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Invasive species in the Northeastern and Southwestern Atlantic Ocean: a review

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Abstract

The spread of non-native species has been a subject of increasing concern since the 1980s when human-mediated transportation, mainly related to ships' ballast water, was recognized as a major vector for species transportation and spread, although records of non-native species go back as far as 16th Century. Ever increasing world trade and the resulting rise in shipping have highlighted the issue, demanding a response from the international community to the threat of non-native marine species. In the present study, we searched for available literature and databases on shipping and invasive species in the North-eastern (NE) and South-western (SW) Atlantic Ocean and assess the risk represented by the shipping trade between these two regions. There are reports of 44 species associated with high impacts for the NE Atlantic and 15 for the SW Atlantic, although this may be an underestimate. Vectors most cited are ballast water and biofouling for both regions while aquaculture has also been a very significant pathway of introduction and spread of invasive species in the NE Atlantic. Although the two regions have significant shipping traffic, no exchange of invasive species could be directly associated to the shipping between the two regions. However, it seems prudent to bring the exchange of ballast water between the two regions under control as soon as possible.

Keywords: Invasive species, NE Atlantic Ocean, SW Atlantic Ocean, ballast water, biofouling, risk assessment.

1. Introduction

The spread of non-native species is a major threat to the biodiversity of the planet (Gurevitch & Padilla, 2014; Butchart *et al.*, 2010; Firn *et al.*, 2015). Humans cause the spread of marine species in various ways (e.g. vessel biofouling and the translocation of shellfish), with ballast water known to be one of the most important vectors for invasions by non-native species (Carlton *et al.*, 1995; Drake, 2015). Ballast water is used to adjust the draught and trim of a ship to improve manoeuvrability and stability with an estimated 3-10 billion tons of ballast water transferred globally each year (Gollasch *et al.*, 2002; Tamelander *et al.*, 2010). As about 80% of international trade, in terms of volume, is carried by sea, shipping routes connect coastal regions worldwide (UNCTAD, 2014). Ballast water was first suggested as a vector for non-native species dispersal more than 90 years ago (Hallegraeff & Bolch, 1992) and it is now considered to be one of the major threats to marine biodiversity (Ruiz *et al.*, 2000; Takahashi *et al.*, 2008; Masson *et al.*, 2013; Fowler & McLay, 2013).

The problem with ballast water is that a myriad of organisms are transported across natural barriers before dispersal, transcending biogeographic regions. Ship's ballast tanks can carry about 3,000 – 7,000 species (Carlton & Geller, 1993; Gollasch *et al.*, 2002; Carlton, 2001; Endrensen *et al.*, 2004) and this wholesale movement of marine life contributes to the spread of disease; it disrupts coastal ecosystems and is causing the homogenization of coastal habitats (Ruiz *et al.*, 2000; Drake & Lodge, 2004; Rahel, 2007, Katsanevakis *et al.*, 2014). The transfer of invasive species in ballast water is an international problem that is currently out of control; increasing shipping trade along with increasing ship size and speed, the opening up of new trade routes such as across the Arctic, man-made coastal habitat modification, the development of offshore windfarms and the global effects of sea-surface warming and acidification are all contributing to marine biological invasions (Williams *et al.*, 2013; Allen & Hall-Spencer, 2015).

Alongside ballast water and biofouling on ships, non-indigenous species can also be introduced and spread by man-made structures at sea, canals, aquaculture activities and releases from aquaria. In many cases the spread of non-indigenous marine life is as a result of multiple pathways of introduction e.g. ballast water releases can be compounded by those from biofouling on hulls, propellers, sea chests and other niche areas (Ruiz *et al.*, 1997). These combinations of vectors can transport aquatic organisms at multiple life stages and include free-living as well as attached forms.

During the United Nations Conference on Environment and Development in 1992, known as the "Rio Earth Summit", the spread of non-native species was recognized as one of the four greatest threats to biodiversity resulting in severe environmental, economic and public health

impacts. This led to Article 8 (h) of the Convention of Biological Diversity which calls for the control and management of invasive species. The International Maritime Organisation (IMO) is a United Nations body that deals with the safety, security and environmental performance of international shipping. It has been working with member states to help control the spread of non-native species in ballast water and vessel biofouling. In 2000, the International Maritime Organisation launched their 'Removal of Barriers to the Effective Implementation of Ballast Water Control and Management Measures in Developing Countries' initiative, widely referred to as the 'Global Ballast Water Management Programme', and this led to the 'Convention on the Control and Management of Ships' Ballast Water and Sediments'. In September, 2016, after more than a decade of delay, this Convention has finally reached the requirements for entry into force.

