



Review

No longer the pristine confines of the world ocean: a survey of exotic marine species in the southwestern Atlantic

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Received 1 October 2001; accepted in revised form 24 April 2002

Key words: Argentina, estuarine, exotics, invasions, marine, Patagonia, southwest Atlantic, Uruguay

Abstract

We conducted a comprehensive survey of existing knowledge about exotic marine organisms introduced to the southwestern Atlantic Ocean, including coastal and shelf areas of Uruguay and Argentina. This domain is equivalent to the so-called Patagonian Shelf Large Marine Ecosystem, and corresponds to two biogeographic provinces: warm-temperate (Argentine Province) and cold temperate (Magellanic Province). The search included species that can be confidently categorized as introduced (31) and cryptogenic species (46). We present a comprehensive picture of recorded introductions (the first for this region) and some prominent ecological consequences. Most coastal ecosystems between the La Plata River estuary and central Patagonia have already been modified, or are expected to be so in the short term. Five recent, human-mediated biological invasions have already had a significant ecological impact. A barnacle (*Balanus glandula*) belt has developed on all rocky shores where none was present 30 years ago, a macro-fouler (*Limnoperna fortunei*) and a reef-builder (*Ficopomatus enigmaticus*) have strongly modified estuarine ecosystems, Pacific oyster (*Crassostrea gigas*) reefs are expanding in shallow bays at a fast rate, and kelp (*Undaria pinnatifida*) is rapidly modifying nearshore benthic communities along the coasts of central Patagonia. At this point, it is uncertain how many of the cordgrasses (*Spartina* spp.) found in coastal salt marshes correspond to exotic forms. Only exposed sandy beaches appear to be free from the pervasive ecological impact of invasion by exotic species. Poor knowledge of the regional biota makes it difficult to track invasions.

Introduction

The accelerating invasion of coastal marine communities by non-indigenous species is a subject of much current concern among ecologists, environmentalists and managers (Carlton 1996; Carlton and Geller 1993; Ruiz et al. 1999, 2000). Comparative studies of patterns, a main avenue for progress towards the

understanding of the processes involved in invasibility and the consequences of invasions, require the existence of comparable data sets. The scientific and technical literature is unevenly distributed, as illustrated by a sample of references recorded during the five-year 1997–2001 period by the Aquatic Sciences and Fisheries Abstracts (ASFA; Figure 1): an overwhelming majority corresponds to the United States,

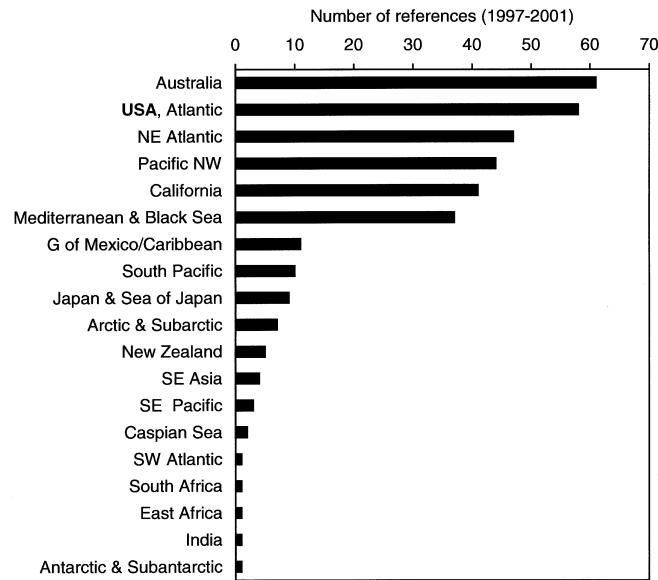


Figure 1. Geographic distribution of references to non-indigenous marine species in a sample from the literature. The latter ($n = 344$ references) was assembled through a search of the Aquatic Science and Fisheries Abstracts (ASFA), using the concatenation of the terms 'introduced species' and 'marine'. Only references that document geographic-specific references on non-indigenous species were retained as part of the sample. The list provides only an indicator; by no means is it presumed to be comprehensive.

Western Europe and Australia. *None to one* references were recovered in the sample for vast expanses of the World oceans, including most of Latin America, Africa, the Indian Ocean and the southeast Pacific, giving the impression that at least some of those regions are relatively pristine with regards to invasions by non-indigenous species. As in other cases, this pattern could be biologically meaningful (reflecting differences in either availability of propagules or invasibility), or just indicative of sampling bias (Ruiz et al. 2000). We explored these hypotheses through a survey of recorded non-indigenous species in the southwestern Atlantic (Figure 2), corresponding to the so-called Patagonian Shelf Large Marine Ecosystem (Sherman 1991; Bisbal 1995), and often regarded as a comparatively pristine confine of the World Ocean. This applies particularly to the Patagonian coastal zone (south of 40° south latitude (SL); Esteves et al. 2000). This zone is sparsely populated, with just a handful of relatively small industrialized spots; in most of the watersheds draining to the sea, there is little to no agricultural development or intensive animal husbandry. Consequently, the risks of land-originated chemical pollution are regarded as relatively minor. Offshore oil-drilling has been considered, particularly for the Malvinas/Falkland Shelf, but remains undeveloped. Spills from oil tankers have

occurred, but the risks are small when compared to the situation in major oil-producing or industrial countries. The eco-tourism industry thrives, based on large colonies of marine birds and mammals.

A casual traveler's glance at most of the Patagonian coastline may, indeed, confirm those expectations. Yet, if man-induced changes in the biodiversity tapestry of coastal seascapes are considered, a closer look at those regions reveals a very different picture. That was the aim of the collaborative effort that we undertook. To this end, we formed an e-discussion group of Argentine and Uruguayan scientists within which information was exchanged and screened in preparation for a working group meeting that took place concurrently with the 4th Jornadas Argentinas de Ciencias del Mar (Puerto Madryn, Argentina, 11–15 September, 2000). The resulting manuscript was circulated among the members of the group until consensus was reached. That was the basis for this overview.

While conducting this literature survey, we had two objectives in mind:

1. To compile all the existing evidence about the introduction of exotics to a region of the World Ocean where marine biodiversity is very poorly documented. Moreover, much of the little that is known is either unpublished or contained in rather cryptic

