



Plastic as a Vector of Dispersion for Marine Species With Invasive Potential. A Review

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Plastic debris constitutes up to 87% of marine litter and represents one of the most frequently studied vectors for marine alien species with invasive potential in the last 15 years. This review addresses an integrated analysis of the different factors involved in the impact of plastic as a vector for the dispersal of marine species. The sources of entry of plastic materials into the ocean are identified as well as how they move between different habitats affecting each trophic level and producing hot spots of plastic accumulation in the ocean. The characterization of plastic as a dispersal vector for marine species has provided information about the inherent properties of plastics which have led to its impact on the ocean: persistence, buoyancy, and variety in terms of chemical composition, all of which facilitate colonization by macro and microscopic species along with its dispersion throughout different oceans and ecosystems. The study of the differences in the biocolonization of plastic debris according to its chemical composition provided fundamental information regarding the invasion process mediated by plastic, and highlighted gaps of knowledge about this process. A wide range of species attached to plastic materials has been documented and the most recurrent phyla found on plastic have been identified from potentially invasive macrofauna to toxic microorganisms, which are capable of causing great damage in places far away from their origin. Plastic seems to be more efficient than the natural oceanic rafts carrying taxa such as Arthropoda, Annelida, and Mollusca. Although the differential colonization of different plastic polymers is not clear, the chemical composition might determine the community of microorganisms, where we can find both pathogens and virulent and antibiotic resistance genes. The properties of plastic allow it to be widely dispersed in practically all ocean compartments, making this material an effective means of transport for many species that could become invasive.

Keywords: plastic debris, alien species, marine exotic species, plastic dispersion, marine ecosystem, nonindigenous species

INTRODUCTION

Marine ecosystems around the world are threatened by several factors related to human activity (Ibabe et al., 2020), such as biological invasions (Ojaveer et al., 2015). Invasive species generally have a strong influence on the invaded environment, altering the structure of the community and the functions of the ecosystem, through competition with native species (Bertness, 1984), introduction of pathogens (Rilov and Crooks, 2009b), or indirect changes in habitat conditions (Crooks, 2002).

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The exponential increase in the rate of invasive alien species (IAS) over the last decades has stimulated the study of biological invasions (Seebens et al., 2017), especially in the marine environment, which has received less attention compared to the terrestrial one (Davis, 2000; Katsanevakis et al., 2014). In addition to traditional marine vectors (biofouling and ballast water), which gained importance with the development of commercial shipping (Carlton, 1987; Clarke Murray et al., 2014), new challenges were added to the study of dispersion factors, such as plastic materials (see Audrézet et al., 2020; previous and complementary article of this review, mainly focused on the biosecurity of marine plastic debris and the knowledge gaps and research priorities that exist on this topic), other materials derived from aquaculture or aquarium hobbies (Rilov and Crooks, 2009b; Walters et al., 2011).

Plastic is a potential dispersal vector of marine species (Rech et al., 2016). It is the most common marine debris, constituting 61-87% of all types of marine debris (Eriksen et al., 2014; Serra-Gonçalves et al., 2019), and is considered as one of the major threats to marine biodiversity (Avio et al., 2017). Plastic production has increased exponentially in the last 60 years, from 0.5 million tons in 1960, to almost 300 million tons in 2013 (PlasticsEurope, 2014) and 360 million tons in 2018 (PlasticsEurope, 2018). About 10% of plastic production has been introduced into marine ecosystems (Thompson, 2006) through land-based sources such as rivers, storm drains (Moore et al., 2011), urban runoff, sewage discharge, effluents from plastic manufacturing factories (Eerkes-Medrano et al., 2015), landfills or recycling points (Alomar et al., 2016), coastal areas due to the action of the wind, illegal dumping, fishing, and other human activities (Derraik, 2002). van Sebille et al. (2015) estimated that microplastics (MPs) in the oceans have reached 52.2 \times 10¹² particles, 236,000 metric tons, mainly distributed in the centers of the subtropical gyres.

The global distribution, buoyancy, and high levels of colonization of plastic debris greatly facilitate the transport of microbial communities (Carson et al., 2013), algae, invertebrates, and fish (Goldstein et al., 2014) to non-native regions (Barnes, 2002). Marine plastic debris is not only a threat to marine wildlife, but also causes significant economic and ecological damage (Keswani et al., 2016) acting both as a vector for the primary introduction of alien species into remote regions, and as a secondary vector for the regional expansion of marine species (Rech et al., 2016; Audrézet et al., 2020).

Several gaps remain to be filled regarding the potential of plastic as a species vector. For example, the harmonization of methodological approaches to study marine litter in different environmental compartments (Galgani et al., 2019) or the impact caused by the secondary propagation, which is not yet sufficiently documented (National Oceanic and Atmospheric Administration Marine Debris Program, 2017). Also, understanding the biosecurity implications associated with plastics could be a vital step toward understanding, monitoring, and eventually mitigating its impacts on a global scale (Audrézet et al., 2020).

This work aims to identify the dispersal potential of plastic as a vector for alien species introductions and to compare it with

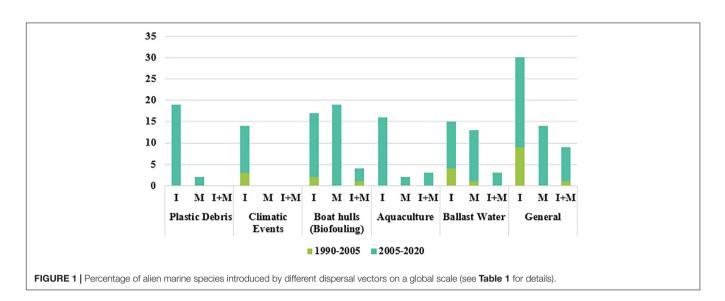
other vectors, as well as to expose the qualitative composition of the communities that inhabit plastic debris. On the other hand, we attempt to synthesize the methodological aspects of the detection of AIS introduced through plastic debris and the prevention of their negative impacts.

METHODOLOGY

Scientific literature published in the last 30 years (1990-2020) was collected from Science Direct, Scopus, Web of Science, and Google Scholar scientific databases, and the most widely consulted publishers and/or scientific internet networks were Elsevier, Springer, ResearchGate, Wiley Online Library, Dialnet, and Academia. The keywords related to invasive species in the ocean, especially those carried by plastic debris, were used in the title and keywords field: "Alien Species," "Ballast Water," "Biofouling," "Ecology," "Ecosystem," "Impact," "Invasive Species," "Marine," "Management," "Microplastics," "Ocean," "Plastic Debris," "Rafting," "Sea," "Threat," "Transport," "Vector," and "Waste." The searches were conducted mostly in March 2020 on the full range of articles or reviews available at that time. The last search was made on April 20, 2020. This initial search yielded a total of 447 articles which included information on invasive and potentially invasive species in the ocean and different dispersal vectors. In this preliminary library, a pre-selection step was carried out according to the presence of at least one of three criteria: (1) articles focused on the impact caused by one or more invasive marine species; (2) articles focused on the management of the invasion of one or more marine species; or (3) articles that include both concepts. After applying these selection criteria, 228 articles were obtained, of which 48 were discarded after analysis because they were not directly related to the topic with respect to the sections considered in the manuscript. Therefore, most of the information presented in this paper was extracted from 180 scientific publications. In addition, other articles named in the literature and previously known to the authors due to their high topic relevance were used for the review.

Selected articles were classified according to the dispersion vector(s) (Plastic Debris, Boat hulls (biofouling), Climatic Events, Ballast Water, Aquaculture, or General), their publication date (1990–2005 or 2006–2020), and the aspect addressed: Impact (I), Management (M) or Impact+Management (I+M). Impacts included articles focused on describing the impacts produced by alien species, and Management included articles focused on the management of these impacts. We separated the last 30 years into two bands to appreciate the differences in the efforts made by scientists regarding different topics in the near past and at present. On the other hand, the label "General" was included for those papers that covered more than one vector.

For the invasive or potentially invasive species listed in **Table 1**, it was specified whether they were sessile or no sessile, in order to draw conclusions about the biology of the species inhabiting plastic. Also, it was specified the transport vector for which they were identified (Plastic Debris, Boat hulls (biofouling), Climatic Events, Ballast Water, Aquaculture, Aquariums, or Transoceanic Channels/Swimming). The native



and non-native locations of the invasive and potentially invasive species were indicated.

Moreover, other relevant information was extracted from the selected and related articles such as plastic as a vector, different types of plastic and how their characteristics affect the colonization of macro and microscopic marine species, recurrent species transported by plastics, associated microorganisms dispersion and species and dispersal patterns of plastic in the ocean and how they can influence horizontal and vertical transport.

PLASTIC DEBRIS COMPARED TO OTHER DISPERSAL VECTORS

With respect to the total number of articles, the labels that yielded the highest number of selected articles were "Boat hulls (biofouling) and Ballast Water" including I, M, and I + M, with 40 and 31 papers, respectively, followed by "Plastic Debris, Aquaculture and Climate Events" (21, 21, 15, respectively) (**Figure 1**).

In the last 15 years, the most frequent labels were "Plastic Debris-Impact," and "Biofouling – Management" with 19 articles each. No articles were selected between 1990 and 2005 for the labels "Plastic Debris" and "Aquaculture." There was also a great difference in the number of research papers on the management of invasive species from the dispersal vectors "Boat hulls (biofouling)" and "Ballast Water," and the vectors "Plastic Debris," "Aquaculture," and "Climatic Events."