According to a comprehensive review on the impact of non-native species on ecosystem services within Europe, the highest number of non-native marine species with described ecological and economic impacts was found in the eastern Mediterranean Sea and in the North Sea (Zenetos et al., 2012; Vilà *et al.* 2009). In 2014, a pan-European review focused on non-indigenous marine species classed 87 species as 'High Impact' with seventeen of these species associated with only negative impacts, the majority (63) were documented as having both positive and negative impacts (Katsanevakis *et al.*, 2014). Among the species with negative impacts on biodiversity is the gastropod *Rapana venosa* that feeds on bivalves and can decimate commercial bivalve stocks. Because of the high densities achieved, the crab *Hemigrapsus sanguineus* was described among the species with a negative impact on native species recruitment, e.g. some species of barnacles and mytilid bivalves (Katsanevakis *et al.* 2014). On the other hand, some species are able to interfere positively in the biological process and may act as a control over other invasive species, e.g. *Crepidula fornicata* that is able to "cause a shift of phytoplankton blooms from toxic flagellates to diatoms" ((Thieltges *et al.* 2006 *apud* Katsanevakis *et al.*, 2014), besides some species known as ecosystem engineering usually associated with both positive and negative impacts, like most macroalgae (Katsanevakis *et al.*, 2014). The problems associated with the spread of non-native marine organisms in Europe are tackled in regional agreements. The Barcelona Convention for the Protection of the Mediterranean Sea against Pollution, originally adopted in 1975 and replaced in 1995, includes invasive species monitoring as one of the key priorities for the next decade and in 2005 adopted an action plan concerning species introductions and invasive species in the Mediterranean Sea; the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Convention), and the Convention on the Protection of the Marine Environment of the Baltic Sea Area, known as HELCOM area (Helsinki Convention) both from 1992, adopted in 2008 joint guidelines with a view to minimizing the risks of introduction and

spread of non-native species in the North-East Atlantic and in the Baltic Sea. These agreements have led to action plans and initiatives designed to tackle the ever increasing problem of non-native species in European seas and in the NE Atlantic.

Unlike the NE Atlantic, South American countries do not have ongoing projects or comprehensive studies on non-native marine species. In a review of non-native marine species along the coast and shelf areas off Argentina and Uruguay, Orensanz *et al.* (2002) listed 31 introduced species, whereas 58 non-native marine species are known to have been introduced along the coastline of Brazil, nine of which categorized as invasive (MMA, 2009). Species classed as invasive for the SW Atlantic were mostly zoobenthos, e.g. *Tubastraea coccinea*, *Isognomon bicolor* and *Styela plicata*. A big problem in the region was caused with the introduction of the golden mussel (*Limnoperna fortunei*), presumably from ballast water tanks. Native from rivers in China and in South-East Asia, this freshwater species invaded South America through the La Plata basin during the 1990's (first record was in 1991, Pastorino *et al.*, 1993) and caused great economic and ecological problems once it is able to attach themselves to any sort of substrates including the settlement on native mussels. Economic losses have been significant since their spreading within South America, where they are known to cause damage in water distribution systems (Darrigran *et al.*, 1999).

The aim of the present study is to assess the amount of shipping that takes place and to update published data on those non-native marine species that have become invasive in the North East and the South West Atlantic Ocean. These two areas were chosen since the two regions may be exchanging non-native species taking into account the significant shipping trade between the two regions.

2. Methods

2.1. Area of study

This study is focussed on the NE and SW Atlantic Ocean. Our NE Atlantic region borders the four non-Arctic areas delimited by the OSPAR Commission, namely; the Greater North Sea (II), the Celtic Seas (III), the Bay of Biscay and Iberian Coast (IV) and the Open Ocean (V). Our SW Atlantic region extends south of the Equator to 55° 00' S and out from the South American continent to 20° W (Figure 1).

