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Research Article

Past and future of the marine bioinvasions along the Southwestern Atlantic

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Abstract

The first comprehensive survey of marine bioinvasions in the southern Southwest Atlantic Ocean (SWA, ca. 33°45'–ca. 54°50'S) published in 2002 reported 31 introduced and 46 cryptogenic species. In this assessment, we update this work by providing a deep historical perspective of marine biological invasions as well as a full new review of introductions that have occurred over the past nearly two decades. We reviewed a variety of sources including peer-reviewed journals and monographs, government reports, and museum databases, among others. The previous survey was re-evaluated and taxonomic experts were also consulted. For each species, the possible status as introduced or cryptogenic, likely vector, likely native region, first collection date if known, and the first authoritative reference of its SWA occurrence were determined. Species were categorized by biogeographical provinces. Our re-evaluation of species status lowered the 2002 survey to 29 introduced and 29 cryptogenic species. The result of our analyses added 100 new introduced and 43 new cryptogenic species, making a total of 129 introduced and 72 cryptogenic marine species for the SWA. Of these 100 species, 67 were found in the literature older than the 2002 survey, and 33 were found as new invasions that occurred since 2002, averaging one new invasion every 178 days. Ships are the most likely vector of invasions with an additional few species introduced with aquaculture, for ornamental purposes or for stabilizing coastal dunes. Most species are native to either the North Pacific or North Atlantic Oceans. Most introduced species (51%) occur in the warm temperate SWA marine ecoregion, while fewer (16%) occur in the cold temperate Magellanic marine ecoregion. Since ships are the main vectors in the region, we forecast that new introductions will continue until regional and international regulations to control ballast water and hull fouling begin to be effective. Our results urge the creation of long-term assessment programs focused on marine coastal biodiversity as a way to avoid inefficient environmental management based on deficient baseline information.

Key words: biological invasions, Argentina, Uruguay, maritime history, shipping

Introduction

The coasts of Uruguay and Argentina, spanning over 20 degrees of latitude from *ca.* 33°44' to 54°50' S in the southern Southwestern Atlantic Ocean (hereafter SWA) have played a critical role in maritime history since European exploration and colonization began in the 1500s. From the rounding of Cape Horn in 1520 by the *Volcano* of the Magellan-Elcano expedition to the opening of the Panama Canal in 1914, the ports and harbors of the southeast coast of South America were key components of major global shipping corridors. Not surprisingly, by the time the *Beagle* arrived in Buenos Aires in 1832, the European cardoon, or artichoke thistle (*Cyanara cardunculus* (L.) Baill.), was so common that in September 1833 Charles Darwin wrote, “I doubt whether any case is on record of an invasion on so grand a scale of one plant over the aborigines” (Darwin 1878). By 1874, the botanist Carlos Berg (1877) reported that fully half of the terrestrial plant species that he found growing wild in the Buenos Aires Province and Patagonia were European.

Despite more than 500 years of maritime traffic, and despite the early recognition of the significant presence of non-native species on lands adjacent to the sea, it was not until 2002 that Orensanz et al. provided the first comprehensive survey of exotic marine organisms in the SWA, reporting 31 introduced and 46 cryptogenic species. Here, we update this work by providing a deep historical perspective of marine biological invasions as well as a full new review of introductions that have occurred over the past nearly two decades. We report the number of introductions to exceed 120 species, more than 4 times the number previously reported.

Materials and methods

Since the publication of Orensanz et al. (2002) we have either kept records of all new reports that have come to our attention, or searched for additional records, of introduced marine viruses, protists, animals, and plants reported from Uruguay and Argentina. Particular attention was paid to taxonomic groups that were either not considered in Orensanz et al. (2002), such as the ocean-dependent plants and animals (i.e., supralittoral, marsh, and dune organisms), or were treated only briefly. For this, we pursued some of the biogeographic and taxonomic categories considered by Carlton (2009) to represent groups that often remain uninvestigated, thus potentially leading to underestimation of invasion diversity. These categories include small-bodied taxa (such as viruses, diatoms, dinoflagellates, foraminifera and others), inshore and shelf-dwelling (neritic) taxa assumed to be dispersed by ocean currents and thus often formerly (and formally) eliminated from consideration as non-native candidates (such as teredinid bivalves, or shipworms), or species with generally presumed cosmopolitan distributions (such as many seaweeds). In addition, anadromous fish were omitted in Orensanz et al. (2002), which we now consider here.

Our sources included peer-reviewed journals and monographs, government reports, conference proceedings and museum databases. We further re-evaluated the biogeographic status of the introduced and cryptogenic species earlier reported in Orensanz et al. (2002). We consulted with taxonomic experts (Supplementary material Table S1, and Acknowledgments) to confirm species identifications or to discuss species' histories and possible origins. For each species under consideration, the possible status as introduced or cryptogenic, likely vector, probable native region, first collection date if known, and the first authoritative reference of its SWA occurrence were determined. If a collection date could not be determined, the publication date was used (and so noted) as the first date of record.

For biogeographical analyses, species were categorized by marine ecoregion as Warm Temperate Southwestern Atlantic and Magellanic (Spalding et al. 2007) and by occurrence between Chuy Creek (33°44'S) to Ushuaia (*ca.* 54°50'S). Native areas for each introduced species were assigned according to the literature, and then largely classified according to Food and Agriculture Organization of the United Nations regions (FAO 2019). FAO regions were used instead of marine ecoregions in order to capture broader origin perspectives. For habitat analyses, species were categorized as occurring in rocky or sandy shores, mudflats, rocky or salt marshes, ports, or other (Bortolus et al. 2009, and herein). Six introduced and seven cryptogenic species of uncertain establishment (Table S1) have been conservatively retained in all of our calculations.

Probable vectors of introduction were determined by taking into account life histories, habitat, and other biological and ecological attributes following the categories of Carlton and Eldredge (2009). These vectors include ballast water, ship fouling, ship boring (organisms boring into wooden ships, or living in such burrows), solid ballast (rocks and sand), releases (intentional or accidental by private individuals or government agencies and species associated with such releases), and other (such as carriage with commercial products, in airplane cabins, resting or egg stages with luggage and clothing, etc.). Ship categories were combined when vectors could not be distinguished, thus all species were assigned to only one of the categories. Binomial names and classifications largely follow the World Register of Marine Species (WoRMS 2019), AlgaeBase (Guiry and Guiry 2019) or FishBase (Froese and Pauly 2019) and specific cases with taxonomic remarks (e.g. Bortolus et al. 2019).

Results

Introduced and Cryptogenic Diversity and Detection

A total of 129 (64%) introduced and 72 (36%) cryptogenic species are here reported in the SWA (Table 1 and Table S1). Our re-evaluation of the status

Table 1. The Introduced and Cryptogenic Marine Animals and Plants of the Southwestern Atlantic Ocean. See Supplementary material Table S1 for first collection dates, vectors, possible origins, detailed remarks, and references.

* Introduced species; unmarked taxa are cryptogenic.