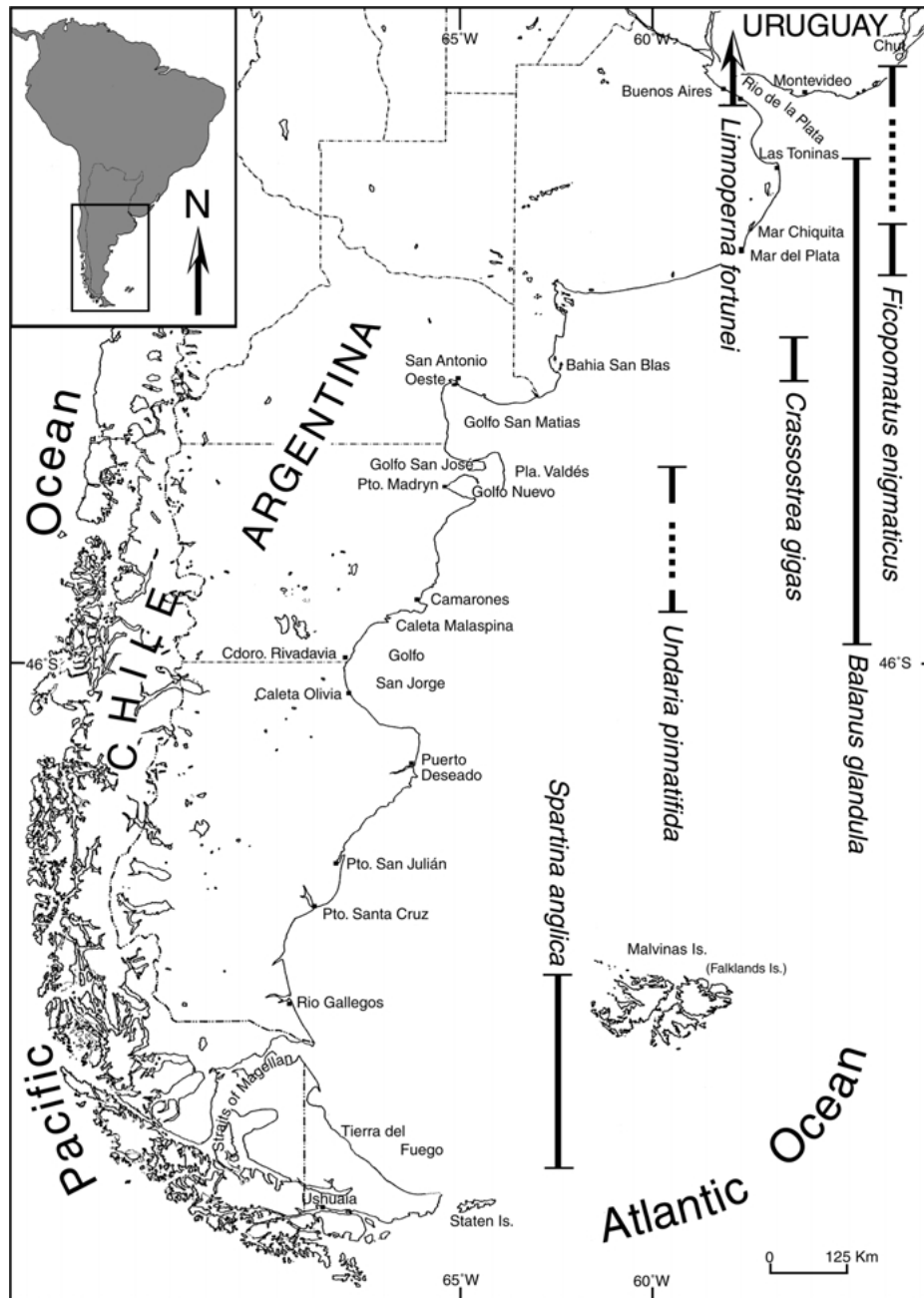


Figure 2. Map of the region considered showing the geographic localities mentioned in the text and latitudinal range of species that have a significant ecological impact. Dotted lines indicate range interruptions.

sources, normally not available to the international scientific community. Thus, it is urgent to compile this information before it is too late.

2. To develop a holistic, 'big picture' of how coastal seascapes of the southwestern Atlantic have

changed as a result of ecologically significant invasions.

The geographic domain covered by our review corresponds to the coastal zone south of the Brazil/Uruguay border (the mouth of Chuy Creek, ca. 34° SL), down

to the southern end of the continent and its adjacencies (including the Malvinas/Falkland Islands, ca. 54° SL), a latitudinal range of about 20 degrees. The latter includes cold-temperate and warm-temperate biotas, usually assimilated to the Magellanic and Argentine Biogeographic provinces, respectively (Instituto de Biología Marina 1964). The transition (in the coastal zone) is located in northern Patagonia, between ca. 41° and 43° SL.

The emerging 'big picture' showed that the impact of recent, human-mediated biological invasions has already had a significant ecological impact. Among the 31 cases identified with certainty as biological invasions, six have had a significant ecological impact. Two occurred in warm-temperate estuarine environments, and four along the coastlines of cold-temperate Patagonia. In this review, we present the results of our literature survey and discuss priorities for management and research.

Scope

Criteria for inclusion

This review is based on the personal knowledge of the members of the working group, and on a careful screening of published information. Much of the latter is contained in rather cryptic sources, many of them not even listed in literature databases like ASFA. We partitioned the specific records into two sets:

1. Species whose 'exotic' status is well documented.
2. Cryptogenic species that are reasonable candidates for the status of invasive exotics.

The second group requires the specification of criteria for inclusion; five were considered:

- (a) Wide geographic distribution, including 'cosmopolitan' species and species showing biogeographically incongruous distribution ranges.
- (b) Invasive potential indicated by documented exotic status in other geographic regions.
- (c) The species is abundant in the vicinity of presumed centers of introduction (e.g. commercial harbors), but rare in (or absent from) the rest of the region. Special consideration was given to species found in communities that are associated with anthropic activities (e.g. fouling communities from harbors).
- (d) Life history suggests high, long-distance dispersive potential, particularly for rafting on man-made structures (fouling on the hull of vessels and other

man-made floating/drifted objects), or the ability to be dispersed with ballast water.

- (e) In the case of species with hard parts, absence from the Quaternary fossil record, which in this region is rich and has been well documented.

Criteria for exclusions

The following cases were excluded from our review:

- (a) Anadromous salmonids, as we have concentrated on benthic/littoral organisms. Salmonids are the only documented exotics present in the region that do not fit the latter condition (Pascual and Orensanz 1996).
- (b) Wood-borers, like limnoriid isopods and teredinid bivalves. While some may have been introduced by man, these organisms are also dispersed on drifting woody substrates of natural origin.
- (c) Species that, within the study area, are *exclusively* associated with floating objects. Many tropical/subtropical species (e.g. some lepadid barnacles, amphinomid polychaetes, etc.) are common on man-made floating objects that, drifting southward along the Brazil Current, reach the coasts of Uruguay and more frequently northern Argentina, but also occur on drifting substrates of natural origin (Barattini and Ureta 1960).
- (d) Hydrozoa with a medusa stage, as their often wide geographic ranges of distribution may be related to natural dispersion. This is best illustrated with the Campanulariid genera *Clytia*, *Gonothyrea* and *Obelia*. Several species have been reported for the region of interest, some based on the polyp stage, some on pelagic medusae, and others on both (Blanco 1964, 1967, 1968, 1976; Blanco and Morris 1977; Bastida 1971; Vervoort 1972; Cornelius 1975, 1982; Zamponi 1987; Zamponi and Genzano 1990; Genzano 1988, 1990, 1995; Genzano et al. 1991, 1998; Genzano and Zamponi 1992). Most of these are cosmopolitan, but there is substantial disagreement between authors regarding the definition of species. Other cases are the bougainvillids *Bougainvillia ramosa* van Beneden (1844) (Genzano and Zamponi 1992; Genzano 1995) and *Bimeria vestita* Wright (1859) (Blanco 1974; Genzano and Zamponi 1992; Genzano 1998).
- (e) Invasive species present only on the freshwater end of estuarine environments, as exemplified by the corbiculid bivalves *Corbicula fluminea* Müller

(1774) and *C. largillierti* Philippi (1844), introduced to the La Plata River estuary during the 1970s (Ituarte 1994). Alternatively, primarily freshwater species extending into the brackish portion of estuaries (e.g. the mytilid bivalve *Limnoperna fortunei* Dunker (1857)) were included.

- (f) Exotics recorded for Brazil, but not from Uruguay/Argentina. This criterion is arbitrary, and was introduced only for practical reasons. North of the boundary between Brazil and Uruguay (marked by the mouth of Chuy Creek), the coast is formed exclusively of exposed sandy beaches over hundreds of kilometers; no exotics have been recorded for that ecosystem.

General survey of recorded species introductions into the southwestern Atlantic

The results of our inquiry are summarized in Tables 1 and 2. Table 1 lists all the cases (31 in total) in which the 'exotic status' is reasonably well established. Six invasions that have had or that are likely to have significant ecological effects are discussed in some detail in the following section. In Table 2, we included cryptogenic species, i.e. species that, according to some of the criteria listed above, are likely candidates to have been introduced to the region through human-mediated activities. These amount to 47 cases. Our survey revealed that crustaceans accounted for ca. one-third of both cryptogenic (34.7%) and exotic (32.2%) species. Next were ascidians and bryozoans among the exotics (respectively with 19.3% and 16%), and annelids and cnidarians (respectively with 26% and 19.5%) among the cryptogenics. Most of the exotic/cryptogenic ascidians, bryozoans and cnidarians, as well as some serpulid polychaetes, are components of the fouling community, and restricted to commercial harbors (Mar del Plata, Ingeniero White). Of the 31 exotic species, only 10% are broadly distributed in Argentina, Uruguay and Brazil, while the majority are concentrated in a few locations. The picture is different for cryptogenics, among which almost half of the species have a broad range of distribution throughout the southwestern Atlantic. Most of the exotic and cryptogenic species are concentrated in Buenos Aires Province (exotics = 79%, cryptogenics = 68%), where major commercial harbors are located. Finally, the area of origin is unknown for most of the exotic species; only 29% of them have a well established area of origin, predominantly the Northeast Pacific and the Far East.