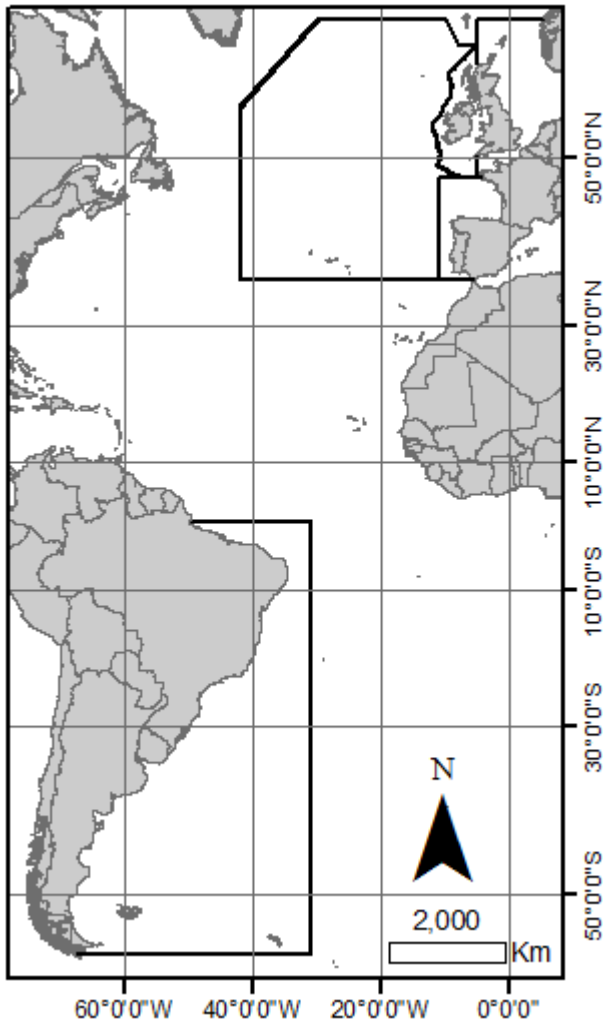


Figure 1: Study area: the NE Atlantic Ocean and the SW Atlantic Ocean.

2.2. Shipping trade data

We assessed the amount of shipping traffic using the United States Coast Guard’s Automated Mutual-Assistance Vessel Rescue System website (www.amver.com). We constructed a shipping density plot to calculate the amount of traffic in June 2013, as this was the most recent month with comprehensive data available.

Data on shipping of all cargo types between Brazil and the fifteen OSPAR countries were obtained from the Brazilian National Waterways Transportation Agency website (www.antaq.gov.br) through the ‘estatística’ link for the year 2014. Data on shipping trade between Argentina and the OSPAR countries were taken from the Argentinian National Institute of Statistics website (<https://opex.indec.gov.ar/>). Finally, for Uruguay, these data were obtained from the websites www.uruguayxxi.gub.uy/ and <http://www.tradingeconomics.com/> which reports on trade for the year 2014.

2.3. Invasive species data

In November 2015, we collated a list of marine and brackish invasive species for our study areas in the NE and SW Atlantic Ocean. We only included non-native species that are known to have had high impacts. For instance, when searching the European Alien Species Information Network the categories we selected were “marine”, “oligohaline”, “high impact” and “alien” for our study areas. The species highlighted by this process were then searched for in the World Register of Marine Species (WoRMS) (<http://www.marinespecies.org/index.php>) to augment the information available. During this iterative process the following databases were consulted: the Global Invasive Species Database (GISD) (<http://www.issg.org/database/welcome/>), the European Network on Invasive Alien Species (<http://easin.jrc.ec.europa.eu/>), Delivering Alien Invasive Species Inventories for Europe (<http://www.europe-aliens.org/default.do>), the European Register of Marine Species, the Information System on Aquatic Non-indigenous and Cryptogenic Species (<http://www.corpi.ku.it/databases/index.php/aquanis>), the GB Non-native Species Secretariat (<http://www.nonnativespecies.org/home/index.cfm>), the North Atlantic Register for Marine Species (<http://www.vliz.be/vmdcdata/narms/>), AlgaeBase (<http://www.algaebase.org/>) and FishBase (<http://fishbase.org/search.php>). A recent review by Katsanevakis *et al.* (2014) for the European seas was also used to cross check and augment our database.