Of the 216 exotic species identified in the present study (**Table 1**), 68% were considered to have been introduced through maritime transport, divided into the categories "Boat hulls (biofouling)" and "Ballast Water," followed by dispersal as a consequence of the "Aquaculture" (16%), and "Plastic debris" (5%) (**Figure 2**).

This result is to be expected, as commercial shipping as a cause of IAS dispersal has been cited long before other vectors such as plastic (e.g., Carlton, 1987). Although it is a more recent

problem, we consider that the studies on plastics as an IAS vector were quite important between 2005 and 2020. Furthermore, it is expected that the number of papers on plastic as a vector of species will increase in the coming years, as its production increases every year and it is currently an emergent topic.

CHARACTERIZATION OF PLASTIC AS A VECTOR

Plastic debris abundance (Winston et al., 1997), artificial origin (Glasby et al., 2007; Pinochet et al., 2020), and properties can affect its potential to act as a vector of IAS: durability, buoyancy (Schoener and Rowe, 1970), size, and structural complexity of the surface determine colonization by marine organisms and the succession of the community associated with plastic debris, with differences in the sessile and mobile organisms (Kiessling et al., 2015).

The increasing introduction of plastic pollution into the ocean increases the chances for alien species to become invasive. For example, the bryozoan Electra tenella [Hickins, 1880; this name is currently not accepted and it is Arbopercula tenella (Hickins, 1880)] previously identified on natural rafts, may be increasing in abundance and distribution due to the increasing amounts of plastic entering the Caribbean currents and the Gulf Stream (Winston et al., 1997). Natural rafts (eg, wood, pumice, and marine vegetation) are generally characterized by low or patchy abundance, limited longevity, and relatively high habitability, due to high surface roughness, structural complexity, and biodegradability (Gil and Pfaller, 2016). Compared to natural rafts, the abundance of plastic debris is increasing (Ebbesmeyer and Ingraham, 1992), and its longevity generally exceeds that of natural debris, taking decades or even centuries to be degraded (Gregory, 1999). The durability of plastic along with its buoyancy in comparison to organic materials (Schoener and Rowe, 1970) allows a greater dispersal potential for organisms that colonize plastic debris (Barnes, 2002; Barnes

TABLE 1 | Compilation of invasive and non-native species which have been introduced or transported into areas far from their origin by the following dispersal vectors: Plastic, boat hulls (biofouling), ballast water, aquaculture, aquarium, and transoceanic channel/swimming.

INVASIVE and		Boat	Climate	Ballast			Transoceanic	Native	Non-native or	
potential		hulls	events	water			channels/	location	invaded	
invasive species	Plastics	(biofouling)			Aquaculture	Aquariums	swimming		location	References
Algae (34)									•	•
Acrothamnion preissii E.M.Wollaston, 1968		Х		Х		X		Indo-Pacific (Australia)	Mediterranean Sea	Bonanno and Orlando-Bonaca, 2019
Agardhiella subulata (C.Agardh) Kraft and M.J. Wynne, 1979					Х			Atlantic North America	United Kingdom	Eno et al., 1997
Anotrichium yagii (Okamura) Baldock, 1976		Х						Japan	Argentina	Horta and Oliveira, 2000
Antithamnionella spirographidis (Schiffner) E.M. Wollaston, 1968		X						Mediterranean Sea	United Kingdom	Eno et al., 1997
Antithamnionella ternifolia (J.D.Hooker and Harvey) Lyle, 1922		Х						Australia	United Kingdom	Eno et al., 1997
Asparagopsis armata Harvey, 1855		Х						Western Australia New Zealand	European coasts Northeast Atlantic Mediterranean Sea South Africa Middle East Indo-Pacific	Pinteus et al., 2018
Bonnemaisonia hamifera Hariot, 1891		×						Northwest Pacific	Europe	Katsanevakis et al., 2014
Caulerpa cylindracea Sonder, 1845				Х		Х		Indo Pacific	Mediterranean Sea	Bonanno and Orlando-Bonaca, 2019
Caulerpa ollivieri Dostál, 1929		Х		Х				Mediterranean Sea	Bahamas	Williams, 2007
Caulerpa taxifolia (M.Vahl) C.Agardh, 1817				Х		Х		Pacific Ocean	Mediterranean Sea	Occhipinti-Ambrogi and Savini, 2003
Codium fragile tomentosoides (1) (van Goor) P.C.Silva, 1955		Х		Х		Х		Japan	Northwest Atlantic	Williams, 2007
Codium fragile atlanticum (A.D.Cotton) P.C.Silva, 1955					X			Pacific coast of Japan	United Kingdom	Eno et al., 1997
Colpomenia peregrina (2) (Sauvageau) Hamel, 1937					Х			Pacific coast of North America	United Kingdom	Eno et al., 1997
Durvillaea antarctica (Chamisso) Hariot, 1892			Х					Chile Southern New Zealand South Atlantic	King George Island (Antarctica)	Fraser et al., 2018

INVASIVE and		Boat	Climate	Ballast			Transoceanic	Native	Non-native or	
potential		hulls	events	water			channels/	location	invaded	
invasive species	Plastics	(biofouling)			Aquaculture	Aquariums	swimming		location	References
Eucheuma denticulatum (N.L.Burman) Collins and Hervey, 1917					Х			Sulu Sea	Indian Ocean	Williams, 2007
Grateloupia doryphora (Montagne) M.Howe, 1914					Х			Pacific North America	United Kingdom	Eno et al., 1997
Grateloupia filicina var. Iuxurians (3) A.Gepp and E.S.Gepp, 1906					Х			Japan	United Kingdom	Eno et al., 1997
Grateloupia imbricata Holmes, 1896		×						Japan Korea	Portugal	Chainho et al., 2015
Grateloupia lanceolata (4) (Okamura) Kawaguchi, 1997		X						East of Asia	Portugal	Chainho et al., 2015
Grateloupia turuturu Yamada, 1941		Х						Pacific ocean	Portugal	Chainho et al., 2015
Halophila stipulacea (Forsskål) Ascherson, 1867			Х					Indo-Pacific	Mediterranean Sea	Hernández-Delgado et al., 2020
<i>Kappaphycus alvarezii</i> (Doty) Doty ex P.C.Silva, 1996					X			Sulu Sea (Philippines)	Southwest Pacific Indian Ocean	Williams, 2007
Lomentaria clavellosa (Lightfoot ex Turner) Gaillon, 1828		Х						Northeast Atlantic	North America	Mathieson et al., 2008
Lophocladia lallemandii (Montagne) F.Schmitz, 1893							Х	Indo-Pacific	Northern Coast Ibiza	García-Gómez et al., 2020
Mastocarpus papillatus (C.Agardh) Kützing, 1843		Х		Х				North Pacific	Chile	Castilla and Neill, 2009
Monostroma oxyspermum (5) (Kützing) Doty, 1947		X						Northeast Atlantic Northwest Pacific	West coast of India	Anil et al., 2002
Neosiphonia harveyi (6) (Bailey) MS.Kim, HG.Choi, Guiry and G.W. Saunders, 2001 Polysiphonia harveyi (6)Bailey, 1848		X		X	X			Japan North-Pacific Pacific coast of Japan	Argentina United Kingdom	Eno et al., 1997; Schwindt et al., 2014
Pikea californica Harvey, 1853		Х						North America	United Kingdom	Eno et al., 1997

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INVASIVE and potential invasive species	Plastics	Boat hulls (biofouling)	Climate events	Ballast water	Aquaculture	Aquariums	Transoceanic channels/ swimming	Native location	Non-native or invaded location	References
Polysiphonia morrowii Harvey, 1857		×		Х				Northeast Asia	Chile	Castilla and Neill, 2009
Rugulopteryx okamurae* (E.Y.Dawson) I.K.Hwang, W.J.Lee and H.S.Kim, 2009	Х	X			Х			Pacífico noroccidental	Strait of Gibraltar (Cádiz, Spain) Thau Lagoon (France) Western Mediterranean	Huang, 1994; Verlaque et al., 2009; García-Góme et al., 2018
Sargassum filicinum (7) Harvey, 1860		Х						Japan and Korea	California (UNITED STATES)	Miller et al., 2006
Solieria chordalis (C.Agardh) J. Agardh, 1842		Х		Х				Northern France	United Kingdom	Eno et al., 1997
Undaria pinnatifida (Harvey) Suringar, 1873		X			X			Northwest Pacific	Spain France Unites Kingdom Belgium The Netherlands New Zealand Australia Argentina	Epstein and Smale, 2017
<i>Womersleyella setacea</i> (Hollenberg) R.E.Norris, 1992		Х		Х				Pacific	Mediterranean Sea	Williams, 2007
Porifera (4)										
Crambe crambe (Schmidt, 1862)		Х		Х				Mediterranean Sea	Portugal	Chainho et al., 2015
Gelliodes fibrosa (8) (Wilson, 1925)		Х						Philippines	Pearl Harbor (Oahu, Hawai)	Godwin, 2003; Therriault et al., 2018
Paraleucilla magna Klautau, Monteiro and Borojevic, 2004		X						Brazil	Portugal	Chainho et al., 2015
Stelletta clarella de Laubenfels, 1930		Х		Х				North Pacific	Chile	Castilla and Neill, 2009
Cnidaria (16)										
<i>Aiptasia diaphana (9)</i> (Rapp, 1829)		Х						Eastern Atlantic Mediterranean Sea	Portugal	Chainho et al., 2015
Amelia aurita (Linnaeus, 1758)				Х				Black Sea Norest Atlantic Chile	Caspian Sea	Korsun et al., 2012
Blackfordia virginica Mayer, 1910		Х		Х				Baltic Sea	Portugal	Chainho et al., 2015
Cladonema radiatum Dujardin, 1843		Х		Х				West Pacific	Northeast Pacific	Williams, 2007
Clavularia viridis Quoy and Gaimard, 1833						Х		Indo-Pacific	Ilha Grande Bay (Brazil)	Mantelatto et al., 2018