Major sources of uncertainty

Poor knowledge of the biota

The single major source of uncertainty regarding biological invasions in the southwestern Atlantic is the poor documentation of the marine biota. This is minimal for some groups, e.g. fungi. The issue of uncertain status due to inaccurate systematics is well illustrated by three genera of ubiquitous, small-sized bivalves: *Crenella* Brown (1827) (Mytilidae), *Lasaea* Leach in Brown (1827) (Lasaeidae) and *Hiatella* Daudin in Bosc (1801) (Hiatellidae). All of them have the potential for long-distance dispersal by vessels, as they tend to live in association with epibenthic communities, including fouling communities. In the three cases, cosmopolitan or widespread species have been reported for the southwestern Atlantic:

1. *Crenella* (Mytilidae) is in dire need of taxonomic revision, even if only shell morphology is considered. The sculpture pattern of the shell in general, and of the protoconch in particular (which under SEM can provide valuable characters), have not been comparatively described. *Crenella divaricata* d'Orbigny (1842) was originally described from Cuba, and later reported for both coasts of the Americas, from the Gulf of California to Perú, and from North Carolina to San Antonio (Argentina). The species may be strictly tropical (Caribbean); records from the southwestern Atlantic (Klappenbach 1970; Figueiras and Sicardi 1970b, 1980b; Scarabino 1977; Rios 1985, and records therein) must be re-evaluated. Melvill and Standen (1912, later listed by Carcelles and Williamson 1951) cited the European species *C. decussata* Montagu (1808) for sub-antarctic waters, but this record is most likely incorrect. This species is distributed along the coasts of the USA, South Japan, the Galapagos Islands, northern Perú, and North Europe (Coan et al. 2000).

2. *Lasaea* is an extremely plastic genus, including sexually-reproducing species as well as clones of parthenogens (Ó Foighil and Smith 1995), all morphologically similar to each other. Three 'cosmopolitan' nominal species have been reported for the southwestern Atlantic: *L. adamsoni* Gmelin (1791) (Figueiras and Sicardi 1980b), *L. rubra* Montagu (1803) (= *L. adamsoni* fide Coan et al. 2000) and *L. consanguinea* Smith (1879) (Zaixso and Pastor 1977), but all these specific records are unsubstantiated.

Table 1. Species for which the 'exotic' status is well documented.

Major taxonomic group and family	Species	Significant references (primary records for the region of interest)	General geographic distribution	Distribution in the southwestern Atlantic	Comments
Spermatophytes Poaceae (Tribe Cynodonteae)	<i>Sparina anglica</i> (Hubbard 1968)	Parodi (1959, as <i>S. × townsendii</i>), Nicora (1978)	Originated as hybrid in the UK	Tierra del Fuego	See text for account of complex origin
Phaeophyta Alariaceae	<i>Undaria pinnatifida</i> (Harvey) (Suringar 1872)	Piriz and Casas (1994), Casas and Piriz (1996)	Japan, China, Korea, SW Australia, Tasmania, New Zealand, Mediterranean coasts, North Europe, SW Atlantic	Golfo Nuevo, Chubut	Apparently introduced through the Ale. Storm Dock (Puerto Madryn). Spreading to other sites along the Argentine coast
Polychaeta, Spionidae	<i>Boeckardiella ligerica</i> (Feronière 1898)	Monro (1938, as <i>Polydora uncatiformis</i>), Orensanz and Estivariz (1972, as <i>Boeckardia hamata</i>), Blake (1983)	W Europe, California, W Indies, S Africa, SW Atlantic	La Plata River estuary and Mar Chiquita coastal lagoon	Presumably native to the Atlantic coast of Europe
Polychaeta, Serpulidae	<i>Ficopomatus enigmaticus</i> (Fauvel 1923)	Monro (1938), Rioja (1943), Orensanz and Estivariz (1972), Bastida (1971), Scarabino et al. (1975), Nion (1979) (all as <i>Mercierella e.</i>), Knight-Jones and Knight-Jones (1991)	Cosmopolitan in subtropical/temperate estuaries	Estuarine environments of Uruguay; Mar Chiquita coastal lagoon (estuarine reefs), Puerto Quequén, Mar del Plata (fouling community) (Argentina)	Area of origin uncertain
Polychaeta, Serpulidae	<i>Hydroides elegans</i> (Haswell 1883)	Bastida (1971, as <i>H. norvegica</i>), Zibrowius (1971), Knight-Jones and Knight-Jones (1991)	Widely distributed in warm and warm-temperate regions	Mar del Plata Harbor (fouling community)	Presumably native to the Indo-Pacific
Polychaeta, Serpulidae	<i>Hydroides dianthus</i> (Verrill 1873)	Valentinuzzi de Santos (1971)	Widely distributed in warm and warm-temperate regions	Puerto Belgrano (fouling community)	
Bivalvia, Ostreidae	<i>Crassostrea gigas</i> (Thunberg, 1793)	Marcela Pascual (pers. obs.)	Intentionally introduced to many temperate regions	San Blas and Anegada Bays	Native to the NW Pacific
Bivalvia, Mytilidae	<i>Linnoperna fortunei</i> (Dunker 1857)	Pastorino et al. (1993), Scarabino and Verde (1995), Darrigran and Pastorino (1995a, b), Darrigran and Ezcurra de Drago (2000)	Originating from rivers from China and SE Asia; fresh and brackish water	La Plata River, including estuarine portion (up to 3 ppt)	
Gastropoda, Muricidae	<i>Rapana venosa</i> (Valenciennes 1846)	Harding and Mann (1999), Scarabino et al. (1999), Pastorino et al. (2000)	Originating from the Sea of Japan, the Yellow Sea and the East China Sea, later introduced to the Black Sea and Chesapeake Bay	La Plata River estuary, both coasts	A record from New Zealand was based on empty shells (Marshall and Crosby 1998)
Gastropoda (Pulmonata), Ellobiidae	<i>Myosotella myosotis</i> (Draparnaud 1801)	Figueiras and Sicardi (1974, as <i>Ovatella</i> (<i>M.</i>) sp.), Zaffaroni (1994, as <i>Ovatella m.</i>)	NE Atlantic, Mediterranean, Nova Scotia to Central America, Bermuda I,	Playa Portezuelo, Maldonado (Uruguay); empty shells presumably originate from	May be native to Europe