For the SW Atlantic Ocean, our main data sources were reviews organized by Lopes (MMA, 2009) for Brazilian coastal waters and by Orensanz *et al.* (2002) for coastal and shelf areas off Argentina and Uruguay. In addition, we consulted the following studies: Genzano *et al.* 2006; Darling *et al.*, 2008; Ignacio *et al.*; 2010; Irigoyen *et al.*, 2011; Lages *et al.*, 2011; Ferrapeira *et al.*, 2011; Guadalupe Vázquez *et al.*, 2012; Sant'Anna *et al.*, 2012; Sylvester *et al.*, 2013; Bonel *et al.*; 2013; Rocha *et al.*, 2013; Riul *et al.*, 2013; Rechimont *et al.*, 2013; Guinder *et al.*, 2013; Schwindt *et al.*, 2014; Freire *et al.*, 2014; Moreira *et al.*, 2014; Marques & Breves, 2014; Altvater & Coutinho, 2015; Ferreira *et al.*, 2015; Carlos-Junior *et al.*, 2015; Sant'Anna *et al.*, 2015. We also searched WoRMS, GISD, National Exotic Marine and Estuarine Species Information System (<http://invasions.si.edu/nemesis/index.jsp>), the Exotics Guide (<http://www.exoticsguide.org/>), the Invasive Species Compendium (<http://www.cabi.org/isc/>) and the Conservation Gateway from the Nature Conservancy Global Marine Invasive Species database (<https://www.conservationgateway.org/ConservationPractices/Marine/Pages/marineinvasives.aspx>).

3. Results

3.1. Shipping trade data

A snapshot of shipping traffic for June 2013 shows the major world shipping routes (Fig. 2) and the numbers of ships travelling in and out of NE and SW Atlantic ports.

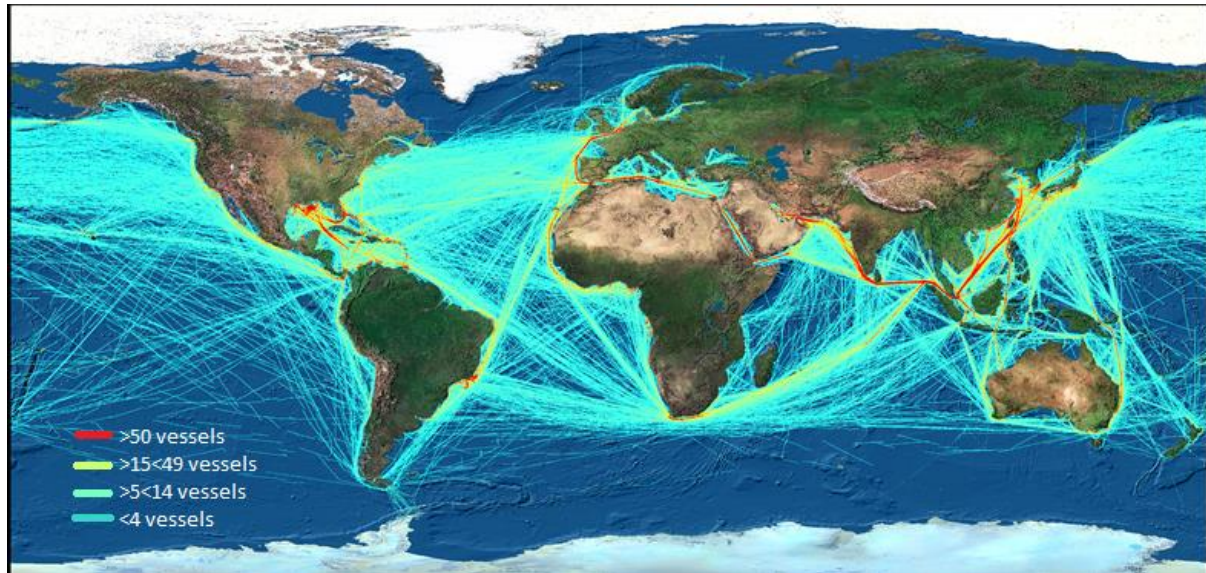


Fig. 2 - World marine traffic density plot for June 2013 (data from the US Coastguard Automated Mutual-Assistance Vessel Rescue System website, www.amver.com).