(Continued)

INVASIVE and		Boat	Climate	Ballast			Transoceanic	Native	Non-native or	
ootential		hulls	events	water			channels/	location	invaded	
nvasive species	Plastics	(biofouling)			Aquaculture	Aquariums	swimming		location	References
Cordylophora caspia (Pallas, 1771)		Х						Caspian Sea Black Sea	Portugal	Chainho et al., 2015
Diadumene lineata Verrill, 1869)	Х	Х	Х	Х				Northwest Pacific (Japan)	Northwest Atlantic Northwestern Hawaii	Williams, 2007; Gregory 2009; Miller et al., 2018
Garveia franciscana (10) Torrey, 1902)					Х			Indo-Pacific	Mediterranean Sea	Marchini et al., 2015b
Gonionemus vertens A. Agassiz, 1862		Х		Х	Х			North Pacific Portugal	Northwest Atlantic United Kingdom	Eno et al., 1997; William 2007
Haliplanella lineata (11) Verrill, 1869)		Х						Pacific Japan	United Kingdom	Eno et al., 1997
Oc<i>ulina patagonica</i> de Angelis, 1908		Х						South West Atlantic	Mediterranean Sea	Fine et al., 2001
Rhizostoma pulmo (Macri, 1778)				Х				Southern North Sea	Black Sea	Boran, 2017
Rhopilema nomadica Galil, Spanier and ⁻ erguson, 1990							Х	Indo-Pacific	Mediterranean Sea	Bonanno and Orlando-Bonaca, 2019
Sansibia spp.						Х		Indo-Pacific	Ilha Grande Bay (Brazil)	Mantelatto et al., 2018
Tubastraea coccinea (Ehrenberg, 1834)		Х						Unknown (widespread distribution)	Southwest Atlantic	Creed et al., 2017
Tubastraea tagusensis Wells, 1982		Х						Galapagos archipelago	Southwest Atlantic	Creed et al., 2017
Ctenophora (2)									•	
Beroe ovato Bruguière, 1789		Х						East Atlantic (North and South America)	Black Sea Denmark	Shiganova et al., 2014
Mnemiopsis leidyi A. Agassiz, 1865				Х				West Atlantic	Black Sea	Shiganova et al., 2019
Platyhelminthes (1)										
Koinostylochus ostreophagus (Hyman, 1955)		X						Northwest Pacific	Strait of Georgia (Canada)	Gartner et al., 2016
Nematoda (1)										
Anguillicola crassus (12) Kuwahara, Niimi and Itagaki, 1974				Х				Taiwan	United Kingdom	Eno, 1996
Mollusca (44)										
Arcuatula senhousia (Benson, 1842)		Х		Х		Х		Indo-Pacific	Mediterranean Sea	Bonanno and Orlando-Bonaca, 2019
Batillaria attramentaria (G. B. Sowerby II, 1855)					Х			Asia	California (UNITED STATES)	Grosholz et al., 2015

(Continued)

INVASIVE and		Boat	Climate	Ballast			Transoceanic	Native	Non-native or	
ootential		hulls	events	water			channels/	location	invaded	
invasive species	Plastics	(biofouling)			Aquaculture	Aquariums	swimming		location	References
Chaetopleura angulata (Spengler, 1797)		Х		Х	X			Brazil	Portugal	Chainho et al., 2015
Chama macerophylla Gmelin, 1791		Х						West Indies	Pearl Harbor (Oahu, Hawaii)	Godwin, 2003; Therriault et al., 2018
Crassostrea gigas (Thunberg, 1793)		Х			×			Asian Pacific Ocean	New Zealand	Chainho et al., 2015
Crassostrea virginica (Gmelin, 1791)		Х			X			Northeast America	North Sea	Gollasch, 2002
Crepidula fornicata (Linnaeus, 1758)		Х			Х			Atlantic coast of North America	Norway	Minchin and Gollasch, 200
Crepidula onyx G. B. Sowerby I, 1824			Х					Northwest Pacific	Northeast Pacific	Miller et al., 2018
Dreissena polymorpha (Pallas, 1771)				Х				Caspian Sea Black Sea	St Clair lake (North America)	Hebert et al., 1991
Ensis americanus (13) (Gould, 1870)				Х				Atlantic North America	United Kingdom	Eno et al., 1997
Haliotis rufescens Swainson, 1822					X			North Pacific	Chile Peru	Castilla and Neill, 2009
Hexaplex trunculus (Linnaeus, 1758)		Х		Х				Mediterranean Sea	Portugal	Chainho et al., 2015
Lopha cristagalli (Linnaeus, 1758)	Х							Indo-Pacific	Southwestern New Zealand	Gregory, 2009
Lyrodus medilobata (Edmonson, 1942)				Х				Indo-Pacific Ocean	West coast of India	Anil et al., 2002
Lyrodus takanoshimensis (Roch, 1929)			Х					Northwest Pacific	Northeast Pacific	Miller et al., 2018
Mactra discors (14) J.E. Gray, 1837		Х						Pacific Ocean (New Zealand)	North Sea	Gollasch, 2002
Magallana angulata (Lamarck, 1819)					Х			Pacific Ocean	Southern Portuguese coast	Rech et al., 2018b
Magallana gigas (Thunberg, 1793)	Х					Х		Indo-Pacific Ocean	Mediterranean Sea Cantabrian Coast	Miralles et al., 2018; Bonanno and Orlando-Bonaca, 2019
Mercenaria mercenaria (Linnaeus, 1758)					Х			West Atlantic	Great Britain	Williams, 2007

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INVASIVE and		Boat	Climate	Ballast			Transoceanic	Native	Non-native or	
otential		hulls	events	water			channels/	location	invaded	
invasive species	Plastics	(biofouling)			Aquaculture	Aquariums	swimming		location	References
<i>Musculista senhousia</i> (15) (Benson, 1842)		Х		X				West Pacific	California	Williams, 2007
Mya arenaria Linnaeus, 1758				Х				Northern Atlantic	Black Sea, Sea of Azov	Occhipinti-Ambrogi and Savini, 2003
Mytella cnarruana (16) (d'Orbigny, 1846)				Х				Atlantic South America Pacific Central South America	South-east North America	Spinuzzi et al., 2013
Mytilopsis sallei (Récluz, 1849)		Х						Central and South America	Australia	Minchin and Gollasch, 200
Mydlus galloprovincialis Lamarck, 1819			Х					Japan	Pearl Harbour (Hawaii)	Therriault et al., 2018
<i>Mydlus trossulus</i> Gould, 1850	Х							North Atlantic North Pacific Baltic Sea	Cantabrian Coast	Miralles et al., 2018
Nassarius costellifera (17) (A. Adams, 1853)		Х						Atlantic Ocean	North Sea	Gollasch, 2002
Nausitora dunlopei E. P. Wright, 1864				Х				Cochin (India)	Goa (India)	Anil et al., 2002
Ocenebra inornata (18) (Récluz, 1851)					Х			Japan Korea	Portugal	Chainho et al., 2015
Ostrea lurida Carpenter, 1864		Х						Pacific North America	North Sea	Gollasch, 2002
Perna viridis (Linnaeus, 1758)	X			Х	X			Tropical Indo-Pacific	Florida Colombian Caribbean	Spinuzzi et al., 2013; Gracia and Rangel-Buitrago, 2020
Philine auriformis Suter, 1909		Х		Х				New Zealand	California	Williams, 2007
Potamocorbula amurensis (Schrenck, 1861)				Х				Asia	San Francisco (UNITED STATES)	Godwin, 2003; Therriault et al., 2018
Potamopyrgus antipodarum (Gray, 1843)		Х		Х				New Zealand	Portugal Baltic Sea	Leppäkoski and Olenin, 2000; Chainho et al., 2015
Rapana venosa (Valenciennes, 1846)				Х				Sea of Japan	Black Sea Adriatic Sea	Occhipinti-Ambrogi and Savini, 2003
Ruditapes philippinarum (A. Adams and Reeve, 1850)					Х			Indo-Pacific	Portugal	Braga et al., 2017
Saccostrea cuccullata (Born, 1778)		Х		Х	Х			Indo-Pacific	South Brazilian coast	do Amaral et al., 2020

(Continued)