Cirripedia, Balanidae	<i>Balanus glandula</i> (Darwin 1854)	Spivak and L'Hoste (1976), Bastida et al. (1980); Newman and Ross (1976), Vallarino and Elfas (1997)	Puget Sound to California, South Africa, Australasia, Uruguay NE Pacific (Aleutians to Baja California); introduced to the SW Atlantic	the mouth of Potrero Creek, which drains on that beach San Clemente del Tuyú to Comodoro Rivadavia, Argentina (Not 'Rio de Janeiro', as stated by Newman and Ross (1976))	Native to the West Coast of North America
Cirripedia, Balanidae	<i>Balanus amphitrite</i> (Darwin 1854)	Bastida (1971), Spivak and L'Hoste (1976), Newman and Ross (1976), Calcagno et al. (1997, 1998)	Cosmopolitan in warm and temperate seas	Introduced in historical times to the harbor of Mar del Plata, where it is a component of the fouling assemblage. Also found in Quequén	Present in the same area during the Quaternary (Plio-Pleistocene in cores 37–41 SL; Newman (1979)). May be originally from the 'Near East' and the <i>Ocean Indian</i> region (Zullo 1966)
Cirripedia, Balanidae	<i>Balanus trigonus</i> (Darwin 1854)	Bastida (1971), Spivak and L'Hoste (1976), Newman and Ross (1976), Zullo (1992)	Cosmopolitan in warm and warm-temperate seas	Introduced to the harbor of Mar del Plata, where it is a component of the fouling assemblage	Presumably introduced in the Atlantic Basin (Zullo 1992)
Amphipoda, Corophidae	<i>Monocorophium insidiosum</i> (Crawford 1937)	Alonso (1997, as <i>Corophium</i> l.)	British Columbia to southern California; both sides of the Atlantic ocean; introduced to Chile, Hawaii and the SW Atlantic	Buenos Aires Province, estuarine, often associated with <i>Ficopomatus</i> reefs	Presumably native to the North Atlantic
Isopoda, Ligiidae	<i>Ligia exotica</i> (Roux 1828)	Giambiagi (1931), Carcelles (1944) (both as <i>Ligyda e.</i>), Barattini and Ureta (1960), Reca (1972), Scarabino et al. (1975, as <i>Ligia</i> sp.), Maytía and Scarabino (1979)	Cosmopolitan along warm and warm-temperate coasts (except Europe); supratidal zone	La Paloma, Montevideo, Quequén and Mar del Plata Harbors	
Isopoda, Halophiloscidae	<i>Halophiloscia couchii</i> (Kinahan 1858)	Giambiagi (1935, as <i>Philoscia bonariensis</i>), Reca (1972)	Europe to NW Africa, introduced to North America and the SW Atlantic	Necochea and San Blas (Argentina), higher intertidal zone	
Isopoda, Idoteidae	<i>Idotea metallica</i> (Bosc 1802)	Wagele (1991), Brandt (1991), Bastida (1971, as <i>I. baltica</i>)	Widely distributed, but not in the Antarctic; often planktonic	Mar del Plata	
Isopoda, Idoteidae	<i>Synidotea laevitorsalis</i> (Miers 1881)	Chapman and Carlton (1991), Giambiagi (1922, as <i>S. marplatensis</i>), Mañé-Garzón (1946, as <i>S. marplatensis</i>), Martínez et al. (1984, as <i>S. brunnea</i>)	Originating from Japan and China; introduced to western North America and the SW Atlantic		Ilha Grande (Brazil) to Bahía Blanca (Argentina)

Table 1. Continued.

Major taxonomic group and family	Species	Significant references (primary records for the region of interest)	General geographic distribution	Distribution in the southwestern Atlantic	Comments
Isopoda, Sphaeromatidae	<i>Sphaeroma serratum</i> (Fabricius 1787)	Roux and Bastida (1990), Kittlein (1991)	NE Atlantic, from Europe to N Africa, Mediterranean and Black Sea; S Africa, W Australia, SW Atlantic	Buenos Aires Province (Argentina)	
Decapoda, Majidae	<i>Pyromaia tuberculata</i> (Lockington 1877)	Schejter et al. (submitted)	NE Pacific, from the West Coast of the USA to Panama	Buenos Aires Province (Argentina)	Also reported as an invading species in Japan (Carlton 1987), Rio de Janeiro and litoral do Paraná, Brazil (de Melo et al. 1989)
Bryozoa, Bugulidae	<i>Bugula flabellata</i> (Thompson in Gray 1848)	Lichtschein de Bastida and Bastida (1980), Ryland (1965), Gordon and Mawatari (1992)	Cosmopolitan	Mar del Plata and Puerto Belgrano harbors (Argentina), fouling community	
Bryozoa, Bugulidae	<i>Bugula neritina</i> (Linnaeus 1758)	Hastings (1943), López-Gappa (1978), Lichtschein de Bastida and Bastida (1980)	Cosmopolitan	Scattered records from harbor areas: Mar del Plata, Puerto Belgrano, Pt. Williams (Falkland I.), as a component of the fouling community	
Bryozoa, Bugulidae	<i>Bugula simplex</i> (Hincks 1886)	Ryland (1965), Lichtschein de Bastida and Bastida (1980), Gordon and Mawatari (1992)	Cosmopolitan	Puerto Belgrano, fouling community	
Bryozoa, Bugulidae	<i>Bugula stolonifera</i> (Ryland 1960)	Ryland (1965), Lichtschein de Bastida and Bastida (1980), Gordon and Mawatari (1992)	Cosmopolitan	Mar del Plata and Puerto Belgrano harbors, in fouling communities	
Bryozoa, Cheiloporinidae	<i>Cryptosula pallastana</i> (Moll 1803)	Ryland (1965), López-Gappa (1978), Lichtschein de Bastida and Bastida (1980), Gordon and Mawatari (1992)	Cosmopolitan	Mar del Plata, Quequén and Puerto Belgrano harbors, fouling community	

Asciaceae, Cionidae	<i>Ciona intestinalis</i> (Linnaeus, 1767)	Van Name (1945), Amor (1964), Kott (1969), Bastida (1971), Pisanó et al. (1971), Traustedt (1885)	Cosmopolitan, often confined to harbor areas; presumably dispersed worldwide by vessels.	Mar del Plata (fouling community), Punta Arenas (Magellan Strait)	Presumably native to one or both coasts of the North Atlantic coast
Asciaceae, Cionidae	<i>Ciona robusta</i> (Hoshino and Tokioka, 1967)	Pisanó et al. (1971)	NE Atlantic, from the Faroe I. and Norway to the Mediterranean, Adriatic, and Black Seas; Australia and New Zealand; NW Atlantic from New England to Florida	Mar del Plata (fouling community)	
Asciaceae	<i>Botryllus schlosseri</i> (Pallas, 1766)	Amor (1964)		Mar del Plata (fouling community)	
Asciaceae, Molgulidae	<i>Molgula manihattensis</i> (DeKay, 1843)	Van Name (1945), Amor (1964), Bastida (1971)	Maine to northern Gulf of Mexico, excluding the Florida peninsula; probably NE Atlantic, from the White Sea to northwestern Africa; West Coast of North America, Japan, Australia	Mar del Plata harbor (fouling community)	Native to the NW Atlantic
Asciaceae, Molgulidae	<i>Molgula robusta</i> (Van Name, 1912)	Van Name (1945), Bastida (1971)	Massachusetts (USA)	Mar del Plata (fouling community)	
Asciaceae, Styellidae	<i>Styela plicata</i> (Lesueur, 1823)	Van Name (1945), F. and C. Monnot (pers. comm., based on materials collected by M. Demichelli, G. Fabiano and G. Riestra)	Widely distributed in warm and warm-temperate seas	Uruguay, mostly from La Paloma Harbor	This and other cosmopolitan congenerics are of Asiatic origin (Kott 1985)

Table 2. Cryptogenic species.