In 2014, ca 100 million tonnes of cargo was exported from Brazil to Europe, down 7% on the previous year. Around 31 million tonnes of cargo were exported from Europe to Brazil in 2014, up 6.4% on 2013 (ANTAQ, 2015). The amount of cargo exported from Brazil to OSPAR countries was ca 80 million tonnes in 2014 (mostly bulk solids), with main destination ports in the Netherlands, France and Spain. In the opposite direction the total reached about 18.5 million tonnes (mostly container vessels), embarked mainly in ports of Spain, Belgium, the Netherlands and German.

In 2014, around 8.5 million tonnes of cargo were exported from Argentina to OSPAR countries, mainly to the Netherlands, Spain and the United Kingdom whereas Germany was the source of most of her OSPAR imports (INDEC - Dirección Nacional de Estadísticas del Sector Externo - <https://opex.indec.gov.ar/>). That year almost 800,000 tonnes were exported from Uruguay to the OSPAR countries, mainly to Portugal and Spain with the latter being the main source of OSPAR country shipping imports to Uruguay (www.uruguayxxi.gub.uy/).

Nevertheless, taking into account the total cargo exported by the three South American Countries in 2014, the amount of cargo exported to OSPAR countries represented a small fraction from the total (Table 1).

Table 1 South American exports to OSPAR Countries and total amounts exported in 2014.

Countries	The Netherlands	Spain	France	UK	Portugal	Total exported in 2014 (T)
Argentina	3%	2%		2%		83,134,257
Brazil	3.5%	1%	1%			968,872,333
Uruguay		1%			4%	13,866,907

3.2. Invasive species data

A search of the EASIN network for records associated with high impact marine and oligohaline non-native species returned >100 species for our NE Atlantic study areas. From that, 49 species are documented as high impact invasive species in our NE Atlantic region (Table 2). For instance, we excluded from this review the amphipod *Dikerogammarus villosus*, native to Ponto-Caspian region as it is mainly a freshwater species with very low salinity tolerance range. We also excluded *Mytilus edulis*, the common blue mussel, since it is considered native to the NE Atlantic (Wonham, 2004) and its invasiveness status is under discussion for the SW Atlantic Ocean (Savoya *et al.*, 2013).

Table 2: Invasive marine and oligohaline species recorded for the NE and SW Atlantic Ocean

For the SW Atlantic Ocean, it was possible to list 15 species to which well documented high impact were described. The list of invasive marine and oligohaline species recorded for the SW waters is presented in Table 3.

Table 3: Invasive marine and oligohaline species recorded for SW Atlantic Ocean

4. Discussion

We have shown that there is a significant volume of shipping traffic between the NE and the SW Atlantic Ocean; cargo is mainly moved in the north-eastern direction and ballast water is mainly moved south-west, which presents a higher risk to export ports and terminals where higher volumes of discharge occur. Propagule pressure is a crucial factor that affects the establishment of non-native species and it is dependent on the number of organisms released and on the number of release events (Lockwood *et al.*, 2005). Propagule pressure can vary according to ship type, size and speed. Large ships with higher volumes of water in their ballast tanks have increase survival of transported organisms and more species are discharged. A good example is the mineral ore shipping trade, which accounted for the majority of goods exported from Brazil to the OSPAR area in 2014; almost 80% of the total

(ANTAQ, 2015). Pereira (2012) estimated volumes between 10,000 to 120,000 m³ of ballast water discharged into Brazilian coastal areas per journey due to the exportation of iron ore.

The shipping pressure is also revealed by the direction each ship takes. We found that the cargo exportation in the NE direction was about 90 million tonnes in 2014, around four times higher than in the opposite direction. From the perspective of possible non-native species introductions and propagule pressure, it represents a higher risk to the SW Atlantic assuming that ships are loading cargo (and, therefore, unloading ballast water) and unloading it in the NE coast of Europe (and, therefore, taking on ballast water). However, the number of invasive species' records for the region doesn't reflect this assumption which is probably related to differences in the salinity of the donor and recipient ports.

