is once again an important indication that even in apparently closely related species there are important ecological differences.

Infaunal alien polychaetes have also been implicated in studies on marine pollution and benthic community composition. In the Mediterranean, alien polychaetes such as *Desdemona ornata*, *F. enigmaticus*, *Polydora cornuta* and *Streblospio gynobranchiata* have contributed up to almost 50% of the polychaete community in polluted areas (Çinar *et al*., 2009). Similarly, changes in benthic community structure near polluted sources indicated the presence of alien polychaetes *Glycinde bonhourei* and *Notomastus mossambicus* (Çinar *et al*., 2012). Furthermore, in an integrative study that included an analysis of biodiversity and its relation with chemical and plastic pollution, alien polychaete species *Kirkegaardia dorsobranchialis*, *Notomastus aberans*, *Pista unibranchia*, *Pseudonereis anomala* and *B. bairdi* were found in polluted areas (D'Alessandro *et al*., 2018). Contrastingly, on the coast of California the presence of the alien species *Pseudopolydora paucibranchiata* did not appear to have a negative impact on the benthic community but was rather associated with high diversity, probably due to the biogenic structures built by this species that enhances the abundance of other macrofauna (Ranasinghe *et al*., 2005).

Taxonomic problems

The 40 polychaete species reviewed here represent only about 13% of species globally reported as probably being alien (Çinar, 2013). Thus, a small proportion of known alien polychaetes have had their impacts investigated, but this is likely an underestimation. There is, for example, no doubt that impacts of alien species were investigated before the 1980s, but these studies and species would not have been included in this review if the species investigated were not identified as alien, or not identified to species level. This is especially relevant to shell-boring pests of mariculture. For example, the impact of an alien *Polydora* species on oysters in Australia was first reported in the late 19th century when Whitelegge (1890) investigated oyster disease – the species was identified as *Polydora ciliata*, which was originally described on the south coast of England (Johnston, 1838). The identification as *P. ciliata* is doubtful, and Blake & Kudenov (1978) suggested that all records of *P. ciliata* in Australia are probably *P. websteri*, also an alien in Australia. Ogburn *et al*. (2007) proposed that a *Polydora* species (possibly the one investigated by Whitelegge (1890)) brought to Australia on oysters imported from New Zealand, may have contributed to the disappearance of oyster reefs from estuaries in Eastern Australia. Impacts of more alien species have therefore probably been conducted before 1980, as reported here. By contrast, the taxonomy of many species purported to be alien are also in need of revision. For example, after thorough revision of the literature and specimens, Langeneck *et al*. (2020) found that of 86 polychaete species previously reported as alien along the Italian coast, only 25 (30%) could be confirmed as alien, while 3 were cryptogenic, 40 questionable and 18 were native or had been misidentified. Thus, estimates of alien polychaetes in many regions may have been exaggerated.

Impacts of species which are alien but erroneously investigated as indigenous (e.g. Rice *et al*., 2018), or not classified as alien (e.g. Schleyer, 1991), would not have been reviewed here. For example, *M. viridis* was initially recorded as *Marenzelleria wireni* in the early 1980s during routine monitoring in the Wadden and Baltic Seas (Essink & Kleef, 1988; Zmudziński, 1996; Thomsen *et al*., 2009) but a revision by specialists indicated that it actually was *M. viridis* (Essink & Kleef, 1988). Similarly, *B. proboscidea* was not always considered an alien in Mar del Plata, Argentina and was reported as *Boccardia polybranchia* in the early 2000s (e.g. Elías *et al*., 2003, 2006). A revision conducted in 2009 by taxonomic specialists determined that the correct identification was *B. proboscidea* (Jaubet *et al*., 2011) so the previously published papers about the polychaetes in this area did not consider it as an alien. It is even possible that the *Boccardia* species identified in the earlier papers (Elias *et al*., 2000; Orensanz *et al*., 2002; Vallarino *et al*., 2002; Adami *et al*., 2004; Martin & Bastida, 2008) were all of *B. proboscidea*.

With regards to the species labelled as CG, although *F. enigmaticus* is one of the most widespread alien polychaetes around the world, its true origin is still unclear (Dittmann *et al*., 2009) and recent molecular studies revealed that it is a species complex (Styan *et al*., 2017; Yee *et al*., 2019). In the case of *H. dianthus*, a higher haplotype diversity in the Mediterranean seems to contradict the currently accepted native range of *H. dianthus sensu stricto* in the USA, while a molecular analysis is necessary to corroborate the status of *H. operculata* as alien in the Mediterranean because it is a complex of at least three cryptic species (Sun *et al*., 2017). For the sabellids *B. bairdi* and *B. boholense*, molecular and morphological evidence suggested important considerations in the identification of these species as alien in the Mediterranean (Del Pasqua *et al*., 2018).

The impact of '*S. kraussii*' was investigated as an alien species in the Mediterranean Sea (Çinar, 2006). However, morphological and molecular analysis conducted by Simon *et al.* (2019) confirmed that this species is restricted to southern African coasts and belongs to a globally distributed complex of morphologically similar species. Similarly, the impact of *P. paucibranchiata* was reported on the Pacific coast of the USA (Ranasinghe *et al.*, 2005) and in the Mediterranean Sea (Dagli & Çinar, 2008), but a recent taxonomic revision concluded that this species must be considered a complex of four pseudocryptic species (Radashevsky *et al.*, 2020). In the case of *P. websteri*, this species was confirmed recently by molecular and morphological analyses as an alien in the Wadden Sea, west coast of the USA and South Africa (Martinelli *et al.*, 2020; Waser *et al.*, 2020; Rodewald *et al.*, 2021; Spencer *et al.*, 2020). However, the native range of this species is now being questioned. It was originally described from the east coast of the USA (Hartman in Loosanoff & Engle 1943), but recent genetic evidence suggests an Asian origin (Rice *et al.*, 2018). However, there are reports of *P. websteri* in South America (Netto & Gallucci, 2003; Breves-Ramos *et al.*, 2005; Sabry & Magalhães, 2005; Diez *et al.*, 2011; Keppel *et al.*, 2019), Canada (Bergman *et al.*, 1982; Bower *et al.*, 1992; Clements *et al.*, 2017), Red Sea (Elnaby, 2019), South Africa (Schleyer, 1991), New Zealand (Handley, 1995) and Australia (Nell, 2001) that need to be confirmed by a molecular and morphological systematic review, as do reports of *P.* cf. *websteri* in some regions of South America (Oscar Díaz & Liñero-Arana, 2009; Barros *et al.*, 2017). It is evident that the identification and distribution of *P. websteri* still needs a careful revision around the world. Finally, *Allita succinea* is reported from the Baltic Sea but its status as alien is uncertain (Thomsen *et al.*, 2009).

In summary, it is clear that taxonomic investigations are key to clarify species' status as indigenous, alien or cryptogenic (Hutchings & Lavesque, 2020; Langeneck *et al.*, 2020; Malan *et al.*, 2020), and will play a vital role in advancing the research on impacts of alien polychaete species.

Management strategies

Once the taxonomic status of an alien polychaete species is confirmed, the next challenge is the evaluation of its impact. It was clear that the scales and contexts of impact evaluations were heterogeneous across the studies considered here and this could introduce bias in the assignment of impact mechanisms. The classification proposed by Blackburn *et al.* (2014) is applicable at different levels of ecological complexity and different spatial and temporal scales. The impact mechanisms assigned in the present review were based on the best available evidence and are by no means definitive or complete. Impact categories are subject to change as more impact studies are undertaken and completed, especially in under-studied studied species. However, despite these limitations, the available data suggest that most species have a major to massive impact on the ecosystems they occupy. This indicates the importance of the study, prevention and management of polychaete alien species. Although, it may also indicate that species are only detected and studied once impacts have become obvious and massive.