Major taxonomic group and family	Species	Significant references (primary records for the region of interest)	General geographic distribution	Distribution in the southwestern Atlantic
Porifera, Clionidae	<i>Cliona celata</i> (Grant 1826)	Cuartas (1991), Genzano et al. (1991)	Cosmopolitan	Rio de Janeiro to Mar del Plata, 0–100 m
Porifera, Halichondriidae	<i>Halichondria panicea</i> (Pallas 1766)	Burton (1934), Cuartas (1991)	Cosmopolitan	Magellanic to 37° S on the Atlantic
Porifera, Hymeniacioniidae	<i>Hymeniacion hirta</i> (Topsent 1889)	Burton (1940, as <i>Stylohalina</i>), Berroa-Belén (1989)	Gulf of Mexico, Gulf of Guinea, SW Atlantic	Uruguay to San Jorge Gulf (Argentina)
Porifera, Hymeniacioniidae	<i>Hymeniacion sanguinea</i> (Grant 1927)	Burton (1940), Cuartas and Excoffon (1993)	Cosmopolitan	La Paloma; Mar del Plata, where it is the predominant sponge species in the rocky intertidal
Hydrozoa, Sertulariidae	<i>Dynamena cornicina</i> (McCrady 1858)	Genzano and Zamponi (1992)	Red Sea, Mediterranean, North Atlantic S to Caribbean	Brazil to Mar del Plata
Hydrozoa, Sertulariidae	<i>Sertularella mediterranea</i> (Hartlaub 1901)	Genzano (1990, 1998), Genzano and Zamponi (1992)	Worldwide scattered records	Apparently only in Mar del Plata (Argentina)
Hydrozoa, Plumulariidae	<i>Plumularia setacea</i> (Ellis 1755)	Blanco (1966, 1976), Genzano et al. (1991), Genzano and Zamponi (1992), Genzano (1998)	Widely distributed in warm and temperate seas (absent from polar seas)	Magellanic region to Mar del Plata
Hydrozoa, Hebellidae	<i>Hebella scandens</i> (Bale 1888)	Genzano and Zamponi (1992)	Cosmopolitan	Mar del Plata
Hydrozoa, Tubulariidae	<i>Tubularia crocea</i> (Agassiz 1862) Status may needs revision (Petersen 1990)	Bastida (1971), Zamponi and Correa (1988), Genzano et al. (1991), Genzano and Zamponi (1992), Genzano (1998)	Cosmopolitan in warm and temperate seas	Magellanic and Argentine provinces. Records from the southwestern Atlantic are in need of review
Hydrozoa, Claviidae	<i>Rhizogetum nudum</i> (Broch 1909)	Genzano and Zamponi (1992)	Worldwide scattered records	Mar del Plata
Actiniaria, Boloceroiidae	<i>Boloceroides mcmurrici</i> Kwietniewski, 1899	Zamponi (1977)	Widely distributed in the Indopacific	Near Mar del Plata (Argentina), intertidal limestone platform
Actiniaria, Actiniidae	<i>Aulactinia reynaudi</i> (Milne-Edwards 1857)	Zamponi (1977, as <i>Bunodactis r.</i>), Acuña and Zamponi (1996, 1997), Acuña (1997)	West and South Africa	Mar del Plata (Argentina), intertidal, rocky shores
Actiniaria, Actiniidae	<i>Oulactis muscosa</i> (Dana 1849)	Zamponi (1977), Excoffon and Zamponi (1995), Acuña and Zamponi (1997)	Australia, Puerto Rico, Argentina	Mar del Plata (Argentina), rocky shores
Polychaeta, Nereidae	<i>Neanthes succinea</i> (Frey and Leuckart 1847)	Dei Cas and Mañé-Garzón (1973), Orensanz and Gianuca (1974)	Widely distributed in warm and temperate seas; common in estuarine environments. Presumably native to the North Atlantic	La Plata River estuary, Mar Chiquita coastal lagoon
Polychaeta, Hesionidae	<i>Syllidia armata</i> (Quatrefages 1865)	Orensanz (pers. obs.)	West Atlantic, from Ireland to South Africa	Mar del Plata Harbor
Polychaeta, Syllidae	<i>Syllis gracilis</i> (Grube 1840)	Orensanz (pers. obs.)	Worldwide in warm and temperate seas	Mar del Plata (rocky intertidal and fouling community)

Table 2. Continued.

Major taxonomic group and family	Species	Significant references (primary records for the region of interest)	General geographic distribution	Distribution in the southwestern Atlantic
Polychaeta, Dorvilleidae	<i>Schistomeringos rudolphi</i> (Delle Chiaje 1828)	Orensanz (1974, as <i>Stauronereis r.</i>)	Cosmopolitan in temperate and tropical seas, in shallow water	Uruguay to San Matias Gulf; most abundant in polluted environments of Mar del Plata harbor and its adjacencies
Polychaeta, Iphitimidae	<i>Ophryotrocha 'puerilis'</i> , auctorum	Orensanz (1990)	Scattered worldwide localities, often in aquaria	Mar del Plata (Argentina), in an aquarium
Polychaeta, Spionidae	<i>Boccardia polybranchia</i> (Haswell 1885)	Blake (1983)	Widespread along warm and temperate coastlines, mostly in the southern Hemisphere	Widespread throughout the region, usually in the high intertidal zone
Polychaeta, Spionidae	<i>Polydora ciliata</i> (Johnston 1838)	Blake (1983)	Europe, S Africa, SW Atlantic	Uruguay to the Falkland I.
Polychaeta, Spionidae	<i>Polydora cornuta</i> (Bosc 1802) ^a	Orensanz and Estivariz (1972, as <i>P. ligni</i>), Blake and Maciolek (1987), Blake (1983)	New England to Florida, California, SW Atlantic; intertidal and estuarine	Mar Chiquita coastal lagoon, associated with colonies of <i>Ficopomatus</i>
Polychaeta, Spionidae	<i>Polydora flava</i> (Claparede 1870)	Blake (1983)	Widely scattered locations in temperate and warm seas	Uruguay to Puerto Madryn
Polychaeta, Spionidae	<i>Polydora socialis</i> (Schmarda 1861)	Blake (1983)	Both coasts of the Americas, Australia and New Zealand	Mar del Plata to San Jose Gulf
Polychaeta, Spirorbidae	<i>Neodexiospira mannarensis</i> (Pillai 1970)	Knight-Jones and Knight-Jones (1991)	Widespread in warm and temperate seas	Puerto Quequén
Polychaeta, Spirorbidae	<i>Simplaria pseudomilitaris</i> (Thiriou-Quievreux 1965)	Knight-Jones and Knight-Jones (1991)	Widespread in warm and temperate seas	Puerto Quequén
Bivalvia, Mytilidae	<i>Perna perna</i> (Linnaeus 1758) ^b	Figueiras and Sicardi (1968, 1980a, b), Bernard (1983), Rios (1985)	Venezuela to Uruguay; rocky shores	
Cirripedia, Balanidae	<i>Balanus pallidus</i> (Darwin 1854)	Newman and Ross (1976)	Scattered records from tropical and subtropical coasts	Argentine Patagonia
Cirripedia, Balanidae	<i>Balanus improvisus</i> (Darwin 1854)	Carcelles (1944, as <i>B. i. communis</i>), Spivak and L'Hoste (1976), Newman and Ross (1976)	East Coast of the Americas; West Coast of Africa; Mediterranean, Black and Red Seas; Washington to San Francisco; Japan; Australia; SW Atlantic	Estuarine environments: Montevideo, Punta Indio, Mar Chiquita coastal lagoon; also Mar del Plata Harbor. Originally described by Darwin (1854) for Montevideo and Patagonia
Amphipoda, Talitridae	<i>Orchestia gammarella</i> (Pallas 1766)	Alonso (1986)	North Atlantic, from Iceland to Canary I. and to Maine, Mediterranean; SW Africa, SW Atlantic	Puerto Deseado area (Argentine Patagonia)
Amphipoda, Talitridae	<i>Orchestia mediterranea</i> (Costa 1857)	Escofet (1973)	Mediterranean, North Atlantic (France, England, Wales, Ireland)	Mar del Plata region

Table 2. Continued.