INVASIVE and		Boat	Climate	Ballast			Transoceanic	Native	Non-native or	
potential		hulls	events	water			channels/	location	invaded	
invasive species	Plastics	(biofouling)			Aquaculture	Aquariums	swimming		location	References
Scapharca inaequivalvis (19) (Bruguière, 1789)				Х				Indo-Pacific	Black Sea Adriatic Sea	Occhipinti-Ambrogi and Savini, 2003
Senilia senilis (Linnaeus, 1758)		Х						North east Atlantic	North Sea	Gollasch, 2002
Teredo fulleri Clapp, 1924				Х				Gulf of Mannar (Southeast India)	Okha (West India)	Anil et al., 2002
Teredo navalis Linnaeus, 1758			Х					Northeast Atlantic	Florida (UNITED STATES)	Miller et al., 2018
Theora lubrica Gould, 1861				Х				Inland Sea (Qatar)	San Francisco Bay (UNITED STATES)	Carlton, 1996
Tonicia atrata (20) Hutton, 1880		Х		Х	Х			Europe	Portugal	Chainho et al., 2015
Urosalpinx cinerea (Say, 1822)					Х			North America	United Kingdom	Eno, 1996
Xenostrobus securis (Lamarck, 1819)		Х						Western Australia New Zealand	North Sea	Gollasch, 2002
Annelida (21)									1	
Branchiomma bairdi (McIntosh, 1885)		Х						Caribbean Sea	Portugal	Chainho et al., 2015
Clymenella torquata (Leidy, 1855)					Х			Western Atlantic	United Kingdom	Eno et al., 1997
Eulalia viridis (Linnaeus, 1767)		Х						North Atlantic	Strait of Georgia (Canada)	Gartner et al., 2016
Eumida sanguinea (Örsted, 1843)		Х						Northeast Atlantic	Strait of Georgia (Canada)	Gartner et al., 2016
Ficopomatus enigmaticus (Fauvel, 1923)		Х		Х				Indian Ocean	Black Sea	Occhipinti-Ambrogi and Savini, 2003
Goniadella gracilis (Verrill, 1873)		Х						North America	United Kingdom	Eno et al., 1997
Hydroides dianthus (Verrill, 1873)		Х			Х			Atlantic North America	United Kingdom	Eno et al., 1997; Katsanevakis et al., 201
Hydroides elegans (Haswell, 1883) [nomen protectum]			Х					Indo-Pacific Northwest Pacific	Australia	Bryan et al., 2004
Hydroides ezoensis Okuda, 1934		Х		Х				Japan	United Kingdom Tropical Northeast Pacific	Eno et al., 1997
Hydroides sanctaecrucis Krøyer in Mörch, 1863		Х						Caribbean Sea	Northern Australia	Lewis et al., 2006
Janua brasiliensis (21) (Grube, 1872)		Х						Tropical areas (e.g., Brazil)	United Kingdom	Eno et al., 1997

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(Continued)

INVASIVE and potential invasive species	Plastics	Boat hulls (biofouling)	Climate events	Ballast water	Aquaculture	Aquariums	Transoceanic channels/ swimming	Native location	Non-native or invaded location	References
Marenzelleria viridis Verrill, 1873)	Flastics	X		Х	Aquaculture	Aquanums	Swinning	North America	Baltic Sea	Leppäkoski and Olenin, 2000
Mercierella enigmatica 22) Fauvel, 1923		Х						Australia	Indian Ocean	Anil et al., 2002
Veodexiospira prasiliensis Grube, 1872)					Х			South America	Northwest Atlantic Great Britain	Williams, 2007
Parougia caeca Webster and Benedict, 1884)		Х						North America	Johnstone Strait (Canada)	Gartner et al., 2016
Pileolaria berkeleyana Rioja, 1942)		Х						Japan	United Kingdom	Eno et al., 1997
Polydora cornuta Bosc, 1802		Х		Х	Х			Unknown	Black Sea	Radashevsky and Selifonova, 2013
Pseudopolydora kempi a ponica majima and Hartman, 1964					Х			Japan	Northwest Pacific	Williams, 2007
Sabaco elongatus (Verrill, 1873)					Х			West Atlantic	Northwest Pacific	Williams, 2007
Sabella spallanzanii (Gmelin, 1791)	Х				Х			Mediterranean Sea	New Zealand	Campbell et al., 2017
Streblospio benedicti Webster, 1879					Х			West Atlantic	Northwest Pacific	Williams, 2007
Arthropoda (51)										
Acaria (Acartiura) omori Bradford, 1976				Х				North Pacific	Chile	Castilla and Neill, 2009
Acaria (Acanthacartia) tonsa Dana, 1849				Х				Indo-Pacific	Portugal	Sobral, 1985
Ammothea hilgendorf (Böhm, 1879)		Х						Japan	United Kingdom	Eno et al., 1997
Amphibalanus amphitrite Darwin, 1854)	X							Unknown	Cantabrian Coast	Miralles et al., 2018
Amphibalanus improvisus Darwin, 1854)		Х						Western Atlantic	Strait of Georgia (Canada, Northwest Pacific)	Gartner et al., 2016

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(Continued)

INVASIVE and potential		Boat hulls	Climate events	Ballast water			Transoceanic channels/	Native location	Non-native or invaded	
invasive species	Plastics	(biofouling)	eventa	water	Aquaculture	Aquariums	swimming	location	location	References
Amphibalanus reticulatus (Utinomi, 1967)		Х Х						Japan	Southern Brazil	Kauano et al., 2016
Ampithoe valida Smith, 1873		Х		Х	Х			Japan	Strait of Georgia (Canada)	Williams, 2007
Austrominius modestus (Darwin, 1854)	Х							Australia New Zealand	North Spain Coast (Cantabria, Asturias, Biscay)	Miralles et al., 2018; Rech et al., 2018b
Balanus amphitrite (23) Darwin, 1854		Х						Japan Korea	North Sea	Gollasch, 2002
Balanus campbelli (24) Filhol, 1886		Х						New Zealand	North Sea	Gollasch, 2002
Balanus eburneus (25) Gould, 1841		Х						North America	North Sea	Gollasch, 2002
Balanus perforatus (26) Bruguière, 1789		Х						Northeast Atlantic	North Sea	Gollasch, 2002
Balanus variegatus (27) Darwin, 1854		Х						Fare East Australia India	North Sea	Gollasch, 2002
Callinectes sapidus Rathbun, 1896				Х				Western Atlantic Ocean	Portugal	Chainho et al., 2015
Caprella drepanochir Mayer, 1890		Х						North Pacific	Strait of Juan de Fuca (Canada) Strait of Georgia (Canada)	Gartner et al., 2016
Caprella mutica Schurin, 1935		Х	Х	Х				Northwestern Pacific Ocean (Japan)	Strait of Georgia (Canada)	Cook et al., 2007; Gartner et al., 2016
Caprella scaura Templeton, 1836		Х		Х	X			Indo Pacific	Girona (Spain)	Martínez and Adarraga, 2008
Carcinus maenas (Linnaeus, 1758)		Х						Northeast Atlantic	North America South Africa	Grosholz and Ruiz, 1995
Centropages abdominalis Sato, 1913		Х		Х				North Pacific	Chile	Castilla and Neill, 2009
Cercopagis pengoi (Ostroumov, 1891)				Х				Caspian Sea	Baltic Sea	Leppäkoski and Olenin, 2000
		Х						Japan Korea	New Zealand	Brine et al., 2013
<i>Cilicaea latreillei</i> Leach, 1818		Х		Х				Indonesia Philippines Sri Lanka South Africa Red Sea Australia	Arabian Sea	Anil et al., 2002
Diamysis lagunaris Ariani and Wittmann, 2000				Х				Mediterranean Sea Black Sea	Portugal	Chainho et al., 2015

(Continued)

INVASIVE and		Boat	Climate	Ballast			Transoceanic	Native	Non-native or	
potential		hulls	events	water			channels/	location	invaded	
invasive species	Plastics	(biofouling)			Aquaculture	Aquariums	swimming		location	References
Dynamene bidentata (Adams, 1800)		Х						Northeast Atlantic	North Sea	Gollasch, 2002
Elminius kingii Gray, 1831		Х						South America	North Sea East cost of Canada	Gollasch, 2002
<i>Elminius modestus</i> (28) Darwin, 1854	Х	Х		Х				New Zealand	United Kingdom Shetland Islands	Eno et al., 1997; Barnes and Milner, 2004
Elminius simplex Linzey (1942)		Х		-				Indian Ocean Australia South America	North Sea East cost of Canada	Gollasch, 2002
Endeis nodosa Hilton, 1942			Х					Northwest Pacific	Tropical Eastern Atlantic	Miller et al., 2018
Eriocheir sinensis H. Milne Edwards, 1853		Х		Х				Japan China	United Kingdom	Eno et al., 1997
Hemigrapsus penicillatus (De Haan, 1835 [in De Haan, 1833-1850])		Х						Fare East (Japan, China, Korea)	North Sea French Atlantic coast	Gollasch, 2002
Hemigrapsus sanguineus (De Haan, 1835 [in De Haan, 1833-1850])			Х					Japan	Hawaii Northeast Pacific	Therriault et al., 2018
Hesperibalanus fallax (Broch, 1927)	Х				Х			Atlantic Coast of tropical Africa	South Portugal	Rech et al., 2018b
Hyas araneus (Linnaeus, 1758)		Х		Х				North Atlantic Arctic Ocean	Antarctic Peninsula	Tavares and De Melo, 2004
laniropsis serricaudis Gurjanova, 1936			Х					Northwest Pacific	North America	Miller et al., 2018
Incisocalliope derzhavini (Gurjanova, 1938)		Х						Northeast Pacific	Strait of Juan de Fuca (Canada) Strait of Georgia (Canada)	Gartner et al., 2016
<i>Ligia oceanica</i> (Linnaeus, 1767)		Х		Х				Northeast Atlantic	Portugal	Chainho et al., 2015
<i>Liocarcinus navigator</i> (Herbst, 1794)	Х							Eastern Atlantic Mediterranean Sea	Adriatic Sea	Tutman et al., 2017

(Continued)