The first strategy to detect and determine the impact of alien polychaete species is implementing a long series of marine ecosystem monitoring (Hoagland & Turner, 1980; Nichols & Thompson, 1985; Essink & Kleef, 1988). The selection of monitoring sites should prioritize entry points for introductions of alien species, such as ballast water discharge areas, docks, marinas and aquaculture sites with imported stocks, as well as nature conservation sites (Olenin & Minchin, 2011). Some monitoring programmes sample sediment (Nichols & Thompson, 1985) or use growth panels, made of wood or artificial substrates such as PVC, submerged in water and/or sediment to analyse the settlement times and cumulative growth of boring and fouling organisms (Hoagland & Turner, 1980; Holloway & Keough, 2002*a*, 2002*b*; Mangano *et al.*, 2019). When alien species are accidentally introduced by aquaculture facilities the application of programmes like the one applied to the sabellid *T. heterouncinata* can lead to extirpation of well-established local pests (Culver & Kuris, 2000). Before the application of such programmes, evaluation using theoretical models such as the one conducted by Soliman & Inglis (2018) to predict the spread and economic impact of *S. spallanzanii* as a biofouler of aquaculture species, are useful to justify the level of biosecurity intervention. When an alien species such as *F. enigmaticus* is introduced in an estuarine system, a routine monitoring and strategic removal programme could limit its spread and negative impacts (Bezuidenhout & Robinson, 2020). However, if an alien polychaete species is established in an open marine ecosystem, there is usually no way to extirpate or control the spread of populations as seen in the case of *M. viridis* in the Baltic Sea. Leppäkoski *et al.* (2002) mentioned that in addition to the monitoring of alien species and studying their biology and ecology, no actions have been undertaken to address the problem in the Baltic Sea. Hence, the prevention of further introductions of alien species should be a priority for any marine biosecurity strategy.

Any national action programme aimed at preventing alien polychaete introductions needs to be supported by international collaboration and regulation, as the primary introduction of alien marine polychaete species have been via aquaculture and shipping activities (Jensen & Knudsen, 2005; Davidson *et al.*, 2010). For example, antifouling paints containing copper on commercial and recreational vessels help to prevent the introduction of alien species. However, the use of these paints is controversial as their accumulation in embayments could simultaneously affect the recruitment of indigenous species or facilitate the transport and establishment of copper-tolerant alien species into disturbed estuarine habitats (Dafforn *et al.*, 2008). For these reasons, an efficient control of the aquaculture industry and the development of new antifouling agents or techniques are key in preventing new introductions of alien species (Thomsen *et al.*, 2009). Finally the application of molecular barcoding and automatic image analysis could be helpful for early detection if followed by an immediate and more detailed taxonomic study of the unusual species (Olenin & Minchin, 2011).

Conclusions

Impacts of alien polychaete species are greatly under-studied and the research field needs to be developed. In the 150 studies included in our systematic review, some aspects of the impacts of 40 alien polychaete species were studied. It identified eight mechanisms of impacts which were mainly massive in magnitude for the alien polychaete species documented. The impact mechanisms (IMos) of alien polychaete species were strongly related to their biology and lifestyles; we found that the species that build conspicuous reefs and tubes mainly showed physical and structural impact on ecosystems and that shell-borers, mainly parasitism and infaunal species, showed mainly chemical, physical and structural impacts on ecosystems. We consider it a priority to produce correct taxonomic identifications using morphological and molecular tools to achieve reliable identifications to confidently determine the alien status of a species. Clearly, evaluating the impacts of an alien polychaete species, even a conspicuous one, is complex and subject to many variables. For this reason, the study of the impacts of alien polychaete species must be conducted in an interdisciplinary manner to integrate different ecological aspects of the species to find the best integrative adaptive solutions for the management of such alien species.

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Data. The authors confirm that the data supporting the findings of this study are available within the article [and/or its supplementary materials].

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Conflict of interest. The authors declare that they have no conflict of interests.

References

Adami ML, Tablado A and López Gappa J (2004) Spatial and temporal variability in intertidal assemblages dominated by the mussel *Brachidontes rodriguezii* (d'Orbigny, 1846). *Hydrobiologia* **520**, 49–59.

Alexander ME, Simon CA, Griffiths CL, Peters K, Sibanda S, Miza S, Groenewald B, Majiedt P, Sink KJ and Robinson TB (2016) Back to the future: reflections and directions of South African marine bioinvasion research. *African Journal of Marine Science* **38**, 141–144.

Anton A, Geraldi NR, Lovelock CE, Apostolaki ET, Bennett S, Cebrian J, Krause-Jensen D, Marbà N, Martinetto P, Pandolfi JM, Santana-Garcon J and Duarte CM (2019) Global ecological impacts of marine exotic species. *Nature Ecology & Evolution* **3**, 787–800.

Appeltans W, Ahyong ST, Anderson G, Angel MV, Artois T, Bailly N, Bamber R, Barber A, Bartsch I, Berta A, Błazewicz-Paszkowycz M, Bock P, Boxshall G, Boyko CB, Brandão SN, Bray RA, Bruce NL, Cairns SD, Chan TY, Cheng L, Collins AG, Cribb T, Curini-Galletti M, Dahdouh-Guebas F, Davie PJF, Dawson MN, De Clerck O, Decock W, De Grave S, De Voogd NJ, Domning DP, Emig CC, Erséus C, Eschmeyer W, Fauchald K, Fautin DG, Feist SW, Fransen CHJM, Furuya H, Garcia-Alvarez O, Gerken S, Gibson D, Gittenberger A, Gofas S, Gómez-Daglio L, Gordon DP, Guiry MD, Hernandez F, Hoeksema BW, Hopcroft RR, Jaume D, Kirk P, Koedam N, Koenemann S, Kolb JB, Kristensen RM, Kroh A, Lambert G, Lazarus DB, Lemaitre R, Longshaw M, Lowry J, MacPherson E, Madin LP, Mah C, Mapstone G, McLaughlin PA, Mees J, Meland K, Messing CG, Mills CE, Molodtsova TN, Mooi R, Neuhaus B, Ng PKL, Nielsen C, Norenburg J, Opresko DM, Osawa M, Paulay G, Perrin W, Pilger JF, Poore GCB, Pugh P, Read GB, Reimer JD, Rius M, Rocha RM, Saiz-Salinas JI, Scarabino V, Schierwater B, Schmidt-Rhaesa A, Schnabel KE, Schotte M, Schuchert P, Schwabe E, Segers H, Self-Sullivan C, Shenkar N, Siegel V, Sterrer W, Stöhr S, Swalla B, Tasker ML, Thuesen EV, Timm T, Todaro MA, Turon X, Tyler S, Uetz P, Van Der Land J, Vanhoorne B, Van Ofwegen LP, Van Soest RWM, Vanaverbeke J, Walker-Smith G, Walter TC, Warren A, Williams GC, Wilson SP and Costello MJ (2012) The magnitude of global marine species diversity. *Current Biology* **22**, 2189–2202.

Arias A, Giangrande A, Gambi MC and Anadón N (2013*a*) Biology and new records of the invasive species *Branchiomma bairdi* (Annelida: Sabellidae) in the Mediterranean Sea. *Mediterranean Marine Science* **14**, 162–171.

Arias A, Richter A, Anadón N and Glasby CJ (2013*b*) Revealing polychaetes invasion patterns: identification, reproduction and potential risks of the Korean ragworm, *Perinereis linea* (treadwell), in the western Mediterranean. *Estuarine, Coastal and Shelf Science* **131**, 117–128.