Major taxonomic group and family	Species	Significant references (primary records for the region of interest)	General geographic distribution	Distribution in the southwestern Atlantic
Amphipoda, Talitridae	<i>Platorchestia platensis</i> (Kroyer 1845)	Bousfield (1973), Escofet (1973) (all as <i>Orchestia</i> sp.)	Nearly cosmopolitan along tropical-temperate coastlines	Montevideo and Mar del Plata
Amphipoda, Melitidae	<i>Melita palmata</i> (Montagu 1804)	Escofet (1973; as <i>Melita</i> sp.), Alonso (1986), Alonso (1997)	NE Atlantic from British I. to Senegal, Mediterranean; SW Atlantic	Mar del Plata area to Golfo Nuevo, intertidal and estuarine, associated with <i>Ficopomatus</i> reefs
Amphipoda, Melitidae	<i>Maera grossimana</i> (Montagu 1808)	Wakabara et al. (1982), Lincoln (1979), Escofet (1973, as <i>Maera</i> sp.)	Mediterranean and North Atlantic	
Amphipoda, Ampithoidae	<i>Ampithoe valida</i> (Smith 1873)	Alonso (1986), Alonso et al. (1996), Alonso (1997)	NW Atlantic, NE Pacific (California and Oregon), Japan, SW Atlantic	Rawson to Puerto Quequén, low intertidal and shallow subtidal
Amphipoda, Ampithoidae	<i>Cymadusa filosa</i> (Savigny 1816)	Escofet (1973, as <i>Cymadusa</i> sp.), Alonso (1986)	Widely distributed in warm and temperate seas	Mar del Plata to San Matías Gulf; low intertidal, among algae
Amphipoda, Caprellidae	<i>Caprella equilibra</i> (Say 1818)	McCain (1968), McCain and Gray (1971)	Almost cosmopolitan, 0–3000 m	Chile and Argentina, interrupted in the Magellanic region
Amphipoda, Caprellidae	<i>Caprella penantis</i> (Leach 1814)	McCain (1968), McCain and Gray (1971)	Almost cosmopolitan	Southern South America
Mysidacea, Mysidae	<i>Neomysis americana</i> (S.I. Smith 1873)	González (1974), Hoffmeyer (1990)	NW Atlantic, from the Gulf of St. Lawrence (Canada) to Florida (USA); SW Atlantic	Uruguay to San Blas (Argentina), in shallow bays and estuaries
Tanaidacea, Tanaidae	<i>Sinelobus stanfordi</i> (Richardson 1901)	Giambiagi (1923), Mañé-Garzón, 1943) (both as <i>Tanais fkuviatilis</i>), Sieg (1983a, b)	Tropical and warm temperate coasts, often estuarine; 0–20 m	La Plata River estuary
Tanaidacea, Tanaidae	<i>Tanais dulongii</i> (Audouin 1826)	Giambiagi (1922, 1923, as <i>T. gallardoii</i>), Sieg (1983a, b)	Scattered regions along temperate coasts	Puerto Madryn
Decapoda, Panopeidae	<i>Panopeus meridionalis</i> (Williams 1983)	Williams (1983), Williams and Boschi (1990), Boschi et al. (1992)		Montevideo (Uruguay), Mar del Plata and Mar Chiquita coastal lagoon (Argentina); intertidal
Decapoda, Grapsidae	<i>Pachygrapsus transversus</i> (Gibbes 1850)	Williams (1984), Zolessi and Philippi (1995)	North Carolina to Uruguay; Bermuda I.; California to Perú, Galápagos I.; Mediterranean Sea to N Angola. Intertidal	Uruguay
Bryozoa, Crisiidae	<i>Crisia eburnea</i> (Linnaeus 1758)	Borg (1944), Lichtschein de Bastida and Bastida (1980)	Cosmopolitan	Tierra del Fuego; fouling community of Puerto Belgrano
Bryozoa, Vesiculariidae	<i>Bowerbankia gracilis</i> (Leidy 1855) ^c	Ryland (1965), Amor and Pallares (1965), Bastida (1971), López Gappa (1978), Lichtschein de Bastida and Bastida (1980), López Gappa et al. (1982), Gordon and Mawatari (1992)	Almost cosmopolitan, in fouling communities	Puerto Deseado, Puerto Belgrano, Mar del Plata (fouling community)

Table 2. Continued.

Major taxonomic group and family	Species	Significant references (primary records for the region of interest)	General geographic distribution	Distribution in the southwestern Atlantic
Bryozoa, Membraniporidae	<i>Conopeum reticulum</i> (Linnaeus 1767)	Marcus (1938), Ryland (1965), Lichtschein de Bastida and Bastida (1980), Bremec (1989)	Cosmopolitan in fouling communities	Puerto Belgrano, Bahía Blanca, Puerto Deseado; common in several localities of Buenos Aires Province (López Gappa, pers. obs.)
Bryozoa, Scrupariidae	<i>Scruparia ambigua</i> (d'Orbigny 1847)	Hastings (1943), Amor and Pallares (1965), López Gappa (1978), Hayward (1995), Lichtschein de Bastida and Bastida (1980), López Gappa and Lichtschein (1990)	NW Atlantic and adjacent seas, Magellanic region, Amsterdam I., Australia, Nueva Zelandia, California, Galapagos I. Often associated with algae; frequent in fouling communities of harbors	Magellanic, N to Pto. Belgrano. Originally described for the Falkland I. by d'Orbigny (1847), as an epibiont of algae. Jullien (1888) recorded it in the 19th century from a remote, presumably pristine region (Orange Bay, Hoste I.). Several locations over the Patagonian Shelf (Hastings 1943; López Gappa and Lichtschein 1990)

^aSeparation of sibling species in the 'ligni' complex may be impossible on the basis of morphological characters alone (Rice 1991).

^bThe genus *Crisia* presents serious taxonomic difficulties. Identification of species is almost impossible in the absence of gonozoids. Lichtschein de Bastida and Bastida (1980) did not illustrate their materials. Other species of the genus have been recorded for the SW Atlantic, including *C. patagonica* (d'Orbigny 1847) described for Bahía Rosas and recorded by Bremec (1989) for Monte Hermoso. The specimens reported by Lichtschein de Bastida and Bastida (1980) could well correspond to the latter.

^cJullien (1888) reported three species of *Bowerbankia* for Orange Bay (Hoste I., Magellanic region), but all were incompletely described. The taxonomic status of those records is still unresolved.

3. Records of *Hiatella* from the southwestern Atlantic have been assigned to two widely spread nominal morpho-species: *H. arctica* Linnaeus (1767) (Figueiras and Sicardi 1980b; Rios 1985) and *H. solida* G. B. Sowerby I (1834) (Richards and Craig 1963; Dell 1964; Figueiras and Sicardi 1970b). Preliminary data (D. Luzzatto and P. Penchaszadeh, pers. obs.) suggest that members of a local population mature at a very small size as compared with *H. arctica* from the Northern Hemisphere, a feature that could suggest the existence of an endemic form. The taxonomic status of records from the southwestern Atlantic requires clarification.

Cosmopolitans: real cases, misidentification, or man-mediated introductions?

According to *Inclusion Criterion* (a) (listed earlier), species with wide or incongruous geographic distribution are suspicious of being exotic invaders. These fall generally within the definition of 'cryptogenic species', i.e. those that are 'not demonstrably native or introduced' (Carlton 1996). In these cases,

three general hypotheses usually compete to explain their origin:

- (H1) The species is truly cosmopolitan, its wide geographic distribution preceding man-mediated dispersal.
- (H2) What is seen as a 'cosmopolitan' morphospecies really corresponds to a cluster of genetically distinct species, each of them with a geographically restricted range of distribution.
- (H3) The current 'cosmopolitan' range of distribution is the result of un-documented man-mediated dispersal.

Unraveling these cases requires the concatenation of systematic, genetic, ecological and historical evidence. It is often the case that complex patterns can be explained by a mixture of the three hypotheses, as has been illustrated by the blue mussels (*Mytilus* spp.; Hilbish et al. 2000).

Natural fluctuations of geographic range

The southern limit of the distribution range of some subtropical species in the southwestern Atlantic has changed in historical times. Natural range expansions,

if not interpreted correctly, could give the false impression of recent introductions. One well-documented example is that of the beach clam *Donax hanleyanus* Philippi (1847), which was absent from exposed sandy beaches south of La Plata River during the 1950s and 1960s, although its presence during the Holocene is attested by the fossil record (von Ihering 1907; Farinati 1985). It was first recorded as living there by Castellanos and Fernández (1965), and afterwards populations exploded (Penchaszadeh and Olivier 1975). The ocypodid *Uca (Celuca) uruguayensis* Nobili (1901), was common in the Mar Chiquita Lagoon during the 1960s (Olivier et al. 1972a), but disappeared for ca. two decades until it reappeared during the 1990s (Spivak et al. 1991). Pelagic larvae of species with established populations north of La Plata River estuary are occasionally transported southward, and settle in northern Argentina. Examples are provided by 'extralimital records' of the mole crab *Emerita brasiliensis* Schmitt (1935) (Scelzo and Boschi 1973), and the portunid crabs *Callinectes sapidus acutidens* Rathbun (1896) (Ringuelet 1963), and *Arenaeus cribarius* Lamarck (1818) (Scelzo 2001).

The case of the mytilid mussel *Perna perna* Linnaeus (1758) is more complicated. Its recent range of distribution extends along the tropical and subtropical coasts of the western Atlantic; it was already reported for Santa Catarina (southeast Brazil) by von Ihering (1897, 1900), but first found in Uruguay during the 1950s (Barattini and Ureta 1960; Klappenbach 1965, p. 335; Amaro 1965). The species is not represented in Quaternary deposits. Some populations were heavily exploited in the intertidal zone during the 1970s. Its abundance declined during the 1980s, but strong recruitment was detected again during the late 1990s (Scarabino, pers. obs.). There is evidence that man contributed to the dispersion of this species during the 19th century, or even earlier (Carlton 1985). Thus, its appearance in Uruguay may reflect a mixture of human-mediated and natural episodes.