INVASIVE and		Boat	Climate	Ballast			Transoceanic	Native	Non-native or	
ootential		hulls	events	water			channels/	location	invaded	
nvasive species	Plastics	(biofouling)			Aquaculture	Aquariums	swimming		location	References
Megabalanus coccopoma (Darwin, 1854)		X		Х				Pacific Central South America	San Diego (California)	Spinuzzi et al., 2013
Melita nitida S.I. Smith in Verrill, 1873		Х						North America	Strait of Georgia (Canada)	Gartner et al., 2016
Metapenaeus monoceros (Fabricius, 1798)					X			Indo-Pacific Ocean	Mediterranean Sea	Bonanno and Orlando-Bonaca, 2019
Monocorophium acherusicum (Costa, 1853)		×						Eastern Atlantic	Strait of Juan de Fuca (Canada) Strait of Georgia (Canada)	Gartner et al., 2016
Monocorophium i nsidiosum (Crawford, 1937)		Х						Eastern Atlantic	Strait of Juan de Fuca (Canada) Strait of Georgia (Canada)	Gartner et al., 2016
Oithona davisae Ferrari F.D. and Orsi, 1984				Х				North Pacific	Chile	Castilla and Neill, 2009
Paracaprella pusilla <i>Mayer,</i> 1890				Х				Western Atlantic	Panama Mediterranean Sea	Ros et al., 2013
Paracaprella tenuis Mayer, 1903		Х						Pacific North America Gulf of Mexico	North Sea	Gollasch, 2002
Penaeus japonicus Spence Bate, 1888					X			Indo-Pacific	Mediterranean Sea	Bonanno and Orlando-Bonaca, 2019
Planes minutus (Linnaeus, 1758)	Х							Indian ocean Atlantic ocean	Adriatic Sea	Tutman et al., 2017
Pyromaia tuberculata (Lockington, 1877)				Х				Southern California (UNITED STATES)	San Francisco (UNITED STATES) Japan Korea New Zealand	Carlton, 1996
Rhithropanopeus harrisii (Gould, 1841)		Х		Х	X			West Atlantic	Portugal	Chainho et al., 2015
Sphaeroma walkeri Stebbing, 1905		Х						Indian Ocean	Hong Kong	Lewis and Coutts, 2010
Striatobalanus amaryllis (Darwin, 1854)		Х						Indian Ocean West Pacific	West Africa	Kerckhof et al., 2010
Temora turbinata (Dana, 1849)				Х				Indian Ocean	Southwest Atlantic	Soares et al., 2018
Bryozoa (15)										
Bowerbankia gracilis (16) Leidy, 1855		Х		Х	X			West Atlantic	California (UNITED STATES)	Williams, 2007
Bugula flabellata (17) Thompson in Gray, 1848)		Х		Х				South Pacific South Atlantic	Chile	Castilla and Neill, 2009

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(Continued)

INVASIVE and		Boat	Climate	Ballast			Transoceanic	Native	Non-native or	
potential		hulls	events	water			channels/	location	invaded	
invasive species	Plastics	(biofouling)			Aquaculture	Aquariums	swimming		location	References
Bugula neritina (Linnaeus, 1758)		X		Х	Х			Pacific Ocean	Chile	Castilla and Neill, 2009
<i>Cryptosula pallasiana</i> (Moll, 1803)			Х					Northwest Pacific	Northeast Pacific	Miller et al., 2018
Disporella novaehollandiae (d'Orbigny, 1853)			Х					Northwest Pacific	Hawaiian Island	McCuller and Carlton, 2018
Jellyella eburnea (Hincks, 1891)	Х							Western Pacific	Central Pacific Eastern Pacific	McCuller and Carlton, 2018
Jellyella tuberculata (Bosc, 1802)	Х		Х					Western Pacific	Central Pacific Eastern Pacific	McCuller and Carlton, 2018
Membranipora membranacea (Linnaeus, 1767)	X							Atlantic Ocean Pacific Ocean	Artic Ocean	Barnes and Milner, 2004
Savignyella lafontii (Audouin, 1826)		Х						Mediterranean Sea	North Sea	Gollasch, 2002
Schizoporella japonica Ortmann, 1890		X	Х	Х	X			Japan	California (UNITED STATES) Columbia (Canada) Northeast Pacific	Williams, 2007; Gartner et al., 2016; Miller et al., 2018
Thalamoporella evelinae Marcus, 1939	Х							Brazil	Florida (UNITED STATES)	Winston et al., 1997
Tricellaria inopinata d'Hondt and Occhipinti Ambrogi, 1985		Х						Pacific ocean	Portugal	Chainho et al., 2015
Watersipora cucullata (Busk, 1854)		Х						Northeast Pacific	New Zealand	Lewis and Coutts, 2010
Watersipora subtorquata (d'Orbigny, 1852)		Х						Unknown	Portugal	Chainho et al., 2015
Zoobotryon verticillatum (18) (Delle Chiaje, 1822)		X		Х				Caribbean Sea	California (UNITED STATES) Portugal	Williams, 2007; Chainho et al., 2015
Entoprocta (2)										
Barentsia benedeni (Foettinger, 1887)				Х				Northeast Atlantic	Black Sea	Rilov and Crooks, 2009a
Barentsia ramosa (Robertson, 1900)				Х				California (UNITED STATES) Belgium	Indian Ocean	Anil et al., 2002
Echinodermata (2)										
Asterias amurensis Lutken, 1871		Х	Х					Northern Pacific (Japan)	South Australia	Godwin, 2003; Therriault et al., 2018

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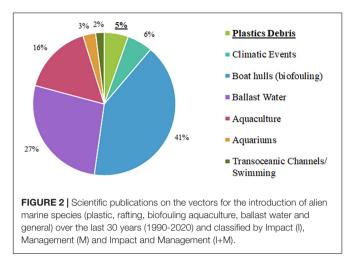
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INVASIVE and		Boat	Climate	Ballast			Transoceanic	Native	Non-native or	
ootential		hulls	events	water			channels/	location	invaded	
nvasive species	Plastics	(biofouling)			Aquaculture	Aquariums	swimming		location	References
Ophiothela mirabilis Verrill, 1867		Х		Х				Indo-Pacific	Ilha Grande Bay (Brazil)	Mantelatto et al., 2018
S. Tunicata (16)										
Ascidiella aspersa (Müller, 1776)		Х		Х	Х			Northeastern Atlantic	Atlantic coast of North America New Zealand Southern Australia India	Lynch et al., 2016
Asterocarpa humilis (Heller, 1878)		Х			×			South Pacific	Chile	Pinochet et al., 2017
Botrylloides violaceus Oka, 1927		Х		Х				West Pacific	Northwest Atlantic Columbia (Canada)	Williams, 2007; Gartner et al., 2016
Botryllus schlosseri (Pallas, 1766)		Х		Х				Northeast Atlantic	East Atlantic Columbia (Canada)	Williams, 2007; Gartner et al., 2016
Ciona intestinalis (Linnaeus, 1767)		Х		Х	Х			North Atlantic	Chile Iceland	Castilla and Neill, 2009; Micael et al., 2020
Oavelina dellavalle (Zirpolo, 1925)		Х		Х				Northeast Atlantic	Portugal	Chainho et al., 2015
Corella eumyota Traustedt, 1882				Х	X			Southern Ocean	Portugal	Chainho et al., 2015
Didemnum vexillum Kott, 2002			Х					Japan	Northwest Pacific Ocean Hawaii	Therriault et al., 2018
Distaplia corolla Monniot F, 1974		Х		Х				West Atlantic Ocean	Portugal	Chainho et al., 2015
Herdmania momus (Savigny, 1816)		Х		Х				Indo-Pacific	Mediterranean Sea	Bonanno and Orlando-Bonaca, 2019
Molgula ficus (Macdonald, 1859)					Х			South Pacific	Chile	Castilla and Neill, 2009
Molgula manhattensis (De Kay, 1843)		Х						North America	Strait of Juan de Fuca (Canada) Strait of Georgia (Canada)	Gartner et al., 2016
Perophora viridis Verrill, 1871		Х		Х				Western-Atlantic	Portugal	Chainho et al., 2015
Pycnoclavella taureanensis Brunetti, 1991		Х						Mediterranean Sea	Portugal	Chainho et al., 2015
Styela canopus (Savigny, 1816)		Х		Х				West Pacific	Northwest Atlantic	Williams, 2007

(Continued)

INVASIVE and		Boat	Climate	Ballast			Transoceanic	Native	Non-native or	
potential		hulls	events	water			channels/	location	invaded	
invasive species	Plastics	(biofouling)			Aquaculture	Aquariums	swimming		location	References
Styela clava Herdman, 1881		Х						Asian Pacific Ocean	Great Britain	Davis and Davis, 2007
Vertebrates (7)										
Lagocephalus sceleratus (Gmelin, 1789)							Х	Indo-Pacific	Mediterranean Sea	Bonanno and Orlando-Bonaca, 2019
Mugil soiuy (32) Basilewsky, 1855				Х				Amur river Sea of Japan	Sea of Azov	Occhipinti-Ambrogi and Savini, 2003
Neogobius melanostomus (Pallas, 1814)				Х				Caspian Sea	Baltic Sea	Holmes et al., 2019
Pterois miles (Bennett, 1828)							Х	Indo-Pacific	Mediterranean Sea	Bonanno and Orlando-Bonaca, 2019
Pterois volitans (Linnaeus, 1758)				Х	X	Х		Indian West Pacific	East coast of North America Caribbean	Padilla and Williams, 2004
Sargocentron rubrum (Forsskål, 1775)							Х	Indo-Pacific	Mediterranean Sea	Bonanno and Orlando-Bonaca, 2019
Siganus rivulatus Forsskål and Niebuhr, 1775		Х					Х	Indo-Pacific	Mediterranean Sea	Bonanno and Orlando-Bonaca, 2019
Total: 216	17	128	18	84	50	9	6			
Sessile species	112									
Mobile species	104									