Atalah J, Floerl O, Pochon X, Townsend M, Tait L and Lohrer AM (2019) The introduced fanworm, *Sabella spallanzanii*, alters soft sediment macrofauna and bacterial communities. *Frontiers in Ecology and Evolution* **7**, 481.

Bacher S, Blackburn TM, Essl F, Genovesi P, Heikkilä J, Jeschke JM, Jones G, Keller R, Kenis M, Kueffer C, Martinou AF, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roy HE, Saul WC, Scalera R, Vilà M, Wilson JRU and Kumschick S (2018) Socio-economic impact classification of alien taxa (SEICAT). *Methods in Ecology and Evolution* **9**, 159–168.

Backer H, Leppänen JM, Brusendorff AC, Forsius K, Stankiewicz M, Mehtonen J, Pyhälä M, Laamanen M, Paulomäki H, Vlasov N and Haaranen T (2010) HELCOM Baltic Sea Action Plan – a regional programme of measures for the marine environment based on the Ecosystem Approach. *Marine Pollution Bulletin* **60**, 642–649.

Ban SM and Nelson WG (1987) Role of *Diopatra cuprea* Bosc (Polychaeta: Onuphidae) tubes in structuring a subtropical infaunal community. *Bulletin of Marine Science* **40**, 11–21.

Barros TL, Gomes Santos CS, De Assis JE and de Souza JRB (2017) Morphology and larval development of *Polydora* cf. *websteri* (Polychaeta: Spionidae) in a tropical region of north-eastern Brazil. *Journal of Natural History* **51**, 1169–1181.

Bastida-Zavala R and García-Madrigal S (2012) First record in the Tropical Eastern Pacific of the exotic species *Ficopomatus uschakovi* (Polychaeta, Serpulidae). *ZooKeys* **238**, 45–55.

Bazterrica MC, Barón PJ, Álvarez G and Obenat SM (2020) Effects of *Ficopomatus enigmaticus* ecosystem-engineered habitat structure on population parameters of the amphipod *Melita palmata*: a NIS-NIS interaction study. *Marine Ecology* **41**, 1–21.

Bazterrica MC, Bruschetti CM, Alvarez MF, Iribarne O and Botto F (2014) Effects of macroalgae on the recruitment, growth, and body condition of an invasive reef forming polychaete in a south-western Atlantic coastal lagoon. *Journal of Sea Research* **88**, 121–129.

Bell SS and Coen LD (1982) Investigations on epibenthic meiofauna I. Abundances on and repopulation of the tube-caps of *Diopatra cuprea* (Polychaeta: Onuphidae) in a subtropical system. *Marine Biology* **67**, 303–309.

Bergamo G, Carrerette O and Nogueira JMDM (2019) Continuous and non-seasonal reproductive cycle of the alien species *Diopatra neapolitana* (Onuphidae, Annelida) in a tropical bay of SW Atlantic. *Estuarine, Coastal and Shelf Science* **231**, 106479.

Bergman KM, Elner RW and Risk MJ (1982) The influence of *Polydora websteri* borings on the strength of the shell of the sea scallop, *Placopecten magellanicus*. *Canadian Journal of Zoology* **60**, 2551–2556.

Bezuidenhout M and Robinson TB (2020) Abundance and distribution of the invasive polychaete *Ficopomatus enigmaticus* in three South African estuaries. *Regional Studies in Marine Science* **39**, 101405.

Biles CL, Paterson DM, Ford RB, Solan M and Raffaelli DG (2002) Bioturbation, ecosystem functioning and community structure. *Hydrology and Earth System Sciences* **6**, 999–1005.

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P and Bacher S (2014) A unified classificaiton of alien species based on the magnitude of their environmental impacts. *PLoS Biology* **12**, e1001850.

Blackburn TM, Lockwood JL and Cassey P (2015) The influence of numbers on invasion success. *Molecular Ecology* **24**, 1942–1953.

Blake JA and Kudenov JD (1978) The Spionidae (Polychaeta) from south-eastern Australia with a revision of the genera of the family. *Memoirs of the National Museum of Victoria* **39**, 171–280.

Boon PJ, Clarke SA and Copp GH (2020) Alien species and the EU Water Framework Directive: a comparative assessment of European approaches. *Biological Invasions* **22**, 1497–1512.

Bower SM, Blackbourn J, Meyer GR and Nishimura DJH (1992) Diseases of cultured Japanese scallops (*Patinopecten yessoensis*) in British Columbia, Canada. *Aquaculture* **107**, 201–210.

Breves-Ramos A, Lavrado HP, Junqueira ADOR and da Silva SHG (2005) Succession in rocky intertidal benthic communities in areas with different pollution levels at Guanabara Bay (RJ-Brazil). *Brazilian Archives of Biology and Technology* **48**, 951–965.

Bruschetti M (2019) Role of reef-building, ecosystem engineering polychaetes in shallow water ecosystems. *Diversity* **11**, 168.

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, Ditomaso JM, Hobbs RJ, Pellant M and Pyke D (2004) Effects of invasive alien plants on fire regimes. *BioScience* **54**, 677.

Bruschetti M, Bazterrica C, Luppi T and Iribarne O (2009) An invasive intertidal reef-forming polychaete affect habitat use and feeding behavior of migratory and locals birds in a SW Atlantic coastal lagoon. *Journal of Experimental Marine Biology and Ecology* **375**, 76–83.

Bruschetti M, Bazterrica C, Fanjul E, Luppi T and Iribarne O (2011) Effect of biodeposition of an invasive polychaete on organic matter content and productivity of the sediment in a coastal lagoon. *Journal of Sea Research* **66**, 20–28.

Bruschetti M, Luppi T and Iribarne O (2016) Effect of an invasive filter-feeder on the zooplankton assemblage in a coastal lagoon. *Journal of the Marine Biological Association of the United Kingdom* **96**, 1201–1210.

Cardoso PG, Bankovic M, Raffaelli D and Pardal MA (2007) Polychaete assemblages as indicators of habitat recovery in a temperate estuary under eutrophication. *Estuarine, Coastal and Shelf Science* **71**, 301–308.

Carlton JT and Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. *Science (New York, N.Y.)* **261**, 78–82.

Catalano B, Moltedo G, Martuccio G, Gastaldi L, Virno-Lamberti C, Lauria A and Ausili A (2012) Can *Hediste diversicolor* (Nereidae, Polychaete) be considered a good candidate in evaluating PAH contamination? A multimarker approach. *Chemosphere* **86**, 875–882.

Çinar ME (2006) Serpulid species (Polychaeta: Serpulidae) from the Levantine coast of Turkey (eastern Mediterranean), with special emphasis on alien species. *Aquatic Invasions* **1**, 223–240.

Çinar ME (2013) Alien polychaete species worldwide: current status and their impacts. *Journal of the Marine Biological Association of the United Kingdom* **93**, 1257–1278.

Çinar ME, Balkis H, Albayrak S, Dagli E and Karhan SÜ (2009) Distribution of polychaete species (Annelida: Polychaeta) on the polluted soft substrate of the Golden Horn Estuary (Sea of Marmara), with special emphasis on alien species. *Cahiers de Biologie Marine* **50**, 11–17.

Çinar ME, Katağan T, Koçak F, Öztürk B, Ergen Z, Kocatas A, Önen M, Kirkim F, Bakir K, Kurt G, Doğan A and Özcan T (2008) Faunal assemblages of the mussel *Mytilus galloprovincialis* in and around Alsancak Harbour (Izmir Bay, eastern Mediterranean) with special emphasis on alien species. *Journal of Marine Systems* **71**, 1–17.