Transformation of a biota: introductions that have already had a significant or potential ecological impact

Ficopomatus enigmaticus

Ficopomatus (= *Mercierella*) *enigmaticus* Fauvel (1923), a serpulid polychaete, is a calcareous reef-builder distributed in brackish waters of temperate zones throughout warm-temperate regions

(ten Hove and Weerdenburg 1978). Presumably originating from Australia (Allen 1953) and originally described from France, it was first observed in the southwest Atlantic in a freshwater creek in Uruguay (Arroyo Las Brujas; Monro 1938) and in an Argentine estuary (Quequén River; Rioja 1943). Along the coasts of Uruguay, it has been reported for the Bay of Montevideo (Scarabino et al. 1975), Valizas Creek (Nion 1979) and Garzón coastal lagoon (J. M. Orensanz, pers. obs.), but has not been observed in the Lagoa dos Patos, an extensive estuarine ecosystem in southern Brazil (Capitoli et al. 1978). It had been long established in the Mar Chiquita coastal lagoon (46 km², Figure 1) in 1964, when Olivier et al. (1972a, b) conducted an ecological survey. However, there is no evidence of the presence of its conspicuous colonies in Holocene deposits of the Querandinean Ingression, a shallow brackish sea with well-documented fossil deposits (Orensanz and Estivariz 1972). This indicates that it is an exotic invader, as is the case over much of its geographic range.

The development of reefs is most spectacular in the Mar Chiquita coastal lagoon (Fasano et al. 1982), where they dot hundreds of hectares (Figures 3A–B). Regions where reefs proliferate are usually embayments where water flow is multidirectional, dominated by wind (E. Schwindt, pers. obs.), and reefs have an approximately circular shape (Figure 3). The size of the reefs is variable (up to 7 m in diameter and 0.5 m in height; Schwindt 2001) with maximum height depending on water level (Obenat and Pezzani 1994). It is common to find pairs of reefs that have coalesced (Obenat and Pezzani 1989; Schwindt and Iribarne 1998). When water flow is unidirectional (i.e. in channels and creeks), the shape of reefs is generally elongated, parallel to current direction. The abundance of reefs decreases towards the mouth of the lagoon (where salinity increases).

Within a reef, live individuals are found around the edges (Figure 3D), where larval settlement occurs between the calcareous tubes (Obenat and Pezzani 1994). Recruitment also takes place on empty molluscan shells (Schwindt and Iribarne 2000), bottles, rocks, pillars, bones, and dislodged reef fragments (Obenat and Pezzani 1994; Schwindt 2001). The accumulation of sediment trapped inside the reef results in the death of the oldest individuals (Keene 1980; Obenat and Pezzani 1989). The maximum recorded length is 55 mm (Obenat and Pezzani 1989). In Mar Chiquita, it is an annual iteroparous whose females may release

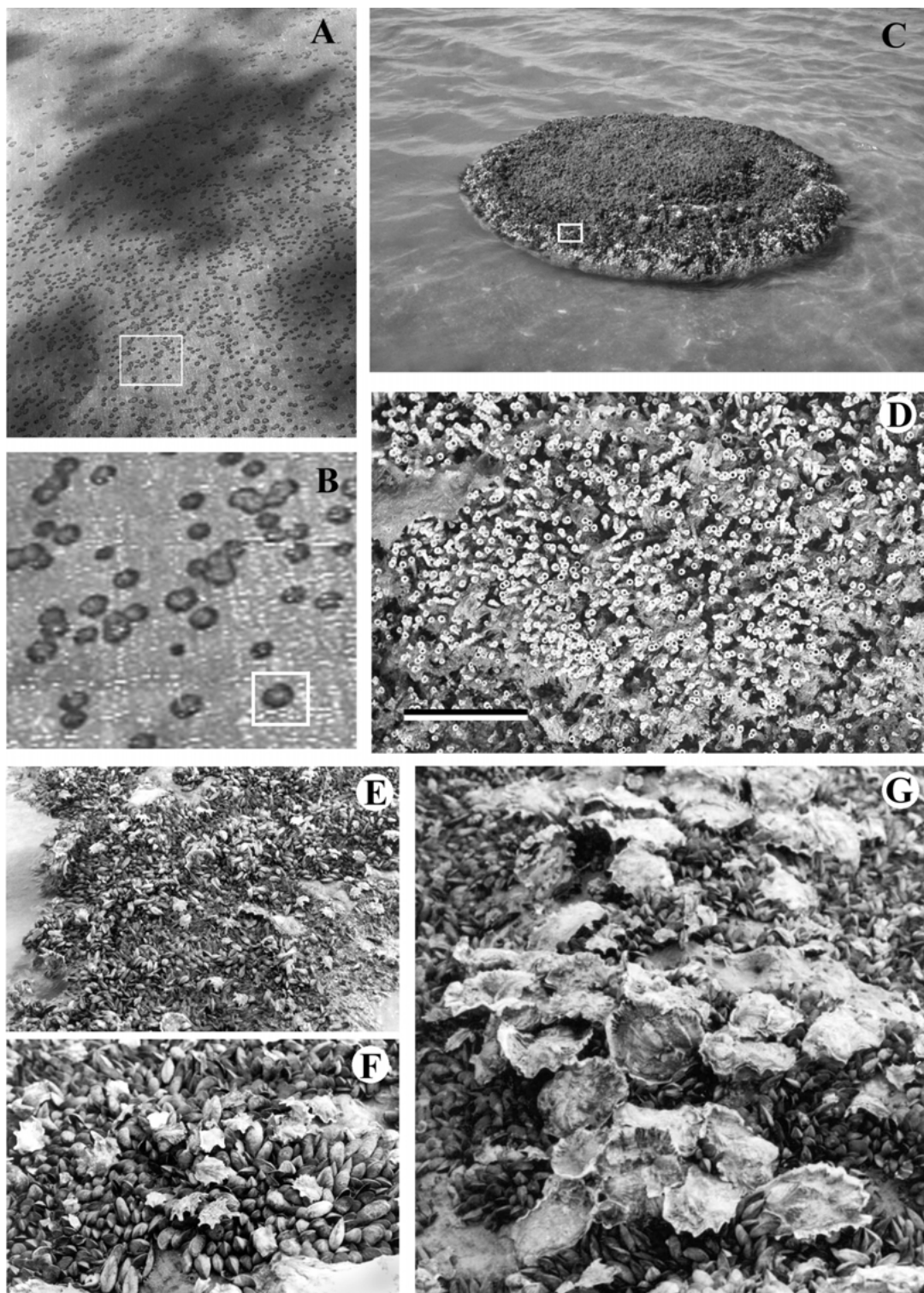


Figure 3. A–D: *Ficopomatus* reefs in Mar Chiquita coastal lagoon. A: Aerial view, B: aerial view at closer range, singling out a reef, C: reef at close range, D: detail of the tubes (scale bar: 5 cm). E–G: *Crassostrea gigas* in San Blas Bay. E: general view of the rocky intertidal, F–G: close-ups. The intertidal mussels are *Brachidontes rodriguezii* and *Mytilus edulis platensis* (both mytilids).

1–2 batches of small eggs per reproductive period; larvae are planktotrophic (Obenat and Pezzani 1994). There are two settlement periods: March–April and November–December (Obenat and Pezzani 1994).

Ficopomatus reefs provide the structural matrix for a complex and diversified community. The tubes, which are white when initially secreted, are steadily covered by bryozoans, green algae and diatoms as they age (Obenat and Pezzani 1989). The reefs provide refuge to numerous organisms, including molluscs, other polychaetes, amphipods and crabs (Orensanz and Estivariz 1972; Schwindt and Iribarne 2000). Among the latter, there is a significant increase in the abundance of juveniles and adults of the grapsid *Cyrtograpsus altimanus* Rathbun (1915) (E. Spivak, pers. obs.), as well as juveniles (4–7 mm) of the congeneric *C. angulatus* Dana (1851) (Spivak et al. 1994). The only predator reported is a reef-inhabiting gobiid fish (*Gobiosoma parri* Ginsburg (1933); Olivier et al. 1972b), a rather infrequent species (Schwindt, pers. obs.). Several aquatic birds (e.g. swans, ducks) use the reefs as resting sites, increasing the local concentration of nutrients (Schwindt and Iribarne 1998).