Viruses

- * WSS VIRUS
- * IHNV VIRUS

Cercozoa

Bonamia exitiosa Hine, Cochennac and Berthe, 2001

Spermatophytina

- * *Spartina alterniflora* Loisel.
- * *Ammophila arenaria* (L.) Link
- * *Leymus arenarius* (L.) Hochst.
- * *Tamarix ramosissima* Ledeb.
- * *Cakile maritima* Scop.
- Sarcocornia perennis* (Mill.) A.J. Scott
- * *Salsola soda* L.
- * *Salsola kali* L.
- * *Mesembryanthemum nodiflorum* L.
- * *Mesembryanthemum crystallinum* L.
- * *Carpobrotus edulis* (L.) N.E.Br.
- * *Carpobrotus chilensis* (Molina) N.E.Br.

Rhodophyta

- * *Anotrichium furcellatum* (J.Agardh) Baldock, 1976
- Antithamnionella ternifolia* (J.D.Hooker and Harvey) Lyle, 1922
- Bangia atropurpurea* (Mertens ex Roth) C.Agardh, 1824
- * *Porphyra linearis* Greville, 1830
- * *Lomentaria clavellosa* (Lightfoot ex Turner) Gaillon, 1828
- * *Melanothamnus harveyi* (Bailey) Diaz-Tapia and Maggs, 2017
- * *Leptosiphonia brodiei* (Dillwyn) A.M.Savoie and G. W. Saunders 2019
- * *Polysiphonia morrowii* Harvey, 1857
- * *Ahnfeltiopsis devoniensis* (Greville) P.C.Silva and DeCew, 1992
- * *Schizymenia dubyi* (Chauvin ex Duby) J.Agardh, 1851
- Hypnea musciformis* (Wulfen) J.V.Lamouroux, 1813
- * *Grateloupia turuturu* Yamada, 1941

Ochrophyta

- Sporochnus pedunculatus* (Hudson) C.Agardh, 1817
- * *Cutleria multifida* (Turner) Greville, 1830
- * *Dictyota dichotoma* (Hudson) J.V.Lamouroux, 1809
- Ectocarpus siliculosus* (Dillwyn) Lyngbye, 1819
- * *Undaria pinnatifida* (Harvey) Suringar, 1873
- Colpomenia sinuosa* (Mertens ex Roth) Derbès and Solier, 1851
- Feldmannia globifera* (Kützting) G.Hamel, 1939
- * *Laminariocolax aecidioides* (Rosenvinge) A.F.Peters, 1998
- * *Saccharina sessilis* (C.Agardh) Kuntze, 1891

Bacillariophyceae

- * *Trieres chinensis* (Greville) Ashworth and E.C.Theriot 2013
- Odontella rostrata* (Hustedt) Simonsen, 1987
- * *Coscinodiscus wailesii* Gran and Angst, 1931

Chlorophyta

- * *Rosenvingiella polyrhiza* (Rosenvinge) P.C.Silva, 1957
- * *Bryopsis rhizophora* M.A.Howe, 1914
- Blidingia minima* (Nägeli ex Kützting) Kylin, 1947

Myxozoa

- * *Alexandrium catenella* (Whedon and Kofoid) Balech
- * *Dinophysis acuminata* Claparède and Lachmann, 1859
- Gymnodinium catenatum* H.W.Graham, 1943
- Perkinsus olsenii* R.J.G.Lester and G.H.G.Davis

Foraminifera

- * *Haynesina germanica* (Ehrenberg, 1840)

Porifera

- Cliona* aff. *celata* Grant, 1826
- Halichondria* (*Halichondria*) *panicea* (Pallas, 1766)
- * *Hymeniacidon perlevis* (Montagu, 1814)
- Dictyonella hirta* (Topsent, 1889)
- Haliclona* (*Haliclona*) *oculata* (Linnaeus, 1759)

Cnidaria: Hydrozoa

- Dynamena disticha* (Bosc, 1802)
- Sertularella mediterranea* Hartlaub, 1901
- Amphisbetia operculata* (Linnaeus, 1758)
- Plumularia setacea* (Linnaeus, 1758)
- Hebella scandens* (Bale, 1888)
- * *Ectopleura crocea* (Agassiz, 1862)
- Obelia bidentata* Clark, 1875
- Obelia dichotoma* (Linnaeus, 1758)
- Obelia longissima* (Pallas, 1766)
- * *Gonothyraea loveni* (Allman, 1859)
- Halecium delicatulum* Coughtrey, 1876
- Rhizogeton nudus* Broch, 1910
- * *Blackfordia virginica* Mayer, 1910
- * *Eutonina scintillans* (Bigelow, 1909)
- * *Cordylophora caspia* (Pallas, 1771)
- * *Bougainvillia muscus* (Allman, 1863)
- Bimeria vestita* Wright, 1859
- * *Gonionemus vertens* A. Agassiz, 1862

Cnidaria: Anthozoa

- * *Diadumene lineata* (Verrill, 1869)

Nemertea

- * *Lineus sanguineus* (Rathke, 1799)

Annelida: Clitellata

- * *Monopylephorus rubroniveus* Levinsen, 1884

Annelida: Polychaeta

- Schistomeringos rudolphi* (Delle Chiaje, 1828)
- Alitta succinea* (Leuckart, 1847)
- Syllis gracilis* Grube, 1840
- Procerastea halleziana* Malaquin, 1893
- * *Eulalia clavigera* (Audouin and Milne Edwards, 1834)
- Ophryotrocha puerilis* Claparède and Mecznikow, 1869
- * *Boccardia proboscidea* Hartman, 1940
- Polydora ciliata* (Johnston, 1838)
- * *Polydora cornuta* Bosc, 1802
- Dipolydora flava* (Claparède, 1870)
- Polydora rickettsi* Woodwick, 1961
- Dipolydora socialis* (Schmarda, 1861)
- * *Boccardiella ligerica* (Ferronière, 1898)
- Neodexiospira pseudocorrugata* (Bush, 1905)
- Simplaria pseudomilitaris* (Thiriot-Quievreux, 1965)
- * *Ficopomatus enigmaticus* (Fauvel, 1923)
- * *Hydroides elegans* (Haswell, 1883)
- * *Hydroides dianthus* (Verrill, 1873)

Mollusca: Gastropoda

- * *Rapana venosa* (Valenciennes, 1846)
- * *Myosotella myosotis* (Draparnaud, 1801)
- * *Tenellia adspersa* (Nordmann, 1845)
- * *Marionia blainvillea* (Risso, 1818)
- * *Pleurobranchaea maculata* (Quoy and Gaimard, 1832)
- Placida dendritica* (Alder and Hancock, 1843)

Table 1. Continued.