Çinar ME, Katagan T, Öztürk B, Dagli E, Açik S, Bitlis B, Bakir K and Dogan A (2012) Spatio-temporal distributions of zoobenthos in Mersin Bay (Levantine Sea, eastern Mediterranean) and the importance of alien species in benthic communities. *Marine Biology Research* **8**, 954–968.

Clements JC, Bourque D, McLaughlin J, Stephenson M and Comeau LA (2017) Siltation increases the susceptibility of surface-cultured eastern oysters (*Crassostrea virginica*) to parasitism by the mudworm *Polydora websteri*. *Aquaculture Research* **48**, 4707–4717.

Cohen BF, Currie DR and McArthur MA (2000) Epibenthic community structure in Port Phillip Bay, Victoria, Australia. *Marine and Freshwater Research* **51**, 689.

Critchley AT, Farnham WF and Thorp CH (1997) On the co-occurrence of two exotic, invasive marine organisms: the brown seaweed *Sargassum muticum* (Yendo) Fensholt and the Spirorbid tube worm *Janua* (Neodexiospira) *brasiliensis* (Grube), in association with the indigenous eelgrass, *Zostera marina* L. and Wrack, *Fucus serratus* L. in the south-west Netherlands and the Channel Islands, Europe. *South African Journal of Botany* **63**, 474–479.

Culver CS and Kuris AM (2000) The apparent eradication of a locally established introduced marine pest. *Biological Invasions* **2**, 245–253.

Cyrino M, Coutinho L, Teixeira VL, Simone C and Santos G (2018) A review of 'Polychaeta' chemicals and their possible ecological role. *Journal of Chemical Ecology* **44**, 72–94.

Dafforn KA, Glasby TM and Johnston EL (2008) Differential effects of tributyltin and copper antifoulants on recruitment of non-indigenous species. *Biofouling* **24**, 23–33.

Dagli E and Çinar ME (2008) Invasion of polluted soft substratum of Izmir Bay (Aegean Sea, eastern Mediterranean) by the spionid polychaete worm, *Pseudopolydora paucibranchiata* (Polychaeta: Spionidae). *Cahiers de Biologie Marine* **49**, 87–96.

D'Alessandro M, Esposito V, Porporato EMD, Berto D, Renzi M, Giacobbe S, Scotti G, Consoli P, Valastro G, Andaloro F, Andaloro F and Romeo T (2018) Relationships between plastic litter and chemical pollutants on benthic biodiversity. *Environmental Pollution* **242**, 1546–1556.

Darling JA and Carlton JT (2018) A framework for understanding marine cosmopolitanism in the anthropocene. *Frontiers in Marine Science* **5**, 1–25.

Dauer DM, Maybury CA and Ewing RM (1981) Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology* **54**, 21–38.

Davidson IC, Zabin CJ, Chang AL, Brown CW, Sytsma MD and Ruiz GM (2010) Recreational boats as potential vectors of marine organisms at an invasion hotspot. *Aquatic Biology* **11**, 179–191.

Davies BR, Stuart V and de Villiers M (1989) The filtration activity of a serpulid polychaete population (*Ficopomatus enigmaticus* (Fauvel)) and its effects on water quality in a coastal marina. *Estuarine, Coastal and Shelf Science* **29**, 613–620.

Delefosse M, Banta GT, Canal-Vergés P, Penha-Lopes G, Quintana CO, Valdemarsen T and Kristensen E (2012) Macrobenthic community response to the *Marenzelleria viridis* (Polychaeta) invasion of a Danish estuary. *Marine Ecology Progress Series* **461**, 83–94.

Del Pasqua M, Schulze A, Tovar-Hernández MA, Keppel E, Lezzi M, Gambi MC and Giangrande A (2018) Clarifying the taxonomic status of the alien species *Branchiomma bairdi* and *Branchiomma boholense* (Annelida: Sabellidae) using molecular and morphological evidence. *PLoS ONE* **13**, e0197104.

Diez ME, Radashevsky VI, Orensanz JM and Cremonte F (2011) Spionid polychaetes (Annelida: Spionidae) boring into shells of molluscs of commercial interest in northern Patagonia, Argentina. *Italian Journal of Zoology* **78**, 497–504.

Dittmann S, Rolston A, Benger SN and Kupriyanova EK (2009) *Habitat Requirements, Distribution and Colonisation of the Tubeworm Ficopomatus enigmaticus in the Lower Lakes and Coorong*. Report for the South Australian Murray-Darling Basin Natural Resources Management Board, Adelaide, 99 pp.

Dong Z, Sun T and Wang L (2018) The biogenic reefs formed by the alien polychaete *Hydroides dianthus* (Serpulidae, Annelida) favor the polyp stage of *Aurelia coerulea* (Cnidaria, Scyphozoa) in a coastal artificial lake. *Marine Pollution Bulletin* **129**, 86–91.

Douglas EJ, Townsend M, Tait LW, Greenfield BL, Inglis GJ and Lohrer AM (2020) *Sabella spallanzanii* and seafloor biodiversity enhancement in a marine soft-sediment system. *Diversity* **12**, 228.

Elgetany AH, van Rensburg H, Hektoen M, Matthee C, Budaeva N, Simon CA and Struck TH (2020) Species delineation in the speciation grey zone—The case of Diopatra (Annelida, Onuphidae). *Zoologica Scripta* **49**, 516–534.

Elías R, Jaubet ML, Llanos EN, Sanchez MA, Rivero MS, Garaffo GV and Sandrini-Neto L (2015) Effect of the invader *Boccardia proboscidea* (Polychaeta: Spionidae) on richness, diversity and structure of SW Atlantic epilithic intertidal community. *Marine Pollution Bulletin* **91**, 530–536.

Elías R, Rivero MS, Palacios JR and Vallarino EA (2006) Sewage-induced disturbance on Polychaetes inhabiting intertidal mussel beds of *Brachidontes rodriguezii* off Mar del Plata (Southwestern Atlantic, Argentina). *Scientia Marina* **70**, 187–196.

Elías R, Rivero MS and Vallarino EA (2003) Sewage impact on the composition and distribution of polychaeta associated to intertidal mussel beds of the Mar del Plata rocky shore, Argentina. *Iheringia, Série Zoologia* **93**, 309–318.

Elias R, Vallarino EA and Bremee CS (2000) *Protoariciella uncinata* Hartmann-Schröeder, 1962 (Polychaeta, Orbiniidae): a new record for intertidal mussel beds of the Southwestern Atlantic shore affected by sewage effluents. *Revista de Biologia Marina y Oceanografia* **35**, 181–184.

Elnaby FAA (2019) New recorded alein polydorid species (Polychaeta: Spionidae) from the Egyptian waters. *Egyptian Journal of Aquatic Biology and Fisheries* **23**, 409–420.

Essink K, Eppinga J and Dekker R (1998) Long-term changes (1977–1994) in intertidal macrozoobenthos of the Dollard (Ems estuary) and effects of introduction of the North American spionid polychaete *Marenzelleria* cf. *wireni*. *Senckenbergiana Maritima* **28**, 211–225.

Essink K and Kleef HL (1988) *Marenselleria viridis* (Verril, 1873) (Polychaeta: Spionidae): a new record from The Ems estuary (The Netherlands/Federal Republic of Germany). *Zoologische Bijdragen* **38**, 1–13.

Etchegoin JA, Merlo MJ and Parietti M (2012) The role of the invasive polychaete *Ficopomatus enigmaticus* (Fauvel, 1923) (Serpulidae) as facilitator of parasite transmission in Mar Chiquita coastal lagoon (Buenos Aires, Argentina). *Parasitology* **139**, 1506–1512.

Fadhullah W and Syakir MI (2016) Polychaetes as ecosystem engineers: agents of sustainable technologies. In Ahmad MI, Ismail M and Riffat S (eds) *Renewable Energy and Sustainable Technologies for Building and Environmental Applications*. Springer, Cham pp. 137–150.