Other important aspect to be considered in a risk assessment is related to ships' route. In our case the main SW-NE route has the Netherlands as the main source of ballast water. It may mean that species recorded for ports in the Netherlands (e.g. Rotterdam) are more likely to be introduced in ports located in the SW Atlantic Ocean. However, previous surveys in the SW Atlantic input a higher risk to routes whose final destinations are located in the Indo-Pacific region, since these account for around 30% of non-native species found in the SW Atlantic (MMA, 2009) possibly reflecting a secondary introduction from a primary site of introduction. Besides ships' influence over the ballast water discharges, there are other aspects that might interfere following discharge and act directly on the species' ability to colonize a new environment. Aspects like the similarity between the places where the water was taken and where it was unloaded, interspecies competition and species-specific tolerances to abiotic factors are crucial in the settlement of non-native species in new environments (Lockwood et al., 2005; Lockwood & Somero, 2011).

Results from the databases and scientific literature researched showed 44 non-native species associated with high impacts for our NE Atlantic while 15 were identified in the SW Atlantic. Species described at least in one database or by an author as freshwater and oligohaline or brackish were included in the present review. Therefore, the two bivalves *Dreissena polymorpha* and *Limnoperna fortunei*, as well as the salmonid *Oncorhynchus mykiss* were included.

In terms of introduced species recorded to European seas and the NE Atlantic, many studies and reviews can be found in the scientific literature. In that respect and according to a recent review, an updated inventory of 87 non-native marine species in European Seas was proposed in 2014, including those species with a documented high impact on ecosystem services or biodiversity (Katsanevakis et al., 2014). When comparing the present list (Table 1) to the one proposed by Katsanevakis et al. for the Celtic and the North Seas, common areas

in both studies, most species are present in both lists. The only exceptions are the amphipod *Chelicorophium curvispinum*, a freshwater / oligohaline species with a salinity tolerance of up to 6 (Van den Brink et al., 1993), and the euryhaline crabs *Rhithropanopeus harrisi* and *Hemigrapsus takanoi*. A dominance of the brush-clawed shore crab over the native European green crab (*Carcinus maenas*) was found in a study along the French coast and in the North Sea (Dauvin et al., 2009). It is worth noting that up to 2005, the name *Hemigrapsus penicillatus* was used for two crabs that are now known to represent two distinct species (*Hemigrapsus penicillatus* and *H. takanoi*). From the invasive species compendium, it is observed that *H. takanoi* was only recently described; therefore first records for Europe, which date back from the mid-1990s, were named *H. penicillatus* (Asakura et al., 2008; Yamasaki et al., 2011). Another similar species *H. sanguineus* is recorded as invasive to Europe and included in Katsanevakis et al. review and in the present study.

In the SW Atlantic Ocean, including Brazilian waters, a comprehensive review compiled by Lopes (MMA, 2009) found 58 marine species recorded as non-native, nine of which have invasive status. A couple of years later, another study along the Brazilian coast increased the known number of non-native species in the region. A total of 343 benthic invertebrate species were recorded (65% non-native and 35% cryptogenic) (Ferrapeira et al., 2011). Nevertheless, an apparent overestimation in the species numbers was highlighted by Rocha et al. (2013) due to some mistakes mainly related to species taxonomy and geographic distributions. For Uruguay and Argentinian coasts, the review conducted by Orensanz (2002) described 31 species with a well-documented exotic status, plus 46 species with a cryptogenic status.

The blue crab (*Callinectes sapidus*) is recorded as a non-native species with high impact in the NE Atlantic Ocean has its natural range described along the western Atlantic coast from Nova Scotia to Argentina (Milliken & Williams 1984; NWARMS). Ballast water is the main vector associated to its introduction outside its native range (Katsanevakis et al, 2012). *Ciona intestinalis* has been identified on both sides of the North Atlantic and has been noted to have spread to the west coast of North America, South America, Australia, New Zealand, Asia and Africa (Kott, 1990; NIMPIS, 2002; Lambert and Lambert, 2003 apud Therriault & Herborg, 2008b). Nevertheless, the native range of *C. intestinalis*, for instance, is a focus of continuing debate (Therriault & Herborg, 2008a).

From the phytoplankton, the diatom *Coscinodiscus wailesii* is among the nine species recorded in Brazilian waters as an invasive species and it is known to be associated with dense blooms causing losses to fisheries and aquaculture. This species is described as euryhaline and eurythermal and tolerant to high concentrations of heavy metals (Proença & Fernandes, 2004; Rick & Dürselen, 1995) and has its native range normally linked to the North

Pacific. Described vectors of introduction are ballast water and aquaculture activities. To the NE Atlantic, the diatom has a recorded range from France to Norway. However, Gómez (2008) described periods of high abundances of *C. wailesii* connected to unusual climatic conditions, being the species currently restricted to residual populations during the winter (Boalch, 1987; Edwards et al., 2001 apud Gómez, 2008).