Mollusca: Bivalvia	
* <i>Perna perna</i> (Linnaeus, 1758)	
* <i>Limnoperna fortunei</i> (Dunker, 1857)	
* <i>Mytilus galloprovincialis</i> Lamarck, 1819	
* <i>Corbicula fluminea</i> (O. F. Müller, 1774)	
* <i>Crassostrea gigas</i> (Thunberg, 1793)	
* <i>Crassostrea talonata</i> (Li and Qi, 1994)	
* <i>Barnea truncata</i> (Say, 1822)	
* <i>Lyrodus pedicellatus</i> (Quatrefages, 1849)	
* <i>Teredo navalis</i> Linnaeus, 1758	
<i>Teredo bartschi</i> Clapp, 1923	
* <i>Teredo furcifera</i> Martens, 1894	
<i>Bankia gouldi</i> (Bartsch, 1908)	
<i>Bankia fimbriatula</i> Moll and Roch, 1931	
<i>Bankia martensi</i> (Stempel, 1899)	
Crustacea: Copepoda	
* <i>Eurytemora americana</i> Williams, 1906	
<i>Parvocalanus crassirostris</i> (Dahl F., 1894)	
Crustacea: Amphipoda	
* <i>Orchestia gammarellus</i> (Pallas, 1766)	
* <i>Orchestia mediterranea</i> Costa, 1853	
<i>Platorchestia platensis</i> (Krøyer, 1845)	
* <i>Melita palmata</i> (Montagu, 1804)	
* <i>Maera grossimana</i> (Montagu, 1808)	
* <i>Ampithoe valida</i> Smith, 1873	
<i>Cymadusa filosa</i> Savigny, 1816	
* <i>Monocorophium acherusicum</i> (Costa, 1853)	
* <i>Monocorophium insidiosum</i> (Crawford, 1937)	
* <i>Crassikorophium bonellii</i> (H. Milne Edwards, 1830)	
* <i>Apocorophium acutum</i> (Chevreux, 1908)	
* <i>Jassa marmorata</i> Holmes, 1905	
* <i>Jassa slatteryi</i> Conlan, 1990	
<i>Podocerus brasiliensis</i> (Dana, 1853)	
<i>Caprella equilibra</i> Say, 1818	
<i>Caprella penantis</i> Leach, 1814	
<i>Caprella dilatata</i> Krøyer, 1843	
* <i>Erichthonius punctatus</i> (Spence Bate, 1857)	
Crustacea: Tanaidacea	
<i>Sinelobus stanfordi</i> (Richardson, 1901)	
<i>Tanais dulongii</i> (Audouin, 1826)	
Crustacea: Isopoda	
* <i>Ligia (Megaligia) exotica</i> Roux, 1828	
* <i>Limnoria tripunctata</i> Menzies, 1951	
* <i>Halophiloscia couchii</i> (Kinahan, 1858)	
* <i>Porcellio lamellatus</i> Budde-Lund, 1885	
* <i>Synidotea laevidorsalis</i> (Miers, 1881)	
* <i>Sphaeroma serratum</i> (Fabricius, 1787)	
* <i>Paracerceis sculpta</i> (Holmes, 1904)	
* <i>Dynamene edwardsi</i> (Lucas, 1849)	
* <i>Joeropsis dubia</i> Menzies, 1951	
Crustacea: Mysidacea	
* <i>Neomysis americana</i> (S.I. Smith, 1873)	
Crustacea: Cirripedia	
* <i>Balanus glandula</i> Darwin, 1854	
<i>Fistulobalanus pallidus</i> (Darwin, 1854)	
<i>Amphibalanus improvisus</i> (Darwin, 1854)	
* <i>Amphibalanus amphitrite</i> (Darwin, 1854)	
<i>Amphibalanus venustus</i> (Darwin, 1854)	
* <i>Balanus trigonus</i> Darwin, 1854	
	<i>Megabalanus tintinnabulum</i> (Linnaeus, 1758)
Crustacea: Decapoda: Caridea	
	* <i>Palaemon macrodactylus</i> Rathbun, 1902
Crustacea: Decapoda: Brachyura	
	* <i>Pyromaia tuberculata</i> (Lockington, 1877)
	* <i>Carcinus maenas</i> (Linnaeus, 1758)
	* <i>Eurypanopeus depressus</i> (Smith, 1869)
Pycnogonida	
	<i>Endeis spinosa</i> (Montagu, 1808)
	<i>Pycnogonum cessaci</i> Bouvier, 1911
Entoprocta	
	<i>Barentsia laxa</i> Kirkpatrick, 1890
Bryozoa	
	<i>Crisia eburnea</i> (Linnaeus, 1758)
	<i>Amathia gracilis</i> (Leidy, 1855)
	<i>Amathia imbricata</i> (Adams, 1798)
	* <i>Amathia verticillata</i> (Delle Chiaje, 1822)
	<i>Conopeum reticulum</i> (Linnaeus, 1767)
	* <i>Conopeum seurati</i> (Canu, 1928)
	<i>Electra monostachys</i> (Busk, 1854)
	* <i>Aspidelectra melolontha</i> (Landsborough, 1852)
	<i>Scruparia ambigua</i> (d'Orbigny, 1841)
	* <i>Bugulina flabellata</i> (Thompson in Gray, 1848)
	* <i>Bugula neritina</i> (Linnaeus, 1758)
	* <i>Bugulina simplex</i> (Hincks, 1886)
	* <i>Bugulina stolonifera</i> (Ryland, 1960)
	* <i>Cryptosula pallasiana</i> (Moll, 1803)
	* <i>Membraniporopsis tubigera</i> (Osburn, 1940)
	<i>Aetea sica</i> (Couch, 1844)
	<i>Aetea anguina</i> (Linnaeus, 1758)
	* <i>Buskia socialis</i> Hincks, 1887
	<i>Victorella pavidia</i> Saville-Kent, 1870
	* <i>Fenestrulina delicia</i> Winston, Hayward and Craig, 2000
	* <i>Schizoporella</i> cf. <i>errata</i>
	* <i>Smittoidea spinigera</i> (Liu, 1990)
Chordata: Tunicata (Ascidacea)	
	<i>Asterocarpa humilis</i> (Heller, 1878)
	<i>Corella eumyota</i> Traustedt, 1882
	* <i>Ciona intestinalis</i> (Linnaeus, 1767)
	* <i>Ciona robusta</i> Hoshino and Tokioka, 1967
	* <i>Ciona savignyi</i> Herdman, 1882
	* <i>Botryllus schlosseri</i> (Pallas, 1766)
	* <i>Molgula manhattensis</i> (De Kay, 1843)
	* <i>Molgula robusta</i> (Van Name, 1912)
	* <i>Styela plicata</i> (Lesueur, 1823)
	* <i>Styela clava</i> Herdman, 1881
	* <i>Asciidiella aspersa</i> (Müller, 1776)
	* <i>Asciidiella scabra</i> (Müller, 1776)
	<i>Ascidia interrupta</i> Heller, 1878
	* <i>Diplosoma listerianum</i> (Milne Edwards, 1841)
	* <i>Lissoclinum fragile</i> (Van Name, 1902)
Chordata: Actinopterygii	
	* <i>Salmo trutta</i> Linnaeus, 1758
	* <i>Oncorhynchus mykiss</i> (Walbaum, 1792)
	* <i>Oncorhynchus tshawytscha</i> (Walbaum, 1792)
	* <i>Cyprinus carpio</i> Linnaeus, 1758
	* <i>Oreochromis niloticus</i> (Linnaeus, 1758)
	* <i>Acipenser baerii</i> Brandt, 1869
	* <i>Arothron firmamentum</i> (Temminck and Schlegel, 1850)

Table 2. Assessments of introduced and cryptogenic marine species in the Southwest Atlantic Ocean.

Study	Number of Introduced Species	Number of Cryptogenic Species	Total
Orensanz et al. 2002: Original calculations	31	46	77
Orensanz et al. 2002: Revised numbers herein; see text	29	29	58
Present study	+ 100	+ 43	+ 143
TOTAL number of species	129	72	201

Table 3. Marine taxa treated in the present study but entirely or largely omitted in Orensanz et al. (2002).