Fauchald K and Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology. An Annual Review* **17**, 193–284.

Fauvel P (1923) Un nouveau serpulien d'eau saumatre *Merceriella* n.g., enigmatica n.sp. *Bulletin de La Société Zoologique de France* **47**, 424–430.

Fidalgo E Costa P, Gil J, Passos AM, Pereira P, Melo P, Batista F and Cancela da Fonseca L (2006) The market features of imported non-indigenous polychaetes in Portugal and consequent ecological concerns. In Sarda R, San Martín G, Lopez E, Martín D and George D (eds), *Scientific advances in polychaete research*, *Scientia Marina*, **70S3**, pp. 287–292.

Fitzhugh K and Rouse GW (1999) A remarkable new genus and species of fan worm (Polychaeta: Sabellidae: Sabellinae) associated with marine gastropods. *Invertebrate Biology* **118**, 357.

Frey RW and Wheatcroft RA (1989) Organism-substrate relations and their impact on sedimentary petrology. *Journal of Geological Education* **37**, 261–279.

Gaonkar CA, Sawant SS, Anil AC, Krishnamurthy V and Harkantra SN (2010) Changes in the occurrance of hard substratum fauna: a case study from Mumbai harbour, India. *Indian Journal of Marine Sciences* **39**, 74–84.

Garaffo GV, Jaubet ML, Sánchez MDLÁ, Rivero MS, Vallarino EA and Elías R (2012) Sewage-induced polychaete reefs in a SW Atlantic shore: rapid response to small-scale disturbance. *Marine Ecology* **33**, 272–279.

Gerovasileiou V, Voultsiadou E, Issaris Y and Zenetos A (2016) Alien biodiversity in Mediterranean marine caves. *Marine Ecology* **37**, 239–256.

Giangrande A, Licciano M and Musco L (2005) Polychaetes as environmental indicators revisited. *Marine Pollution Bulletin* **50**, 1153–1162.

Gibson G, Paterson IG, Taylor H and Woolridge B (1999) Molecular and morphological evidence of a single species, *Boccardia proboscidea* (Polychaeta: Spionidae), with multiple development modes. *Marine Biology* **134**, 743–751.

Handley SJ (1995) Spionid polychaetes in Pacific oysters, *Crassostrea gigas* (Thunberg) from Admiralty Bay, Marlborough Sounds, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **29**, 305–309.

Hartman O (1940) *Boccardia proboscidea*, a new species of spionid worm from California. *Journal of the Washington Academy of Sciences* **30**, 382–387.

Haupt TM, Griffiths CL, Robinson TB and Tonin AFG (2010) Oysters as vectors of marine aliens, with notes on four introduced species associated with oyster farming in South Africa. *African Zoology* **45**, 52–62.

Hayes KR, Cannon R, Neil K and Inglis G (2005) Sensitivity and cost considerations for the detection and eradication of marine pests in ports. *Marine Pollution Bulletin* **50**, 823–834.

Hendrix PF, Callaham MA, Drake JM, Huang C-Y, James SW, Snyder BA and Zhang W (2008) Pandora's box contained bait: the global problem of introduced earthworms. *Annual Review of Ecology, Evolution, and Systematics* **39**, 593–613.

Hoagland KE and Turner RD (1980) Range extensions of teredinids (shipworms) and polychaetes in the vicinity of a temperate-zone nuclear generating station. *Marine Biology* **58**, 55–64.

Holloway MG and Keough MJ (2002*a*) An introduced polychaete affects recruitment and larval abundance of sessile invertebrates. *Ecological Applications* **12**, 1803–1823.

Holloway MG and Keough MJ (2002*b*) Effects of an introduced polychaete, *Sabella spallanzanii*, on the development of epifaunal assemblages. *Marine Ecology Progress Series* **236**, 137–154.

Hutchings P (1998) Biodiversity and functioning of polychaetes in benthic sediments. *Biodiversity and Conservation* **7**, 1133–1145.

Hutchings P (1999) The limits to our knowledge of introduced marine invertebrates. In Ponder WF and Lunney D (eds), *The Other 99%: The Conservation and Biodiversity of Invertebrates*. Mosman, NSW: Transactions of the Royal Zoological Society of New South Wales, pp. 26–29.

Hutchings P and Kupriyanova E (2018) Cosmopolitan polychaetes – fact or fiction? Personal and historical perspectives. *Invertebrate Systematics* **32**, 1–9.

Hutchings P and Lavesque N (2020) I know who you are, but do others know ? Why correct scientific names are so important for the biological sciences. *Zoosymposia* **163**, 151–163.

Jaubet ML, Bottero MAS, Hines E, Elías R and Garaffo GV (2018) *Boccardia proboscidea* (Polychaete: Spionidae) in the SW Atlantic: how far has the invasion spread? *Aquatic Invasions* **13**, 351–363.

Jaubet ML, Garaffo GV, Sánchez MA and Elías R (2013) Reef-forming polychaetes outcompetes ecosystem engineering mussels. *Marine Pollution Bulletin* **71**, 216–221.

Jaubet ML, Sánchez MA, Rivero MS, Garaffo GV, Vallarino EA and Elías R (2011) Intertidal biogenic reefs built by the polychaete *Boccardia proboscidea* in sewage-impacted areas of Argentina, SW Atlantic. *Marine Ecology* **32**, 188–197.

Jensen K and Knudsen J (2005) A summary of alien marine benthic invertebrates in Danish waters. *Oceanological and Hydrobiological Studies* **34** (Suppl.1), 137–162.

Jewett EB, Hines AH and Ruiz GM (2005) Epifaunal disturbance by periodic low levels of dissolved oxygen: native vs. invasive species response. *Marine Ecology Progress Series* **304**, 31–44.

Johnston G (1838) Miscellanea Zoologica. III.-The British Ariciadae. *Magazine of Zoology and Botany, Edinburgh* **2**, 63–73.

Jones CG, Lawton JH and Shachak M (1994) Organisms as ecosystem engineers. *Oikos* **69**, 373–386.

Jumars PA, Dorgan KM and Lindsay SM (2015) Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science* **7**, 497–520.

Kalejta B and Hockey PAR (1991) Distribution, abundance and productivity of benthic invertebrates at the Berg River estuary, South Africa. *Estuarine, Coastal and Shelf Science* **33**, 175–191.

Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Çinar ME, Oztürk B, Grabowski M, Golani D and Cardoso AC (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquatic Invasions* **9**, 391–423.

Keppel E, Keith I, Ruiz GM and Carlton JT (2019) New records of native and non-indigenous polychaetes (Annelida: Polychaeta) in the Galapagos islands. *Aquatic Invasions* **14**, 59–84.

Kocak F, Ergen Z and Çinar ME (1999) Fouling organisms and their developments in a polluted and an unpolluted marina in the Aegean Sea (Turkey). *Ophelia* **50**, 1–20.

Koricheva J, Gurevitch J and Mengersen K (eds) (2013) Handbook of meta-analysis in ecology and evolution. In *Handbook of Meta-Analysis in Ecology and Evolution*. Princeton, NJ: Princeton University Press, pp. 37–51.

Kotta J and Ólafsson E (2003) Competition for food between the introduced polychaete *Marenzelleria viridis* (Verrill) and the native amphipod *Monoporeia affinis* Lindström in the Baltic Sea. *Journal of Sea Research* **50**, 27–35.

Kristensen E, Hansen T, Delefosse M, Banta G and Quintana C (2011) Contrasting effects of the polychaetes *Marenzelleria viridis* and *Nereis diversicolor* on benthic metabolism and solute transport in sandy coastal sediment. *Marine Ecology Progress Series* **425**, 125–139.