Plastic and boat hulls are highlighted because of their importance in our study. 216 species were included, classified as sessile (pink cells) and no sessile species (blue cells) and sorted mainly by phylum (except the group Algae, subphylum Tunicata and the group Vertebrates). Next to each group, the number of species in the group is indicated in parentheses. The species name coincides with the name used in the citation. Species whose currently accepted name has changed are indicated by numbers in parentheses, and the currently accepted name is clarified at the end of the table. Accepted names: (1) Codium fragile subsp. fragile (Suringar) Hariot, 1889 (2) Colpomenia sinuosa var. peregrina Sauvageau, 1927 (3) Grateloupia subpectinata Holmes, 1912 (4) Pachymeniopsis lanceolata (K.Okamura) Y.Yamada ex S.Kawabata, 1954 (5) Gayralia oxysperma (Kützing) K.L.Vinogradova ex Scagel et al., 1989 (6) Melanothamnus harveyi (Bailey) Diaz-Tapia and Maggs, 2017 (7) Sargassum horneri (Turrer) C.Agardh, 1820 (8) Gelliodes wilsoni Carballo, Aquilar-Camacho, Knapp and Bell, 2013 (9) Exaiptasia diaphana (Rapp, 1829) (10) Calyptospadix cerulea Clarke, 1882 (11) Diadumene lineata (Verrill, 1869) (12) Anguillicola (Anguillicolaides) crassus Kuwahara, Niimi and Itagaki, 1974 (13) Ensis leei M. Huber, 2015 (14) Spisula discors (Gray, 1837) (15) Arcutula senhousia (Benson, 1842) (16) Mytella strigata (Hanley, 1843) (17) Nassarius magaritifer (Dunker, 1847) (18) Ocinebrellus inomatus (Récluz, 1851) (19) Anadara inaequivalvis (Bruguière, 1789) (20) Plaxiphora (Plaxiphora) aurata (Spalowsky, 1795) (21) Neodexiospira brasiliensis (Grube, 1872) (22) Ficopomatus enigmaticus (Fauvel, 1923) (23) Amphibalanus amphitrite (Darwin, 1854) (24) Notomegabalanus campelli (Filhol, 1885) (25) Amphibalanus eburneus (Gould, 1841) (26) Perforatus perforatus (Bruguière, 1789) (27) Amphibalanus variegatus (Darwin, 1854) (28) Amathia gracilis (Leidy, 1855) (30) Bugulina flabellata (Thompson in Gray, 1848) (31) Amathia verticillata (delle Chiaje, 1822) (32) Pl



and Milner, 2004), by increasing their potential travel distance (Thiel and Gutow, 2005).

Wasson et al. (2005) suggested that alien species preferred hard artificial materials (rip rap, gravel bars, pilings, and docks), while native species were found mainly on soft substrates. Pinochet et al. (2020) affirmed that native species are more commonly found on natural surfaces; for example, native algae such as Sargassum sp. and Corallina sp. are prevalent on natural reefs but not on artificial structures (Glasby et al., 2007). Pinochet et al. (2020) found that the settlement of the larvae of two invasive species of the genus Bugula on plastic surfaces was 70% higher than in cement or wood. Furthermore, settlement on plastic substrates was extremely rapid, with 50% of the larvae settling only after 5 min. For some species of invasive bryozoans, it has been suggested that their prevalence in artificial structures and settlement on plastic panels is explained by their ecology, since they are early successional species (Vail and Tranter, 1981), they show a faster growth, an early initiation of reproductive stages and have higher metabolic rates, allowing them to outgrow their competitors in the early successional stages of the developing community (Pettersen et al., 2016; Lagos et al., 2017). Astudillo et al. (2009) reported that approximately 60% of the fauna found on plastic buoys in Coquimbo Bay, a temperate zone of the Southeast Pacific Ocean, had direct development or short larval durations, so they were capable of maintaining persistent populations in floating elements, suggesting a high potential for long-distance dispersal of fauna on buoys.

Recent data suggest that larger pieces of plastic debris support greater biological diversity, which is consistent with the classic species-area relationships inherent in the biogeography of islands (Simberloff, 1976; Gil and Pfaller, 2016; Garcia-Vazquez et al., 2018). Debroas et al. (2017) observed a higher bacterial and eukaryotic richness in polyethylene (PE) of mesoplastic size (5 mm–20 cm) compared to MPs of 300 μ m–5 mm, mainly PE. However, it is necessary to consider the complexity of the debris materials, since those with greater structural complexity (for example, groups of tangled ropes) support greater diversity (Goldstein et al., 2014). Plastic debris of all sizes often has limited structural complexity and smooth, rigid surfaces (e.g., buoys, containers, balls, liners). These characteristics can limit the habitability of plastic waste for many species, since a wide variety of organisms require shelter to persist (Gil and Pfaller, 2016). Even floating harbor pontoons, which carry well-established biofouling communities, can be an important vector for the massive expansion of native species in the face of extreme events that destroy them, such as tsunamis (Wang et al., 2016), displacing them thousands of kilometers away (**Figures 3A–D**).

Gil and Pfaller (2016) studied the relationship between the area and the structural complexity of marine plastic debris and the colonization of species. The study revealed contrasting patterns for the richness of sessile and mobile taxa. Regarding the number of sessile taxa on debris, the increase in surface had a significant positive effect, while the cover of barnacles of the genus Lepas had a significant negative effect. However, regarding the number of mobile taxa on the debris, the increase in surface area had a trivial positive effect, while the number of barnacles had a significant positive effect. These results suggest that barnacles of the genus Lepas act as base species in communities on plastic debris, providing a complex structural habitat on otherwise structurally limited plastic debris. In agreement with these data, Astudillo et al. (2009) carried out a study on biota inhabiting buoys in the sea and observed that the number of mobile species on buoys was positively related to the number and biomass of sessile species. Thus, benthic species which colonize plastic surfaces are considered eco-engineers, since they provide a habitat for mobile species that otherwise would not be able to colonize these surfaces (Astudillo et al., 2009).

Differential Colonization in the Different Types of Plastic Polymers

The five main classes of plastic polymers, which comprise about 90% of polymer production, are polyethylene (PE), polypropylene (PP), polyvinyl chloride (PVC), polystyrene (PS), and polyethylene terephthalate (PET), with the latter being the most abundant in the ocean (Andrady and Neal, 2009).

While many authors have observed no evidence that the type of polymer is relevant for the composition of the macrobiota associated with plastics, Gündoğdu (2017) have found that the type of plastic (PE, PET, and PP) shows significant differences with respect to the diversity and abundance of species. On the other hand, it is commonly accepted that the difference in structural and/or chemical properties (plasticizers and colorants) observed among polymer families influences bacterial communities and dynamics (De Tender et al., 2015). Pinochet et al. (2020) observed that the bryozoan larvae of two invasive species of the genus Bugula showed preferences for colonizing PS and polycarbonate (PC) substrates within the polymer possibilities (PP, PVC, PET, and PC). Furthermore, antifouling treatments applied to different plastic materials, such as nylon fishing nets, could influence the community of organisms adhering to them (Núñez et al., 2006).

Although the reason for association with certain polymers is not clear, some authors have indicated that it might be due to the biofilm that develops on each polymer (Shin et al., 2013; Lagos et al., 2016; Morohoshi et al., 2018). According to



FIGURE 3 | Plastic fouling examples: (A) in floating boxes of polystyrene docks covered with pvc carrying fauna such us the invasive species *Amathia verticillata* (their breakage, due to a storm or tsunami (see text) can lead to their dispersion in the sea over great distances); (B,C) plastic bottle and plastic bag taken from the bottom of a port, with incipient cauloids of the possible fine morphotype of the Asian invasive algae, *Rugulopteryx okamurae*; (D) loose end nylon net, extracted from the bottom of a port, completely covered with biofouling. Pictures were taken at Leisure port La Alcaidesa (La Línea), Bay of Algeciras.

Oberbeckmann et al. (2014) the composition of the polymer not only influences the abundance of microorganisms associated with polymers, but also shapes the structure of the biofilm community, which could play a role in the establishment of other species associated with the biofilm (Shin et al., 2013; Lagos et al., 2016; Morohoshi et al., 2018).

Macrobiota Transported by Plastics

Barnes (2002) highlighted the importance of marine debris as a distribution vector for marine species and estimated that it doubled the probability of transport of the species. After analyzing more than 200 pieces of debris from 30 different islands, he concluded that the most abundant groups were bryozoans, barnacles, polychaetes, hydroids and molluscs. Astudillo et al. (2009) found in the Southeastern Pacific 134 species in a total of 40 sampled buoys, mostly belonging to the Arthropoda, Annelida, and Mollusca phyla, 4 of them classified as invasive on the Chilean coast (Castilla et al., 2005): *Ciona intestinalis (Linnaeus, 1767), Bugula neritina (Linnaeus, 1758), B. flabellata* [Thompson in Gray, 1848; this name is currently not accepted and it is *Bugulina flabellata* (Thompson in Gray, 1848)] and the macroalgae *Codium fragile* (Suringar) Hariot, 1889 (frequencies of 73, 82, 59 and 9%, respectively). Later, in 2014, Goldstein et al. (2014) found 95 taxa in 242 pieces of plastic debris, most of them from the phylum Arthropoda, followed by Mollusca and Cnidaria. These data are consistent with the results obtained in our study (**Table 1**), as the phylum observed on plastic were Arthropoda (6), Bryozoa (4), Mollusca (4), Annelida (1) and Cnidaria (1), and the group Algae (1).