Taxonomic groups entirely omitted or largely not treated in Orensanz et al. (2002)	Number of Introduced Species (I)	Number of Cryptogenic Species (C)	Total	Number of species known in the SWA			
				Before 2002		After 2002	
				I	C	I	C
VIRUSES	2	0	2			2	
CERCOZOA: Haplosporida	0	1	1		1		
SPERMATOPHYTINA (vascular plants) ¹	11	1	12	11	1		
RHODOPHYTA, OCHROPHYTA ² , CHLOROPHYTA (macroalgae)	16	8	24	10	8	6	
BACILLARIOPHYCEAE (diatoms)	2	1	3	2	1		
MYZOOZOA							
Dinoflagellata (dinoflagellates)	2	1	3	2	1		
Protalveolata (parasitic protozoans)	0	1	1				1
FORAMINIFERA (forams)	1	0	1			1	
NEMERTEA (ribbon worms)	1	0	1	1			
ANNELIDA: Clitellata (oligochaetes)	1	0	1	1			
MOLLUSCA							
Gastropoda: Opisthobranchia (sea slugs)	3	1	4	1		2	1
Bivalvia: Teredinidae (shipworms)	3	4	7	3	4		
CRUSTACEA							
Copepoda (copepods)	1	1	2	1	1		
Tanaidacea (tanaids)	0	2	2		2		
Mysidacea (mysids)	1	0	1	1			
Caridea (shrimp)	1	0	1	1			
PYCNOGONIDA (sea spiders)	0	2	2		1		1
ENTOPROCTA (nodding heads)	0	1	1		1		
CHORDATA: Actinopterygii (fish)	7	0	7	7			
TOTAL number of species	51	24	75	40	21	11	3
TOTAL number newly added species	51 ³	24	75 ³	40 ³	21	11	3

¹ Only one species of maritime plant, *Spartina anglica* (Hubbard, 1968), was treated as introduced in Orensanz et al. (2002); it is now considered extinct in Argentina (see text).

² Only one species of introduced seaweed, *Undaria pinnatifida* (Harvey) Suringar, 1873, discovered in 1992, was treated in Orensanz et al. (2002).

³ Excluding the seaweed *Undaria pinnatifida*, already treated by Orensanz et al. (2002).

of species treated in Orensanz et al. (2002), detailed below, revised the species treated therein to 29 introduced and 29 cryptogenic species (Table 2). Our present work thus adds 100 introduced and 43 cryptogenic species, for a total of 201 species now under consideration as confirmed or possible marine bioinvasions (Table 3). Overall, since Orensanz et al. (2002), 33 introduced species have been newly documented in the SWA.

Of these 100 introduced species, half (51) represent numerous taxonomic groups that were either entirely omitted from, or with two exceptions, largely not treated by Orensanz et al. (2002) (Table 3). One of the exceptions is the wakame *Undaria pinnatifida* (Harvey) Suringar, 1873,

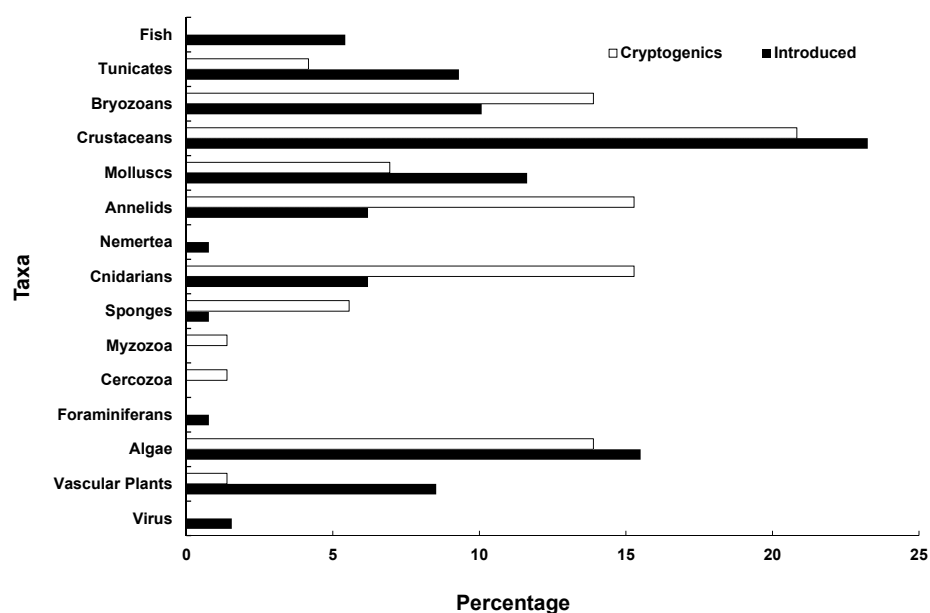


Figure 1. Percentage of introduced and cryptogenic species in the Southwestern Atlantic Ocean separated by major taxonomic groups.

which was included in the previous survey. We have now added 16 introduced algae species. The other exception was a salt marsh plant, *Spartina anglica* C.E. Hubb. which was deleted from the list because it is considered extinct in Argentina (Nicora 1978), while 11 additional introduced maritime plants were added. In turn, we note that the majority (40, or 78%) of these 51 species were present (Table 3) at the time of the Orensanz et al. (2002) review, while only 11 species (22%) of the 51 have been documented in the SWA since 2002. Thus, unexplored groups have newly contributed more than one-third (51 of 129) of all added records of introduction.

The taxon that was most represented were crustaceans with 30 introduced and 16 cryptogenic species (Figure 1), mostly represented by amphipods with 12 and 6 introduced and cryptogenic species, respectively. The second most speciose group was algae, with 20 introduced and 10 cryptogenic species, followed by bryozoans with 13 introduced and 10 cryptogenics, and annelids and cnidarians with 8 introduced and 11 cryptogenics for each group. The detection of introduced and cryptogenic species increased constantly over time (Figure 2), but a pulse occurred between 1960 and 1970 when 19% of the introduced species were first observed, mainly crustaceans and tunicates (Figure 3). Nearly 70% of introduced species were reported during the last 50 years (Figure 2).

Re-Assessment of Species Treated in Orensanz et al. (2002)

Of the 31 species treated as introduced in Orensanz et al. (2002) to the SWA, we have retained 29. The two deleted species are the salt marsh cordgrass *Spartina anglica* C. E. Hubb (see above), and the isopod *Idotea metallica* Bosc, 1802, a native pelagic, oceanic species. Of the 46 cryptogenic species, we have retained only 29. Ten species reported as cryptogenic in