Kuk-Dzul JG, Gold-Bouchot G and Ardisson PL (2012) Benthic infauna variability in relation to environmental factors and organic pollutants in tropical coastal lagoons from the northern Yucatan Peninsula. *Marine Pollution Bulletin* **64**, 2725–2733.

Kuris AM (2002) Eradication of introduced marine pests. In Rapport DJ, Lasley BL, Rolston DE, Nielsen NO, Qualset CO and Damania AB (eds), *Managing for Healthy Ecosystems*. New York, NY: Lewis Publishers, pp. 549–556.

Langeneck J, Lezzi M, Del Pasqua M, Musco L, Gambi MC, Castelli A and Giangrande A (2020) Non-indigenous polychaetes along coasts of Italy: a critical review. *Mediterranean Marine Science* **21**, 238–275.

Lehtiniemi M, Ojaveer H, David M, Galil B, Gollasch S, McKenzie C, Minchin D, Occhipinti-Ambrogi A, Olenin S and Pederson J (2015) Dose of truth – monitoring marine non-indigenous species to serve legislative requirements. *Marine Policy* **54**, 26–35.

Leighton DL (1998) Control of sabellid infestation in green and pink abalones, *Haliotis fulgens* and *H. corrugata*, by exposure to elevated water temperatures. *Journal of Shellfish Research* **17**, 701–705.

Leppäkoski E (2002). Harmful non-native species in the baltic sea — An ignored problem. In Heidelberg SB (Ed), *Baltic Coastal Ecosystems*. Springer-Verlag: Berlin, Heidelberg, pp. 253–275.

Levin LA and Crooks JA (2011) Functional consequences of invasive species in coastal and estuarine systems. In: Wolanski E and McLusky D (eds), *Treatise on Estuarine and Coastal Science*, Academic press, pp. 17–51.

Lezzi M and Giangrande A (2018) Seasonal and bathymetric effects on macrofouling invertebrates' primary succession in a Mediterranean non-indigenous species hotspot area. *Mediterranean Marine Science* **19**, 572–588.

Llanos EN, Jaubet ML and Elías R (2019) The intertidal benthic community of SW Atlantic as an environmental indicator of 50 years of human-mediated changes. *Marine Biology Research* **15**, 458–475.

Mach ME, Levings CD, McDonald PS and Chan KMA (2012) An Atlantic infaunal engineer is established in the Northeast Pacific: *Clymenella torquata* (Polychaeta: Maldanidae) on the British Columbia and Washington Coasts. *Biological Invasions* **14**, 503–507.

Magalhães WF, Hutchings PA, Oceguera-Figeroa A, Martin P, Schemelz RM, Wetzel MJ, Wiklund H, Maciolek NJ, Kawauchi GY and Williams

JD (2021) Segmented worms (Phylum Annelida): a celebration of twenty years of progress through *Zootaxa* and call for action on the taxonomic work that remains. *Zootaxa* **4979**, 190–211.

Malan A, Williams JD, Abe H, Sato-Okoshi W, Matthee CA and Simon CA (2020) Clarifying the cryptogenic species *Polydora neocaeca* Williams & Radashevsky, 1999 (Annelida: Spionidae): a shell-boring invasive pest of molluscs from locations worldwide. *Marine Biodiversity* **50**, 51.

Mangano MC, Ape F and Mirto S (2019) The role of two non-indigenous serpulid tube worms in shaping artificial hard substrata communities: case study of a fish farm in the central Mediterranean Sea. *Aquaculture Environment Interactions* **11**, 41–51.

Maranho LA, Baena-Nogueras RM, Lara-Martín PA, DelValls TA and Martín-Díaz ML (2014) Bioavailability, oxidative stress, neurotoxicity and genotoxicity of pharmaceuticals bound to marine sediments. The use of the polychaete *Hediste diversicolor* as bioindicator species. *Environmental Research* **134**, 353–365.

Marchini A, Galil BS and Occhipinti-Ambrogi A (2015) Recommendations on standardizing lists of marine alien species: lessons from the Mediterranean Sea. *Marine Pollution Bulletin* **101**, 267–273.

Martin JP and Bastida R (2008) Contribución de las comunidades bentónicas en la dieta del róbalo (*Eleginops maclovinus*) en la ría Deseado (Santa Cruz, Argentina). *Latin American Journal of Aquatic Research* **36**, 1–13.

Martinelli JC, Lopes HM, Hauser L, Jimenez-Hidalgo I, King TL, Padilla-Gamiño JL, Rawson P, Spencer LH, Williams JD and Wood CL (2020) Confirmation of the shell-boring oyster parasite *Polydora websteri* (Polychaeta: Spionidae) in Washington State, USA. *Scientific Reports* **10**, 1–14.

Martinez LE, Bazterrica MC and Hidalgo FJ (2020) Influence of complexity and habitat heterogeneity on macrofaunal assemblages provided by an invasive ecosystem engineer in Mar Chiquita coastal lagoon. *Estuarine, Coastal and Shelf Science* **246**, 107038.

Mauri M, Baraldi E and Simonini R (2003) Effects of zinc exposure on the polychaete *Dinophilus gyrociliatus*: a life-table response experiment. *Aquatic Toxicology* **65**, 93–100.

McQuaid KA and Griffiths CL (2014) Alien reef-building polychaete drives long-term changes in invertebrate biomass and diversity in a small, urban estuary. *Estuarine, Coastal and Shelf Science* **138**, 101–106.

Miranda NAF, Kupriyanova EK, Rishworth GM, Peer N, Bornman TG, Bird MS and Perissinotto R (2016) An invasive polychaete species found in living marine stromatolites. *Aquatic Invasions* **11**, 257–266.

Mito T and Uesugi T (2004) Invasive alien species in Japan: the status quo and the new regulation for prevention of their adverse effects. *Global Environmental Research* **8**, 171–191.

Moher D, Liberati A, Tetzlaff J and Altman DG (2009) Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *Annals of Internal Medicine* **151**, 264.

Moore JD, Juhasz CI, Robbins TT and Grosholz ED (2007) The introduced sabellid polychaete *Terebrasabella heterouncinata* in California: transmission, methods of control and survey for presence in native gastropod populations. *Journal of Shellfish Research* **26**, 869–876.

Moreno RA, Neill PE and Rozbaczylo N (2006) Native and non-indigenous boring polychaetes in Chile: a threat to native and commercial mollusc species. *Revista Chilena de Historia Natural* **79**, 263–278.

Murugesan P, Muniasamy M, Muthuvelu S, Vijayalakshmi S and Balasubramanian T (2011) Utility of benthic diversity in assessing the health of an ecosystem. *Indian Journal of Marine Sciences* **40**, 783–793.

Neill PE, Rozbaczylo N, Villaseñor-Parada C, Guzmán-Rendón G, Sampértegui S and Hernández CE (2020) Patterns of association of native and exotic boring polychaetes on the southeastern Pacific coast of Chile: the combined importance of negative, positive and random interactions. *PeerJ* **8**, e8560.

Nell JA (2001) The history of oyster farming in Australia. *Marine Fisheries Review* **63**, 14–25.

Netto SA and Gallucci F (2003) Meiofauna and macrofauna communities in a mangrove from the Island of Santa Catarina, South Brazil. *Hydrobiologia* **505**, 159–170.

Nichols F and Thompson J (1985) Persistence of an introduced mudflat community in South San Francisco Bay, California. *Marine Ecology Progress Series* **24**, 83–97.

Nygård H, Lindegarth M, Darr A, Dinesen GE, Eigaard OR and Lips I (2020) Developing benthic monitoring programmes to support precise and representative status assessments: a case study from the Baltic Sea. *Environmental Monitoring and Assessment* **192**, 795.