Some recurrent characteristics have been noted in the biology and ecology of species associated with plastic debris in the sea, such as cosmopolitan distributions, suspensivorous feeding (Astudillo et al., 2009) and sessile with short-lived larval development without natural potential means of dispersal (Barnes, 2002).

Kiessling et al. (2015) found 335 taxa associated with plastic garbage items in the ocean and stranded on the coast. In a study in the Atlantic Ocean, Barnes and Milner (2004) found several species of barnacles with a high incidence; the balanomorph *Semibalanus balanoides* (*Linnaeus, 1767*) were present in marine debris at all arctic and subarctic study sites; the invasive species *Elminius modestus* Darwin, 1854 [this name is currently not accepted and it is *Austrominius modestus* (Darwin, 1854)] was also found on plastic items in the Shetland Islands. The genus *Lepas* (one of the most common colonizers of plastic litter) (Miralles et al., 2018) shows a wide distribution associated with debris: from high latitudes in the Shetland Islands [*Lepas (Anatifa) anatifera Linnaeus, 1758*] to the Malvinas Islands [*L. (Anatifa) australis Linnaeus, 1758*], including locations closer to the equator such as the Ligurian Sea [*L. (Anatifa) pectinata* Spengler, 1793] (Aliani and Molcard, 2003). Other plastic colonizers include several species of hydroids and bryozoans (Aliani and Molcard, 2003; Barnes and Milner, 2004). The suspensivorous bivalve family Mytilidae form dense aggregations (Mikkelsen and Bieler, 2008) in specific vectors (e.g., marine debris, artificial substrates, ship hulls, and ballast water). This family includes invasive species carried by plastic debris such as *Perna viridis (Linnaeus, 1758*) (Gracia and Rangel-Buitrago, 2020).

Nikula et al. (2013) documented the transport of algae in debris, mostly plastic, between islands separated by more than 500 km. After a 30-year examination of the impact of the invasion of *Undaria pinnatifida* (Harvey) Suringar, 1873 in Australasia, South et al. (2017) indicated that its ability to settle and develop on any hard substrate until it reaches reproductive maturity, among those who frequented plastic products such as buoys, could be a key factor toin the initial success of its invasion. Recently, a study of the distribution and impact of *Rugulopteryx okamurae* in the Strait of Gibraltar also showed the highly competitive capacity of the algae to settle onto hard substrates, describing its ability to adhere to nets and ropes (made of nylon), and hooks of nets, constituting a problem for the fishing sector, and showing the potential of polyamides for the dispersal of species (García-Gómez et al., 2018).

Plastic as a Vector for the Dispersal of Microorganisms and Associated Diseases

Plastics, including MPs and NPs, adsorb organic and inorganic nutrients from water (Frère et al., 2018), which, along with its physical properties and widespread distribution provides a unique and stable habitat (Zettler et al., 2013; Oberbeckmann et al., 2015; Keswani et al., 2016), thus attracting bacteria, viruses, plankton, and other microorganisms which adhere to its surface (Frère et al., 2018), and enhancing their dispersion to different oceanic regions (Zettler et al., 2013; Oberbeckmann et al., 2015; Keswani et al., 2016). This adhesion is facilitated by the complexity of plastic surfaces, such as roughness and braiding (Núñez et al., 2006).

Zettler et al. (2013) introduced the term "plastisphere" to define a community of microorganisms associated with marine plastic debris found on the surface of seawater. "Plastisphere" differs from the bacterial populations found in other marine ecosystems, both in the water column and in other natural substrates (Zettler et al., 2013; Harrison et al., 2014; Dussud et al., 2018; Curren and Leong, 2019) and host a diverse community, including heterotrophs, autotrophs, predators, and symbionts, which generally begin with microbial colonization and biofilm conformation, which at the same time facilitate the settlement of other species, for example bryozoans (Bryant et al., 2016). Oberbeckmann et al. (2014) show that microbial communities in plastic change in structure and composition with respect to geographic location, season and type of polymer, but that there are also similarities between these plastic communities, such as the predominance of the phyla Proteobacteria and Bacteroidetes (Zettler et al., 2013; Oberbeckmann et al., 2014; Frère et al., 2018; Curren and Leong, 2019) and some microalgal species such as diatoms and dinoflagellates (Carson et al., 2013).

Different cases of dissemination of potentially toxic species have been documented, including pathogens and invasive algae, which can invade new habitats and modify their structure, becoming a threat to the ecosystem (Zettler et al., 2013; Kirstein et al., 2016). The toxic bacterial genus Vibrio has been commonly detected in MPs (Zettler et al., 2013; Frère et al., 2018; Curren and Leong, 2019); Kirstein et al. (2016) confirmed the presence of Vibrio spp. in 13% of all MP particles collected in the sea, identifying the potentially pathogenic species V. parahaemolyticus (Fujino et al., 1974) Sakazaki et al., 1963 and V. fluvialis Lee et al., 1981. Masó et al. (2003) detected members of the potentially harmful dinoflagellate genera Ostreopsis, Coolia, and Alexandrium in plastic debris floating in Mediterranean coastal waters. These infectious organisms can reach their hosts through the ingestion of plastic (Harrison et al., 2011; Zettler et al., 2013).

Several authors found antibiotic resistance genes (ARG; Miller et al., 2009; Laganà et al., 2019), metal resistance genes (MRG; Yang et al., 2019) and virulence genes (Radisic et al., 2020) in different species of bacteria in marine environments. Radisic et al. (2020) findings of virulence genes and new ARG variants in the fish pathogen *Aeromonas salmonicida* (Lehmann and Neumann, 1896; Griffin et al. 1953) isolated from plastic debris in Norway showed their potential for causing infections.

Audrézet et al. (2020) highlight the importance of the study of the succession of plastiphere communities and the different factors that influence the transmission of microorganisms mediated by plastic through the combination of molecular and microscopic approaches, and the use of genetic markers.

Therefore, there is concern that MP pollution, which is increasing in the marine environment, may cause serious marine ecological effects, influence the dynamics of its population and, ultimately, the emergence of pathogens (Frère et al., 2018; Shen et al., 2019). The introduction of MPs colonized by non-native microbial communities is likely to alter microbial communities and genetic exchange in natural water and consequently affect the ecological function of microbial communities (Miao et al., 2019).

SPATIOTEMPORAL DISPERSION PATTERNS OF PLASTIC DEBRIS IN THE MARINE ENVIRONMENT AND VULNERABLE AREAS

Plastic horizontal dispersion in the ocean is driven by different large-scale processes, such as the action of ocean currents, wind, tides (**Figure 4**; Law et al., 2010; Kim et al., 2015) and extreme

meteorological events, such as hurricanes (Wang et al., 2019; Lo et al., 2020) and tsunamis (Wang et al., 2016). Sea state, wind (Astudillo et al., 2009; Thiel et al., 2011), and particle size and type (Reisser et al., 2015) influence the duration of transport. A Plastic particle from the east coast of the United States may reach the subtropical gyre of the Atlantic North in less than 60 days (Law et al., 2010). Six years after the 2011 tsunami in Japan, Carlton et al. (2017) documented 289 living species on the coasts of North America and Hawaii in marine debris originating after the catastrophe, among which plastic debris was abundant. On the ocean surface, downwind and slow current habitats are potential sinks for plastic debris (Browne et al., 2010). Currently, 5 ocean gyres have been identified, located in the North Atlantic, South Atlantic, South Indian, South Pacific, and North Pacific (Eriksen et al., 2014), which accumulate on their surfaces at least 79 thousand tons of plastic (Lebreton et al., 2018). Moreover, the appearance of another patch in the Barents Sea has been predicted (van Sebille et al., 2012). These areas can accommodate quantities of up to 21,290 tons of plastic in the North Pacific gyre (Law et al., 2010). In addition, in the convergence regions, surface water is pumped down to depths of a few hundred meters (van Sebille et al., 2020).

The vertical transport of plastic is both size- and densitydependent. MPs are more abundant than larger plastic debris, both on the sea's surface and in the water column (Kooi et al., 2017). On the other hand, plastic materials with a density lower than water (LD) (1.02 g/cm^3) are usually found on the surface and in neustonic environment (Moore et al., 2011), while those with a higher density (HD) reach the marine benthic environments (Moret-Ferguson et al., 2010; Ballent et al., 2012).

During plastic debris stay in the marine environment, their density can change over time due to the physical/chemical/biological degradation or biofouling attachment Figure 4) (Moret-Ferguson et al., 2010) of suspended matter, contamination by epiphytes or the formation of microbial biofilms (Lobelle and Cunliffe, 2011; Collignon et al., 2014; Bagaev et al., 2017). Increased density could cause the debris to sink, to be transported by underlying currents (Engler, 2012), trapped by turbulent currents of the benthic boundary layer, resuspended by deep currents, or finally to settle onto the seafloor (Bagaev et al., 2017; Figure 4). In many cases, sedimentation is facilitated by oceanographic processes (Wang et al., 2016) such as dense shelf water cascading (Canals et al., 2006), severe coastal storms (Sanchez-Vidal et al., 2012), offshore convection (Durrieu de Madron et al., 2013), and saline subduction (Talley, 2002). Predicting this vertical mixing could be essential, as it affects the horizontal drifting patterns and ecological impacts of plastic pollution (Reisser et al., 2015). Plastic concentrations have been shown to decrease exponentially with depth (Reisser et al., 2015). However, Woodall et al. (2014) reported an abundance of MPs on the seafloor four orders of magnitude greater than in surface water gyres, while Peng et al. (2018) reported abundant MP particles in the Mariana Trench, the deepest part of the world's ocean.