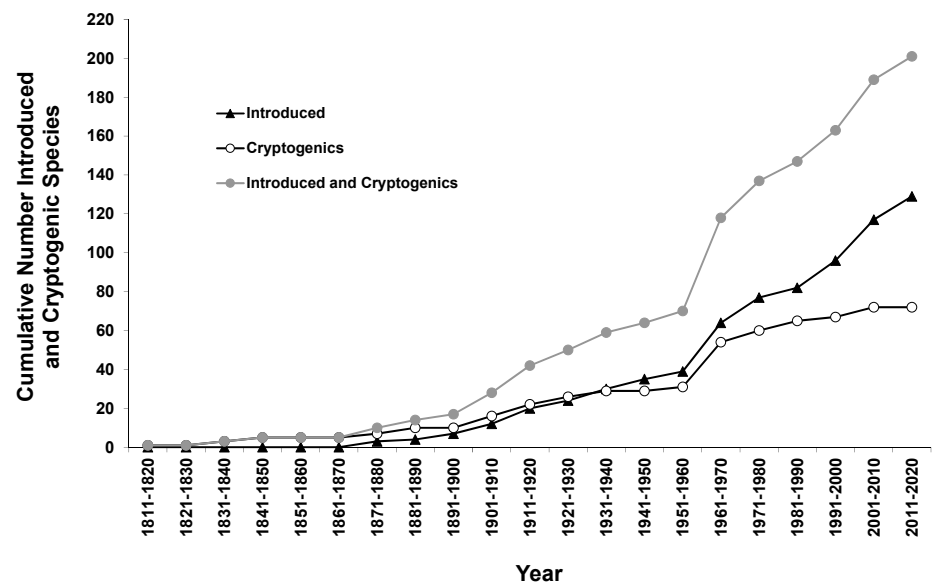


Figure 2. Cumulative number of introduced species (▲), cryptogenic species (○) and the sum of both species (●) detected in the Southwestern Atlantic Ocean over 10-year intervals from 1811 to 2019.

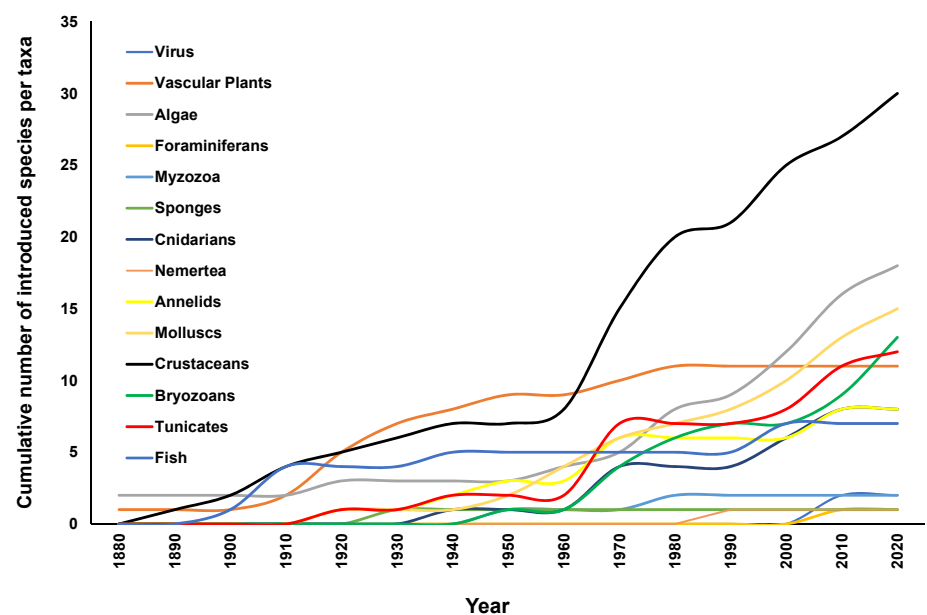


Figure 3. Cumulative numbers of introduced species for 14 taxa in the Southwestern Atlantic Ocean over 10-year intervals from 1880 to 2019.

Orensanz et al. (2002) are here regarded as introduced, based upon reanalyses of their systematics and biogeography (Table S1). These are the sponge *Hymeniacidon perlevis* (Montagu, 1814), the hydroid *Ectopleura crocea* (Agassiz, 1862), the polychaete *Polydora cornuta* Bosc, 1802, the amphipods *Orchestia gammarellus* (Pallas, 1766), *Orchestia mediterranea* Costa, 1853, *Ampithoe valida* Smith, 1873, *Maera grossimana* (Montagu, 1808), and *Melita palmata* (Montagu, 1804), the mysid *Neomysis americana* (S.I. Smith, 1873) and the bivalve *Perna perna* (Linnaeus, 1758). Three species of cryptogenic anemones and two species of polychaete worms noted in Orensanz et al. (2002) are of either uncertain identification

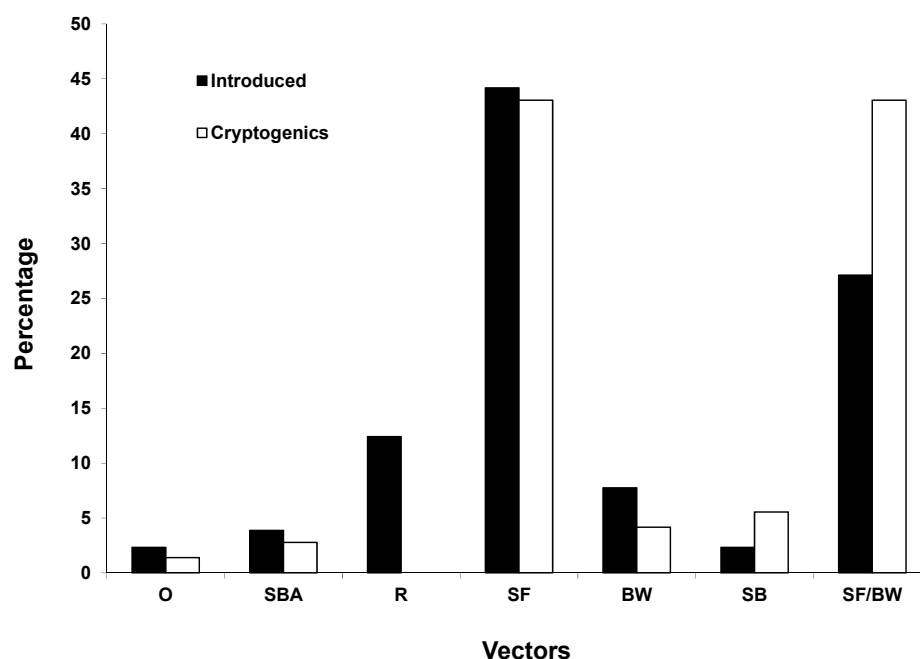


Figure 4. Percentage of introduced (black) and cryptogenic (white) species in the Southwest Atlantic Ocean according to the most likely vectors. Other (O), solid ballast (SBA), releases (R), ship fouling (SF), ballast water (BW) and ship boring (SB). The category SF/BW includes species that may have been transported either by SF or BW. All the species were assigned to only one of the categories.

or are under further study and thus were deleted. Two species of crabs previously listed as cryptogenic we now consider as native (*Panopeus meridionalis* Williams, 1983) or of uncertain identity regarding the original record considered (*Pachygrapsus transversus* (Gibbes, 1850)), thus they were also deleted.

Earliest Records

The earliest records of introduced marine species in the SWA are the red algae *Melanothamnus harveyi* (Bailey) Díaz-Tapia and Maggs, 2017, an introduced species mistakenly considered as native (i.e. pseudoinigenous species), collected in 1872 in San Antonio Bay (40°S) by the Hassler expedition and described as *Polysiphonia argentinica* W.R. Taylor, 1939, and *Lomentaria clavellosa* (Lightfoot ex Turner) Gaillon, 1828, collected no later than 1876. The earliest records of cryptogenic species are the bryozoan *Scruparia ambigua* (d'Orbigny, 1841), collected in 1820 in the Malvinas/Falkland Islands, the barnacle *Amphibalanus improvisus* (Darwin, 1854) collected in 1833, and the hydroid *Amphisbetia operculata* (Linnaeus, 1758), collected no later than 1839.