Obenat SM and Pezzani SE (1994) Life cycle and population structure of the polychaete *Ficopomatus enigmaticus* (Serpulidae) in Mar Chiquita coastal lagoon, Argentina. *Estuaries* **17**, 263–270.

O'Brien AL, Ross DJ and Keough MJ (2006) Effects of *Sabella spallanzanii* physical structure on soft sediment macrofaunal assemblages. *Marine and Freshwater Research* **57**, 363.

Ogburn DM, White I and Mcphee DP (2007) The disappearance of oyster reefs from eastern Australian estuaries – impact of colonial settlement or mudworm invasion? *Coastal Management* **35**, 271–287.

Olenin S and Minchin D (2011) Biological introductions to the systems: macroorganisms. In Wolanski E and McLusky DS (eds), *Treatise on Estuarine and Coastal Science*. Waltham: Academic Press, pp. 149–183.

Orensanz JM and Estivariz MC (1971) Los anélidos poliquetos de aguas salobres de la Provincia de Buenos Aires. *Revista Del Museo de La Plata (Nueva Serie), Sección Zoología* **11**, 95–104.

Orensanz JM, Schwindt E, Pastorino G, Bortolus A, Casas G, Darrigran G, Elías R, López Gappa JJ, Obenat S, Pascual M, Penchaszadeh P, Piriz ML, Scarabino F, Spivak ED and Vallarino EA (2002) No longer the pristine confines of the world ocean: a survey of exotic marine species in the southwestern Atlantic. *Biological Invasions* **4**, 115–143.

Oscar Díaz D and Liñero-Arana I (2009) Porcentaje del grado de infestación de polydora cf. websteri Hartman, 1943 (Polychaeta: Spionidae) por clase de talla de *Crassostrea rhizophorae* (Guilding, 1828) de la Laguna La Restinga (Isla Margarita, Venezuela). *Revista Cientifica de La Facultad de Ciencias Veterinarias de La Universidad Del Zulia* **19**, 113–118.

Pan J and Marcoval MA (2014) Top-down effects of an exotic serpulid polychaete on natural plankton assemblage of estuarine and brackish systems in the SW Atlantic. *Journal of Coastal Research* **298**, 1226–1235.

Peters K, Griffiths C and Robinson TB (2014) Patterns and drivers of marine bioinvasions in eight Western Cape harbours, South Africa. *African Journal of Marine Science* **36**, 49–57.

Pires A, Almeida Â, Calisto V, Schneider RJ, Esteves VI, Wrona FJ, Soares AMVM, Figueira E and Freitas R (2016) *Hediste diversicolor* as bioindicator of pharmaceutical pollution: results from single and combined exposure to carbamazepine and caffeine. *Comparative Biochemistry and Physiology Part – C: Toxicology and Pharmacology* **188**, 30–38.

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, Kleunen M, Vilà M, Wingfield MJ and Richardson DM (2020) Scientists' warning on invasive alien species. *Biological Reviews* **95**, 1511–1534.

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U and Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology* **18**, 1725–1737.

Quintana CO, Hansen T, Delefosse M, Banta G and Kristensen E (2011) Burrow ventilation and associated porewater irrigation by the polychaete *Marenzelleria viridis*. *Journal of Experimental Marine Biology and Ecology* **397**, 179–187.

Radashevsky VI, Malyar VV, Pankova VV, Gambi MC, Giangrande A, Keppel E, Nygren A, Al-Kandari M and Carlton JT (2020) Disentangling invasions in the sea: molecular analysis of a global polychaete species complex (Annelida: Spionidae: *Pseudopolydora paucibranchiata*). *Biological Invasions* **22**, 3621–3644.

Radashevsky VI and Olivares C (2005) *Polydora uncinata* (Polychaeta: Spionidae) in Chile: an accidental transportation across the Pacific. *Biological Invasions* **7**, 489–496.

Ranasinghe JA, Mikel TK, Velarde RG, Weisberg SB, Montagne DE, Cadien DB and Dalkey A (2005) The prevalence of non-indigenous species in southern California embayments and their effects on benthic macroinvertebrate communities. *Biological Invasions* **7**, 679–686.

Read G and Fauchald K (2021) *World Polychaeta Database*. Available at http://www.marinespecies.org/polychaeta/ (Accessed online 21 September 2021).

Read GB, Inglis G, Stratford P and Ahyong ST (2011) Arrival of the alien fanworm *Sabella spallanzanii* (Gmelin, 1791) (Polychaeta: Sabellidae) in two New Zealand harbours. *Aquatic Invasions* **6**, 273–279.

Renz JR and Forster S (2013) Are similar worms different? A comparative tracer study on bioturbation in the three sibling species *Marenzelleria arctia*, *M. viridis*, and *M. neglecta* from the Baltic Sea. *Limnology and Oceanography* **58**, 2046–2058.

Ricciardi A, Hoopes MF, Marchetti MP and Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* **83**, 263–282.

Rice LN, Lindsay S and Rawson P (2018) Genetic homogeneity among geographically distant populations of the blister worm *Polydora websteri*. *Aquaculture Environment Interactions* **10**, 437–446.

Richardson DM, Pyšek P and Carlton JT (2011) A compendium of essential concepts and terminology in biological invasions. In Richardson DM (ed) *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*. Oxford: Wiley, pp. 409–420.

Robinson T, Alexander M, Simon C, Griffiths C, Peters K, Sibanda S, Miza S, Groenewald B, Majiedt P and Sink K (2016) Lost in translation? Standardising the terminology used in marine invasion biology and updating South African alien species lists. *African Journal of Marine Science* **38**, 129–140.

Rodewald N, Snyman R and Simon CA (2021) Worming its way in – *Polydora websteri* (Annelida: Spionidae) increases the number of non-indigenous shell-boring polydorin pests of cultured molluscs in South Africa. *Zootaxa* **4969**, 255–279.

Rodriguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions* **8**, 927–939.

Rosenberg R, Hellman B and Lundberg A (1996) Benthic macrofaunal community structure in the Norwegian Trench, Deep Skagerrak. *Journal of Sea Research* **35**, 181–188.

Ross D, Keough M, Longmore A and Knott N (2007) Impacts of two introduced suspension feeders in Port Phillip Bay, Australia. *Marine Ecology Progress Series* **340**, 41–53.

Ross DJ, Longmore AR and Keough MJ (2013) Spatially variable effects of a marine pest on ecosystem function. *Oecologia* **172**, 525–538.

Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE and Kay MC (2005) Introduction of non-native oysters: ecosystem effects and restoration implications. *Annual Review of Ecology, Evolution, and Systematics* 36, 643–689.

Sabry RC and Magalhães ARM (2005) Parasites in cultured oysters (*Crassostrea rhizophorae* and *Crassostrea gigas*) from Ponta do Sambaqui, Florianópolis, SC. *Arquivo Brasileiro de Medicina Veterinaria e Zootecnia* **57**, 194–203.

Saracho Bottero MA, Jaubet ML, Llanos EN, Becherucci ME, Elías R and Garaffo GV (2020) Spatial-temporal variations of a SW Atlantic macrobenthic community affected by a chronic anthropogenic disturbance. *Marine Pollution Bulletin* **156,** 111189.

Sato-Okoshi W, Okoshi K and Shaw J (2008) Polydorid species (Polychaeta: Spionidae) in south-western Australian waters with special reference to *Polydora uncinata* and *Boccardia knoxi*. *Journal of the Marine Biological Association of the United Kingdom* **88**, 491–501.

Schleyer MH (1991) Shell-borers in the oyster, *Striostrea margaritacea*: pests or symbionts? *Symbiosis* **10**, 135.