Plastic debris is widely distributed throughout our oceans and colonize from latitudes near the equator to the poles (Obbard

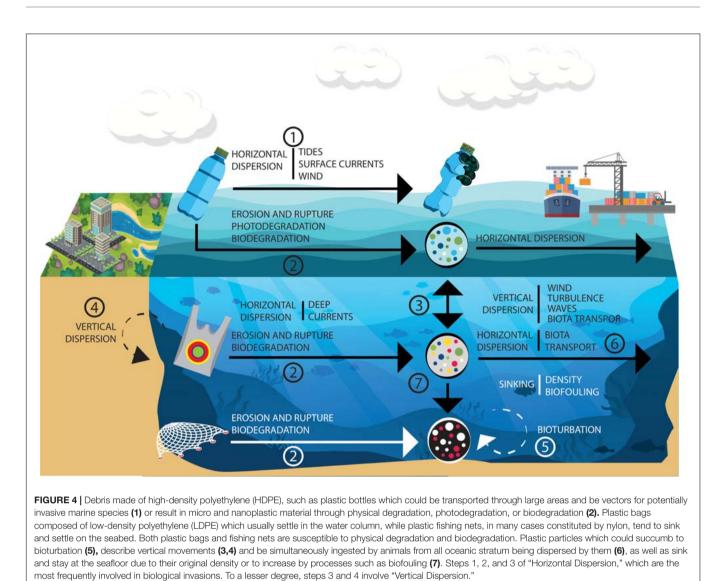
et al., 2014), with the tropical regions being the areas where it is most frequent and predominant (Barboza et al., 2019). Regardless of the geographical region, the most vulnerable areas with respect to the colonization of exotic species transported by this debris are those where endemisms abound and endangered species are present (Gregory, 2009; Thevenon et al., 2014).

Therefore, given the spatial "cosmopolitanism" of plastic materials and their increasing abundance in the marine environment, generalist invasive species (or with invasive potential) in the surface waters of all oceans which can be transported by this vector, constitute an increasing threat within the bathymetric range to which they are adaptive especially to pristine and highly biodiverse ecosystems, with particular relevance to Marine Protected Areas.

EARLY DETECTION AND SURVEILLANCE OF AIS IN MARINE PLASTIC DEBRIS

Rech et al. (2018a) found that the frequency of a specific taxon attached to plastic litter in a coastal area can be predicted based on the characteristics of biological communities associated with each litter material and the composition of beach litter. This approach, after being tested in other regions, may contribute as a simple and cost-effective tool for risk assessment in the future (Rech et al., 2018a). On the other hand, Fazey and Ryan (2016a,b) showed that small samples of plastic litter lost buoyancy due to biofouling much faster than larger ones, providing the first estimates of the longevity of different sizes of plastic debris at the surface of the ocean. This finding could be used to improve model predictions of the distribution and abundance of floating plastic debris globally.

Ports are often export areas for native generalist species and entry areas for alien species (Mineur et al., 2006; Keller et al., 2010; Airoldi et al., 2015; López-Legentil et al., 2015; Ferrario et al., 2017). A sport or recreational vessel whose hull is made of fiberglass-reinforced polyester can import or export native and alien species. But also, by accumulation and subsequent sinking, ports and marinas can import and export plastic trash with alien species. In many cases the plastic sinks (especially bags), because of the weight of the biofouling, remain at shallow depths (especially in ports and marinas, which tend to accumulate plastic garbage on their bottoms). For their control and environmental monitoring, a modification of the SBPQ (Sessile Bioindicators Permanent Quadrats) method could be applied, as recently proposed by García-Gómez (2015) and García-Gómez et al. (2020a) for the early detection of alien species and environmental impacts of a local nature (e.g., urban discharges) or global (climate change) in rocky natural habitats. It is a non-invasive method focuses on the monitoring of preselected sensitive (indicators) sessile target species associated with rocky coralligenous habitats using permanent quadrats in underwater sentinel stations. It could be adapted to plastic panels (completed with other types of non-plastic panels) which are susceptible to colonization by opportunistic sessile species that could become invasive, and act as "traps" for the early



detection of alien species. In this regard, the installation of underwater sentinel stations should be tested at various inland points of ports, with plastic panels of at least five panels per point, of 25 cm \times 25 cm, with different roughness and nature (e.g., polyamide or nylon, polyester, polyethylene, high density polyethylene and polypropylene), which serve to recognize the species which establish easily on this type of material and those which are more frequent and with a structural and adaptive profile of higher risk for invasion. This method could contribute to the early detection of alien species with invasive potential, and to the implementation of immediate mitigation and/or eradication measures.

ADDITIONAL CONSIDERATIONS

From the foregoing, it can be deduced that plastic debris represents a ubiquitous vector with great potential for transporting both sessile and mobile species associated with it, capable of traveling long distances because plastic, due to its composition, is not biodegradable and, therefore, very durable over time.

We could ask ourselves which species of those transported by plastic (or that could be transported by this type of substrata) may have a greater risk of invasion. They would be sessile generalist arborescent species (e.g., seaweeds, hydrozoans, bryozoans) that, according to Bradshaw et al. (2003), are common components of fouling communities. So, they can provide food, shelter or hiding conditions for other mobile species that can travel with them (both non-native and native). About this, Marchini et al. (2015a) reported three mobile NIS associated with the introduced sessile species Amathia verticillata (= Zoobotrion verticillatum) (Bryozoa) and suggested this species as substrate for transport between ports, facilitating its distribution. Also, Gavira-O'Neill et al. (2018) found 19 species associated with the invasive bryozoan Tricellaria inopinata-in list of "100 Worst Invasives" in the Mediterranean (Streftaris and Zenetos, 2006)-between them the three mobile introduced species *Caprella scaura*, *Monocorophium* sextonae (Amphipoda), and the *Paracerceis sculpta*, adding that these species represented over half of the quantified individuals and discussing the possibility of a potential case of "invasional meltdown"—expression by Simberloff and Von Holle (1999) during which introduced species provide suitable habitat for other non-native species, favoring their establishment. Other studies also support this hypothesis for *T. inopinata* as a host for other mobile species introduced from other zoological groups, such as isopods and nudibranchs (Keppel et al., 2012; Hobbs et al., 2015). So, such arborescent sessile species (hosts of mobile fauna) are those that need to occupy the substrate surfaces of the bottom (even as epibionts) and, therefore, those that can generate the greatest environmental impact on the native sessile biota.

In order to improve biosecurity, the best mechanism is prevention and, in this sense, it is important to start acting against this ongoing problem; for example, through protocols for the sighting (from small boats and large ships) of accumulations of plastic adrift within 20 miles off the coasts, where the presence of accumulations of floating with well-established biofouling is detected. In the same way, ports and marinas must be involved in environmental surveillance for the early detection of alien species before they can become widespread.

Actions to manage the problem should be put into place, such as the collection of floating plastic by cleaning boats employed in coastal areas at risk of the entry of plastic accumulations due to winds and/or currents. International regulations or legal provisions must be implemented in this regard. Collaboration on the part of society must also be encouraged. Environmental education and the emerging "Citizen Science" movement (Wiggins and Crowston, 2011) should be stimulated and coordinated from public administrations, as well as large industries, companies or institutions that have large coastal infrastructures. In addition, large industries and companies should also participate in mitigating the problem under the influence of the emerging philosophy of "Working with nature" (PIANC, 2014; Martin et al., 2017; Nebot et al., 2017). which has generated an awareness of respect for nature, by which it is intended to act with it and not against it, collaborating in environmental monitoring and surveillance studies of threatened species naturally established in port breakwaters (García-Gómez et al., 2010, 2014) and, in the present case, for the early detection of alien species with invasive potential.

CONCLUSION

1. The number of articles published of plastic debris as a vector for the introduction of alien species has increased enormously in recent years. This increase could be related

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- 2. Several of the biological characteristics of marine species commonly associated with plastic, such as the short life cycle and larval development, are also characteristics of a large portion of the known invasive species; so these species that travel on plastic debris across the ocean could generally be perceived as a major threat to their destination.
- 3. A wide variety of organisms colonize plastic materials, both microorganisms (e.g., species of the genus *Vibrio* or different species carrying virulent and antibiotic resistance genes) and macrofauna species (e.g., algae or bryozoan species). This fact increases the threat to ocean life caused by plastic and turns it into a means for spreading disease.
- 4. There are large gaps in knowledge about the functioning of plastic objects as vectors and the lack of studies on colonization processes on different plastic polymers by marine species generate contradictions between different authors. Despite the great advances produced today in the knowledge of plastic debris in the ocean, greater research are necessary to mitigate the threat of biological invasions linked to this type of pollutant.

AUTHOR CONTRIBUTIONS

MG and JG made **Figures 1**, **2**, and **4**. JG-G provided the photographs of **Figure 3**. All authors decided the consensus on the structure of the manuscript and accomplished the literature search, and participated for the conclusion and formal aspects.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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