Vectors

Ships are the most likely vector (85%) for transporting introduced species, either in fouling (44.5%) or by fouling or ballast water (26.5%) (Figure 4). Aquaculture-related releases of anadromous fish and Japanese oysters are

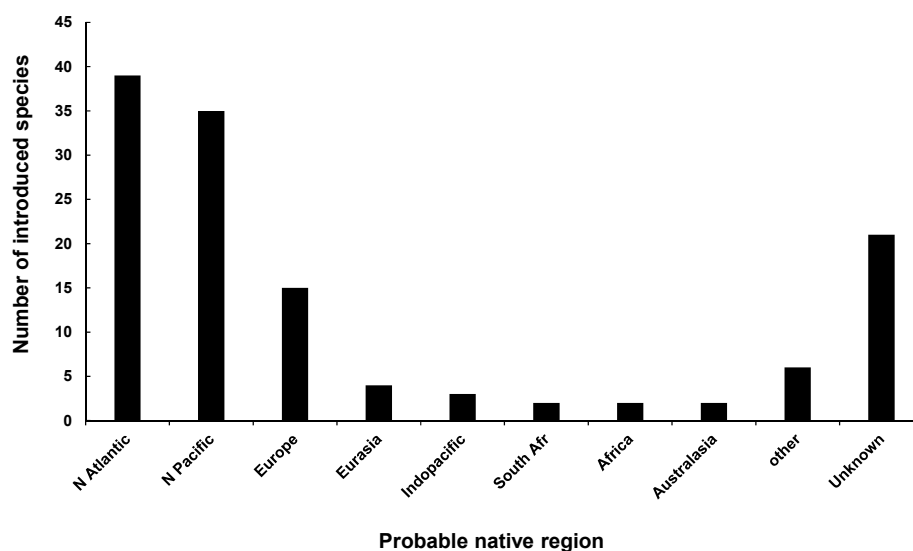


Figure 5. Number of introduced species in the Southwest Atlantic Ocean by probable native region.

intentional. Several other intentional introductions of species occurred for ornamental purposes or for the purpose of stabilizing coastal dunes. The latter included vascular plants such as *Ammophila arenaria* (L.) Link, *Leymus arenarius* (L.) Hochst., *Tamarix ramossissima* Ledeb., *Carpobrotus edulis* (L.) N.E. Br. and *C. chilensis* (Molina) N.E. Br. (Figure 4). Cryptogenic species followed a similar pattern of introduced species, with ships the most likely vector (98%), either as fouling (43%) or fouling/ballast water (44%).

Source Regions and Regional and Habitat Distribution

Most introduced species appear to be native to the northern hemisphere (93%, Figure 5), specifically from the Northeast and Northwest Atlantic, the Northwest Pacific, Asia or Southeast Asia, and Europe (Table S1). Regarding the biogeographical distribution, most introduced species (51%) are found only in the warm temperate SWA marine ecoregion, while fewer (16%) occur only in the cold temperate Magellanic ecoregion (Figure 6). Most cryptogenic species are widely distributed in both marine ecoregions (Figure 6). Mar del Plata, in the warm temperate SWA (38°S) and its surrounding areas have the highest number of both introduced and cryptogenic species (Figure 7), while this number diminishes at higher and lower latitudes. Most introduced and cryptogenic species are found in ports as well as in rocky shore habitats (Figure 8).

Discussion

Invasion Diversity and Potential Underestimation

While the diversity of introduced and cryptogenic species in the Southwest Atlantic Ocean (SWA) reported here has increased the number of recognized invasions or possible invasions nearly 4.5 times and 2.5 times, respectively (based upon revised calculations of the data in Orensanz et al.

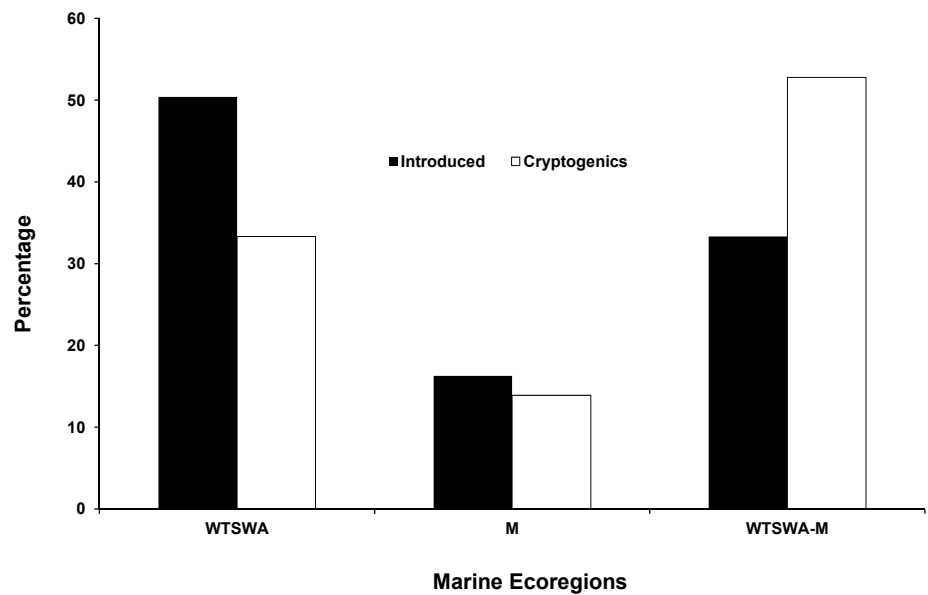


Figure 6. Distribution of introduced and cryptogenic species in Southwestern Atlantic marine ecoregions: (WTSWA) the warm temperate SWA, (M) the cold temperate, Magellanic and (WTSWA-M) for species distributed in both provinces (this category does not include species in the other two categories).