Schwindt E, Bortolus A and Iribarne OO (2001) Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure. *Biological Invasions* **3**, 137–149.

Schwindt E and Iribarne OO (2000) Settlement sites, survival and effects on benthos of an introduced reef-building polychaete in a SW Atlantic coastal lagoon. *Bulletin of Marine Science* **67**, 73–82.

Schwindt E, Iribarne OO and Isla FI (2004) Physical effects of an invading reef-building polychaete on an Argentinean estuarine environment. *Estuarine, Coastal and Shelf Science* **59**, 109–120.

Shine R (2010) The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *Quarterly Review of Biology* **85**, 253–291.

Sierra-Correa PC and Cantera Kintz JR (2015) Ecosystem-based adaptation for improving coastal planning for sea-level rise: a systematic review for mangrove coasts. *Marine Policy* **51**, 385–393.

Simon CA, Ludford A and Wynne S (2006) Spionid polychaetes infesting cultured abalone *Haliotis midae* in South Africa. *African Journal of Marine Science* **28**, 167–171.

Simon CA and Sato-Okoshi W (2015) Polydorid polychaetes on farmed molluscs: distribution, spread and factors contributing to their success. *Aquaculture Environment Interactions* **7**, 147–166.

Simon CA, Thornhill DJ, Oyarzun F and Halanych KM (2009) Genetic similarity between *Boccardia proboscidea* from Western North America and cultured abalone, *Haliotis midae*, in South Africa. *Aquaculture* **294**, 18–24.

Simon CA, van Niekerk HH, Burghardt I, Ten Hove HA and Kupriyanova EK (2019) Not out of Africa: *Spirobranchus kraussii* (Baird, 1865) is not a global fouling and invasive serpulid of Indo-Pacific origin. *Aquatic Invasions* **14**, 221–249.

Simon CA, Worsfold TM, Lange L and Sterley J (2010) The genus Boccardia (Polychaeta: Spionidae) associated with mollusc shells on the south coast of South Africa. *Journal of the Marine Biological Association of the United Kingdom* **90**, 585–598.

Soliman T and Inglis GJ (2018) Forecasting the economic impacts of two biofouling invaders on aquaculture production of greenlipped mussels Perna canaliculus in New Zealand. *Aquaculture Environment Interactions* **10**, 1–12.

Spencer LH, Martinelli JC, King TL, Crim R, Blake B, Lopes HM and Wood CL (2020) The risks of shell-boring polychaetes to shellfish aquaculture in Washington, USA: a mini-review to inform mitigation actions. *Aquaculture Research* **00**, 1–18.

Stabili L, Licciano M, Lezzi M and Giangrande A (2014) Microbiological accumulation by the Mediterranean invasive alien species *Branchiomma bairdi* (Annelida, Sabellidae): potential tool for bioremediation. *Marine Pollution Bulletin* **86**, 325–331.

Stenton-Dozey JME, Jackson LF and Busby AJ (1999) Impact of mussel culture on macrobenthic community structure. *Marine Pollution Bulletin* **39**, 357–366.

Streftaris N and Zenetos A (2006) Alien marine species in the Mediterranean – the 100 'worst invasives' and their impact. *Mediterranean Marine Science* **7**, 87–118.

Styan CA, Mccluskey CF, Sun Y and Kupriyanova EK (2017) Cryptic sympatric species across the Australian range of the global estuarine invader *Ficopomatus enigmaticus* (Fauvel, 1923) (Serpulidae, Annelida). *Aquatic Invasions* **12**, 53–65.

Sun Y, Al-Kandari M, Kubal P, Walmiki N and Kupriyanova EK (2017) Cutting a Gordian knot of tubeworms with DNA data: the story of the Hydroides Operculata-complex (Annelida, Serpulidae). *Zootaxa* **4323**, 39–48.

Svendsen LMB, van der Bijl L and Norup S (2005) NOVANA. National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environments. Programme Description-Part 2. *NERI Technical Report* 1483 **537**, pp. 91–111.

Tait LW, Lohrer AM, Townsend M, Atalah J, Floerl O and Inglis GJ (2020) Invasive ecosystem engineers threaten benthic nitrogen cycling by altering native infaunal and biofouling communities. *Scientific Reports* **10**, 1–11.

Thomsen MS, Wernberg T, Silliman BR and Josefson AB (2009) Broad-scale patterns of abundance of non-indigenous soft-bottom invertebrates in Denmark. *Helgoland Marine Research* **63**, 159–167.

Vallarino EA, Rivero MS, Gravina MC and Elías R (2002) The community-level response to sewage impact in intertidal mytilid beds of the Southwestern Atlantic, and the use of the Shannon index to assess pollution. *Revista de Biología Marina y Oceanografía* **37**, 25–33.

Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M and Westbrooks R (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* **21**, 1–16.

Volkenborn N, Robertson DM and Reise K (2009) Sediment destabilizing and stabilizing bio-engineers on tidal flats: cascading effects of experimental exclusion. *Helgoland Marine Research* **63**, 27–35.

Waser AM, Lackschewitz D, Knol J, Reise K, Wegner KM and Thieltges DW (2020) Spread of the invasive shell-boring annelid *Polydora websteri* (Polychaeta, Spionidae) into naturalised oyster reefs in the European Wadden Sea. *Marine Biodiversity* **50**, 63.

Watson GJ, Murray JM, Schaefer M and Bonner A (2017) Bait worms: a valuable and important fishery with implications for fisheries and conservation management. *Fish and Fisheries* **18**, 374–388.

Weigert A and Bleidorn C (2016) Current status of annelid phylogeny. *Organisms Diversity & Evolution* 16, 345-362.

Whitelegge T (1890) Report on the worm disease affecting the oysters on the coast of New South Wales. *Records of the Australian Museum* **1**, 41–54.

Williams L, Matthee CA and Simon CA (2016) Dispersal and genetic structure of *Boccardia polybranchia* and *Polydora hoplura* (Annelida: Spionidae) in South Africa and their implications for aquaculture. *Aquaculture* **465**, 235–244.

Witte U, Aberle N, Sand M and Wenzhöfer F (2003) Rapid response of a deep-sea benthic community to POM enrichment: an *in situ* experimental study. *Marine Ecology Progress Series* **251**, 27–36.

Woodwick K (1963) Comparison of *Boccardia columbiana* Berkeley and *Boccardia proboscidea* Hartman (Annelida, Polychaeta). *Bulletin of the Southern California Academy of Sciences* **62**, 132.

Yee A, Mackie J and Pernet B (2019) The distribution and unexpected genetic diversity of the non-indigenous annelid *Ficopomatus enigmaticus* in California. *Aquatic Invasions* **14**, 250–266.

Yeung C, Yang MS, Jewett SC and Naidu AS (2013) Polychaete assemblage as surrogate for prey availability in assessing southeastern Bering Sea flatfish habitat. *Journal of Sea Research* **76**, 211–221.

Zenetos A (2010) Trend in alien species in the Mediterranean. An answer to Galil, 2009 'Taking stock: inventory of alien species in the Mediterranean Sea'. *Biological Invasions* **12**, 3379–3381.

Zenetos A, Çinar ME, Crocetta F, Golani D, Rosso A, Servello G, Shenkar N, Turon X and Verlaque M (2017) Uncertainties and validation of alien species catalogues: the Mediterranean as an example. *Estuarine, Coastal and Shelf Science* **191**, 171–187.

Zmudziński L (1996) The effect of the introduction of the American species *Marenzelleria viridis* (Polychaeta: Spionidae) on the benthic ecosystem of Vistula Lagoon. *Marine Ecology* **17**, 221–226.

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