The dinoflagellate *Alexandrium tamarense*, usually considered a harmful species (associated to Paralytic Shellfish Poisoning toxins) is native in the North Atlantic Ocean as well as in the North Sea. On the other hand this species is considered invasive to the SW Atlantic Ocean where it is widely spread.

Species listed as invasive in both regions of study are *Spartina townsendii* var. *anglica*, (native of southern England) *Ficopomatus enigmaticus* (native range described as unknown), *Crassostrea gigas* (NW Pacific Ocean) and *Bugula neritina* which is a cosmopolitan species. From those, the common cord-grass (*Spartina anglica*) is described as a hybrid from one species native to North America (*Spartina alterniflora*) and other from Europe (*Spartina maritima*). The resultant species is now considered native to southern England and first introductions of *Spartina alterniflora* in Europe in the late 1870s are associated with ballast water while later introductions of the hybrid were intentional for coastal protection purposes (Nehring & Adersen, 2006).

The recorded invasive species' list for the NE doesn't present any native species that exclusively inhabit the SW Atlantic Ocean. Species like the Australian tubeworm, *Ficopomatus enigmaticus*, has its native range associated with the Southern Hemisphere and, in some records to the eastern coast of South America. Nonetheless, it is also recorded as an introduced species to Argentina (WoRMS and DAISIE databases). The amphipod, *Platorchestia platensis*, originally described to Uruguay had its native range updated to unknown (Jensen, 2010). Finally, the ctenophore *Mnemiopsis leidyi* has its native range described for the Atlantic Coast of North and South Americas (Costello, 2001).

Regarding the vectors involved in the transport of non-native species, for the NE Atlantic ballast water is the most cited vector of introduction / dispersion wither alone or as one of the possible vectors / pathways, present in almost 48% of the records. In some records, however, the pathway of introduction was identified as "shipping", probably referring to both ballast water and biofouling vectors, which might increase ballast water as the main vector of introduction to more than 65% of the total. Applying the same reasoning for the biofouling vector, the latter reaches almost 55% of the records as preferential vector of introduction / spread. In sequence, biofouling and aquaculture activities (around 38% each) are the most cited while natural dispersion was cited as the pathway in six of records. For the SW Atlantic, ballast water was

cited in thirteen records as the most probable vector of introduction alone or together with other vectors or pathways (73%) followed by biofouling (47%).

Successful establishment of exotic species in a new environment is usually highly associated with the environmental similarity between the donor and the receptor areas (Keller et al., 2011). This reduced the chance of exchange for the tropical regions of the SW Atlantic although the temperate regions are more at risk from invasion by non-native species from Europe.

4. Conclusion

This review updates information on invasive species recorded for the NE and SW Atlantic Ocean. The number of non-native species that have become invasive with high ecological impacts are 44 in the NE Atlantic and 15 in the less well studied south-western Atlantic. The main vector of introduction and spread of these invasive species is shipping (both ballast water and biofouling). Aquaculture is also an important pathway of introduction, particularly in the NE Atlantic. However in most cases where more than one vector and pathway were cited it is difficult to disentangle the level of influence of the different vectors and/or pathways. In many cases a combination of vectors may carry species at multiple life stages. No clear evidence for the exchange of species between the NE and the SW Atlantic has been noted in this review, although this does not negate international efforts that are underway to improve biosecurity.

The development of scientific research and case studies focused on non-native marine species' vectors as a whole instead of focusing on individual species or individual vectors seems to be a way forward with a view to avoiding impacts and associated losses and costs (Williams *et al.*, 2013). Integrated studies might be the best way to produce valuable forecasts of ecological and economic importance of invasion on ecosystems around the world (Ibanez *et al.*, 2014). Non-native species are certainly a crucial issue that needs to be addressed to raise general awareness and publicity, alongside scientific surveys and monitoring, improved data availability, regulations (preferably international ones in order to avoid legal uncertainties), management tools, risk assessment, stakeholders' commitment, enforcement, best practices and constant surveillance (Costello *et al.*, 2007; Williams *et al.*, 2013; Lehtiniemi *et al.*, 2015).

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