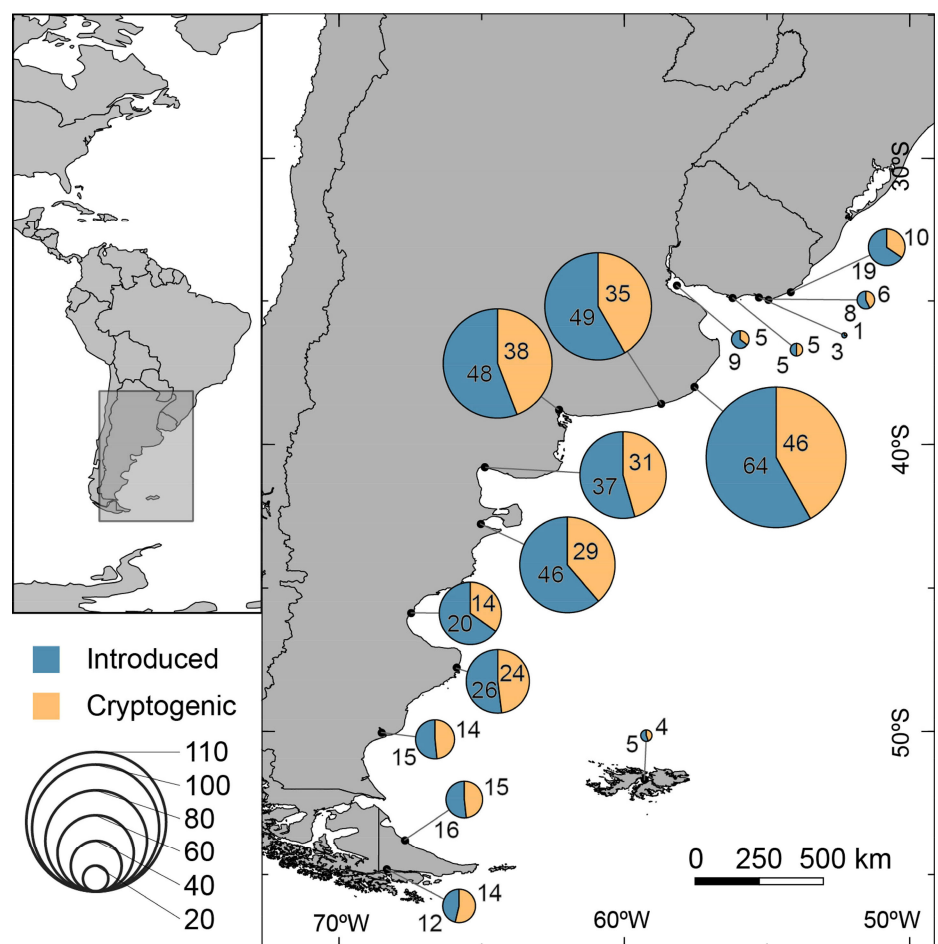


Figure 7. Distribution and number of introduced and cryptogenic species along the Southwestern Atlantic Ocean, from 33°45' to ca. 54°50'S, at different localities and surrounding areas. The size of each circle represents the number of introduced (in blue) and cryptogenic (in orange) species for each location, being Mar del Plata (38°S) and Piriápolis (34°52'S) with the highest (n total = 110) and the lowest (n total = 4) values respectively.

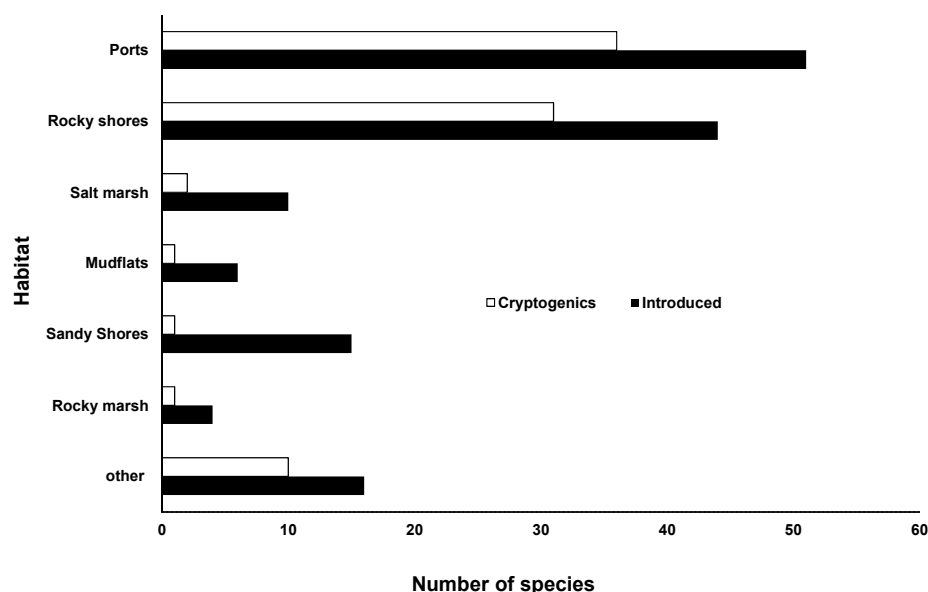


Figure 8. Number of introduced and cryptogenic species in the Southwestern Atlantic Ocean distributed per habitat type. Note that the same species can be found in several habitats.

2002; Table 2 herein), we have no doubt that the actual number of bioinvasions along the southeast coast of South America is significantly higher than previously thought. In the past 17 years, 33 new invasions have been documented (based upon first new records of non-native species from 2002 and later), averaging one new invasion every 178 days (Orensanz et al. 2002; Schwindt and Bortolus 2017). This invasion rate is itself an underestimate, given the number of probable new but undetected invasions in many unstudied or understudied groups of protists, invertebrates, and algae (Carlton 2009; Bortolus et al. 2015).

This said, most new records represent the results of investigations of taxa not explored in an earlier study or of re-evaluation of species previously reported as cryptogenic (Table 3). Around the world, regions that were thought to have sustained relatively few invasions were found, upon detailed study, to have significant numbers of both introduced and cryptogenic species. Examples include California (San Francisco Bay, Cohen and Carlton 1995), the Hawaiian Islands (Carlton and Eldredge 2009, 2015), Australia (Hewitt et al. 2004; Sliwa et al. 2009), New Zealand (Cranfield et al. 1998; Hayden et al. 2009), South Africa (Mead et al. 2011), Brazil (Lopes 2009; Rocha et al. 2013), and most recently the Galapagos Islands (Carlton et al. 2019). Despite this, in all of these regions, a very large suite of taxa continue to remain unstudied due to long-term challenges in interpreting the historical and modern biogeography of many groups (Carlton 2009; Bortolus et al. 2015) as well as a steadily increasing dearth of taxonomic expertise (Carlton and Fowler 2018).

As an example, one of many obfuscated taxonomic and biogeographic puzzles encountered in our work was the red-tide producing dinoflagellate *Alexandrium*. It was first recorded in the SWA as *Gonyaulax excavata*

(Braaerud) Balech, 1971, following the first human intoxication reported in 1980 in Argentina in the Valdes Peninsula (Carreto et al. 1981). Although long considered as *Alexandrium tamarense* (Lebour, 1925) Balech, 1995, after global genetic and taxonomic comparisons, it has now been accepted as *A. catenella* (Whedon & Kofoid) Balech (John et al. 2014; Fraga et al. 2015, Table S1) and considered probably native to the North Atlantic or North Pacific oceans. Another toxic-bloom producing dinoflagellate, *Dinophysis acuminata* Claparede and Lachmann, 1859, was first recorded in 1941 by Balech (1944). Neither of these species were discussed in the regional phytoplankton literature as exotic invasive species, due to the assumption that they had been transported by ocean currents from some unknown overseas shores, despite the lack of evidence for this dispersal mechanism, and the concomitant abundance of data on the role of ballast water in transporting phytoplankton (including these species of dinoflagellates) globally (Bailey 2015). Further efforts should be directed to determine how many additional species of introduced phytoplankton remain undetected in the SWA.

In many regions worldwide—with Argentina and Uruguay being no exception—long expanses of coastline remain unexplored. We found that most of the introduced species are concentrated in the warm temperate SWA of Uruguay and in Mar del Plata in the northern portion of the coast of Argentina. This pattern, as previously highlighted (Orensanz et al. 2002), likely reflects long-term sampling biases. Most historical and recent biofouling harbor studies were in this marine ecoregion (Bastida 1971; Brankevich et al. 1984, 1988; López Gappa and Liuzzi 2016, 2018; Rumbold et al. 2018; Albano and Obenat 2019). Since 2002, however, there has been an increase in invasion research in colder regions, including Puerto Madryn, Comodoro Rivadavia and San Antonio Este, three important port areas of Patagonia (Rico et al. 2010, 2012; Schwindt et al. 2014), leading to a significant uptick in our understanding of the scale of invasions and their impact in Patagonia, with 21 introduced species now reported for this region. This is a striking shift since only two introduced species (*Undaria pinnatifida* (Harvey) Suringar, 1873 and *Spartina anglica*) were reported for Patagonia by Orensanz et al. (2002). Indeed, several new and well-known introduced species, such as the European green crab *Carcinus maenas* (Linnaeus, 1758) and the club tunicate (ascidian) *Styela clava* Herdman, 1881 were first detected along these cold temperate shores (Hidalgo et al. 2005; Pereyra et al. 2015). Even more striking perhaps is the finding that some of the introduced species have not only colonized different environments than in their place of origin, but also showed novel unpredicted behaviors, such as a rocky shore barnacle colonizing soft bottom saltmarshes (Schwindt et al. 2008), or soft bottom benthic snails traveling fast across long distances as biofouling on sea turtles (Lezama et al. 2013).

Vectors and Donor Routes

The primary vector for marine introduced and cryptogenic species in the SWA is ships. There is no surprise there, as the same pattern has been observed worldwide (Hewitt et al. 2004; Mead et al. 2011; Carlton et al. 2019). Since the early 1500s when ships and explorers arrived to the region, many species (such as algae, barnacles, and tunicates) were transported in external hull fouling and inside the wooden hulls (such as shipworms), as well as mixed with solid ballast (such as the cordgrass *Spartina alterniflora*; Bortolus et al. 2015). As vessel technology evolved, water replaced rocks and sand as ballast. Nevertheless, in the past 20 years, half of the introduced species we report in this work were likely transported by hull fouling, highlighting the current importance of this vector.

The introduction of species along the SWA due to escape from aquaculture activities was not yet reported as important since this activity is not highly developed as in other countries within the region. Besides the white spot syndrome virus (WSSV) presumably associated with unregulated aquaculture activities (Schwindt et al. 2018), only one invertebrate species, the Japanese oyster *Crassostrea gigas* (Thunberg, 1793), was intentionally introduced in the SWA from Chile in 1982 during an aquaculture farming initiative that later failed, with the oysters then being abandoned (Orensanz et al. 2002). While the Japanese oyster is no longer economically exploited, it is spreading along SWA muddy and rocky shores making difficult to walk bare footed along some of the invaded touristic beaches (dos Santos and Fiori 2010; Schwindt et al. *pers. obs.*). Aquaculture farms are widespread along the Chilean coast, and they are recognized as an economically important activity. Nevertheless, none of the introduced species established in that country were reported from escapes (Castilla et al. 2005), except for salmon (Arismendi et al. 2014) where escapes are documented. For example, a massive escape of 900,000 salmon occurred recently in southern Chile after a heavy storm and with only 28% of the fish recovered (Gómez-Uchida et al. 2018). Within this context, Argentina keeps debating whether to install salmon farms in the southern part of the country despite the intense opposition of global and local communities and the lack of support from expert scientists who predict dramatic negative effects on the nearby marine protected areas and surroundings (Bortolus and Schwindt 2018; FCMPAI 2018; Summers 2019).

Most introduced species reported for the SWA appear to have originated in the northern hemisphere, mostly from the North Atlantic and specifically from Europe. Nevertheless, it would be wrong to assume that native regions are always the donor sources since many introduced species follow complex unpredicted travel routes. For instance, genetic studies on two of the most aggressive invaders worldwide, the green crab *Carcinus maenas* and the seaweed *Undaria pinnatifida*, native to the Northeast

Atlantic and Northwest Pacific respectively, demonstrated that individuals found in Argentina were genetically more closely related to populations from Australia, where both species were also introduced (Voisin et al. 2005; Darling et al. 2008). The Austral cordgrass *Spartina densiflora* Brongn., native to the SWA, was introduced to the Pacific coast of North America where it currently has invaded most salt marshes. In this case, the donor region was Chile, and not the Atlantic coast of South America (Bortolus 2006; Fortuné et al. 2008). In a similar vein, the dune marram grass *Ammophila arenaria*, although native to Europe, was most likely introduced to continental Argentina from the Malvinas/Falkland Islands, where its date of arrival, amount of imported seeds and exact location were recorded in detail (Hubbard 1937).

With an increasing global connectivity during the 20th century, the reports of introduced species in the SWA native to Southeast Asia, the Indo-Pacific and other Pacific regions became also increasingly common (Table S1). During the last 50 years, one third of the introduced species reported here arrived from the Pacific Ocean. A similar result was observed in Australia by Hewitt et al. (2004), documenting that a shift in trade led to a change of marine invasions from the North Atlantic to the North Pacific after 1950. A continuing future trend is expected for the SWA, where by 2050 a high number of introduced species are predicted to arrive from Asia (Sardain et al. 2019). A first example of this change in global trade may be the introduction of the sea slug *Pleurobranchaea maculata*, native to the Pacific region and recently reported in Argentina as the only country outside its native range (Farías et al. 2015, 2016; Battini et al. 2019).

Conclusions

We cannot make progress in our understanding of the impact of invaders if the scale of invasion diversity remains poorly assessed, and if the abundance and distribution of already established invaders remain uncertain. The most direct consequences of delays in recognizing invasions are delays in early detection of and rapid response to new invasions, and the hampering of the design of strong, effective management strategies to prevent future introductions. Our results argue strongly for regularly updated regional assessments of marine coastal biodiversity. While the United States and many European countries maintain online databases (such as NEMESIS (Fofonoff et al. 2019) and NOBANIS), for other less-known regions such as Central and South America, Africa and much of Asia, data availability for marine introduced species remains both sorely limited and urgently needed. In this vein, the specific support to the marine biodiversity with emphasis on taxonomy has a central role (e.g. Orensanz et al. 2002; Scarabino 2006; Salazar-Vallejo et al. 2008).

Like in a rearview mirror, the notion of a pristine region associated with the SWA fades away while we progress in our analysis. However, Argentina

and Uruguay have indeed started to work in the right direction with the National Strategy of Invasive Exotic Species (<https://www.argentina.gob.ar/ambiente/biodiversidad/especiesinvasoras> and <https://bit.ly/2NgLum9>) and the online database provided by the Inter-American Biodiversity Information Network (IABIN) through the Invasives Information Network (I3N, <http://www.inbiar.uns.edu.ar/>), as well as the production of new identification field guides focused on marine-coastal introduced species (Schwindt et al. 2018). However, since these initiatives tend to be threatened by disrupted or unreliable long-term governmental support, marine biodiversity is still often either unrepresented or under-represented in many cases. Since ships are the main vectors, we forecast that new introductions will continue to occur until regional and international regulations directed to control ballast water and hull fouling are effectively and globally integrated across oceans, seas, river basins and political borders.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Introduced (I) and cryptogenic (C) marine species of the Southwest Atlantic Ocean (SWA).

Appendix 1. List of References for Table S1.

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2020/Supplements/AI_2020_Schwindt_et_al_SupplementaryTable.xlsx