Reefs have affected sedimentation in their adjacencies as well as the biota of the flats. Reef structures are efficient traps for sediments that would otherwise be transported out of the lagoon (Schwindt 2001). They serve as a refuge for adult *Cyrtograpsus angulatus*, whose abundance is positively correlated with reef size (Schwindt and Iribarne 2000). Crabs, in turn, have a negative effect on the density of polychaetes inhabiting the adjacent mudflats. Density of *Heteromastus cf. similis* Southern (1921) and *Laonereis acuta* Treadwell (1923) decreases, while density of *Nephtys fluviatilis* Monro (1937), increases close to the reefs (Schwindt and Iribarne 2000). Among the meiofaunal organisms inhabiting the top 3 cm of the sediments, only the abundance of ostracods is affected by crabs taking refuge under the reefs (Schwindt 2001).

The introduction and subsequent spread of *Ficopomatus enigmaticus* in Mar Chiquita resulted in dramatic, large-scale modification of the lagoon's ecological and sedimentary dynamics, as well as in constraints to recreational navigation. Similar phenomena have been reported for other coastal lagoons (Fornós et al. 1997).

Limnoperna fortunei

Three important commercial harbors (Buenos Aires, Montevideo and La Plata) make the La Plata River

estuary (Figure 1) a likely entry port for invasive exotics. *Limnoperna fortunei*, the 'golden mussel', was first detected in 1991 in Balneario Bagliardi, on the southern coast of the estuary (Pastorino et al. 1993). Darrigran (1995) predicted that its introduction could create serious environmental problems. This was the first warning regarding freshwater macrofouling in the Neotropics, where that problem had been restricted to marine and brackish water habitats.

The golden mussel, originating from river systems in China and southeast Asia, invaded Hong Kong in 1965, then Japan and Taiwan in the 1990s (Darrigran 2000). Darrigran and Pastorino (1995a,b) hypothesized that the species reached the La Plata River system accidentally, presumably from ballast water discarded from merchant vessels. Like other mytilid mussels, it is epifaunal, adhering to hard substrates, natural (logs, aquatic vegetation, compacted silt-sandy bottoms) as well as artificial (docks, pipes, etc.). Its wide environmental tolerance enables its rapid dispersion. Between 1991 and 2000, it invaded three major rivers in the La Plata Basin (La Plata, Paraná and Paraguay Rivers). It has spread at an average rate of 240 km year⁻¹. Its rate of population growth has been high in a region where it has no competitors. In 1991, when first detected, density was 4 to 5 mussels m⁻² on rocks of Balneario Bagliardi (where its presence was first detected). Average density (on the same rocks) exploded to 30,000 mussels m⁻² in 1992, and 82,000 mussels m⁻² in 1993; presently, it is in the order of 150,000 mussels m⁻² (Darrigran et al. 1999).

The economical impact of the invasion, which affects both natural communities and the human environment, parallels the case of the zebra mussel (*Dreissena polymorpha* Pallas (1771)) in North America (Darrigran and Ezcurra de Drago 2000). Significant effects include the clogging of pipes and filters (Figures 4B and D), changes in flow at the boundary layer, accumulation of empty shells, and the contamination of water coming through pipes due to mussel mass mortality. These problems have been observed in the water intake of water treating plants of La Plata City (Darrigran and Pastorino 1995a, b) and Esquina, as well as in the water intake of industrial and power-generating plants (Darrigran 1997a, b; Codina et al. 1999). Operating costs increase due to lowered pump efficiency, tube corrosion due to the enhanced proliferation of bacteria and fungi, and service interruptions for the cleansing and changing of filters.

Ecologically, the invasion by *L. fortunei* has had an impact on native communities. It has become a component in the diet of several fishes (Montalto et al. 1999), and even changed the diet of a native species (Penchaszadeh et al. 2000). In Bagliardi Beach (where it was first recorded), two gastropods that were commonly found have vanished: *Chilina fluminea* Maton (1809) has no longer been found, while *Gundlachia concentrica* d'Orbigny (1835) has become very rare. In contrast, other species appeared in the modified habitats, including eight species of oligochaetes, one aphanoneuran, eight leeches, and crustacea and insects not observed before (Darrigran et al. 1998). Finally, native bivalves (e.g. *Anodontites trapesialis* Lamarck (1819)) and *A. tenebricosus* Lea (1834) are smothered by *L. fortunei*, in a way similar to what has been described for *Dreissena polymorpha*'s smothering of native unionid mussels in North America (Figures 4A and C). According to Scarabino and Verde (1995), it may have also displaced *Mytella charruana* d'Orbigny (1842) (an indigenous mytilid) on the Uruguayan coast of the estuary.

Crassostrea gigas

Crassostrea gigas Thunberg (1795), the 'Pacific oyster', is a relatively large species originating from Japan, where several races or morphotypes are found in different regions. Best known among these varieties are the Hokkaido, Miyagi, Hiroshima and Kumamoto. This is a fast growing species that tolerates a wide range of environmental conditions (Shatkin et al. 1997), which has resulted in its wide spread over warm and temperate seas following intentional or accidental introductions. In South America, it has been introduced to Chile and Perú on the Pacific, and Brazil and Argentina on the Atlantic. Presently, the Pacific oyster constitutes 98% of the World's oyster production (FAO 1999).

Its introduction to Argentina resulted from an uncontrolled event in 1982, when a fisheries firm (API) brought ca. 500 specimens to San Blas Bay (40°32' S; 62°18' W, Figure 1) with the intention of starting an oyster-culture operation. An inquiry conducted by one of us (M. Pascual) indicates that the specimens were 4 bought in Buenos Aires, where ca. 40 tons year⁻¹ were imported that year for local consumption. According to a local informer (Gianni, pers. comm.), the transplanted lot had originated in Coquimbo (Chile), where the Pacific oyster was cultivated experimentally at the Universidad Católica del Norte. The San Blas operation

was conducted by a countryman of Korean origin who had acquired some basic knowledge of oyster-culture during his childhood. The initial culture operation was interrupted after a few months, and the oysters abandoned.

In 1987, local folks began finding large adult oysters (up to 35 cm long) with juveniles attached to their shells. Thus, five years after the introduction, there was a small population of reproductively active adults. By 1995, there was incipient colonization of intertidal limestone terraces at Los Pocitos, a site located 25 km from San Blas. Average oyster density in Los Pocitos was ca. 2 m⁻² in 1995 and 3 m⁻² in 1996 (M. Pascual, pers. obs.); new recruits were still scarce.

Settlement increased explosively between 1998 and 2000; a density of up to 120 recruits m⁻² was observed in Los Pocitos in 1999. North of San Blas lays Bahía Anegada, an extensive system of ca. 2830 km² of tidal flats, salt marshes and flat islands. Although there has not been a systematic survey of this region, scattered observations indicate that the Pacific oyster is widespread, colonizing preferentially the middle and low intertidal zone of limestone outcrops. Spat is also found attached to boulders, empty shells, the basal portion of *Spartina*, and to the shells of a native small mussel (*Brachidontes rodriguezii* d'Orbigny (1842)) (Figures 3E–G) that typically forms monocultures along the rocky shores of the southwestern Atlantic. The spatial architecture of intertidal communities has become more complex than it was before the introduction, with increased availability of refuge space. A dramatic change is underway, as oyster reefs have started to develop.

In recent years, a hatchery located in San Antonio Oeste (the only one in the region, Figure 1) has begun producing Pacific oyster 'seed'. Oysters have been transplanted for experimental aquaculture to Las Toninas (Buenos Aires Province, 1998 and 1999, Figure 1), Río Gallegos and San Julián (southern Santa Cruz Province, 1998), and Caleta Olivia (northern Santa Cruz Province, 1999, Figure 1). So far no invasion of natural ecosystems has been detected at these locations.

Balanus glandula Darwin (1854)

Early descriptions of the intertidal rocky shores of the southwestern Atlantic (Olivier et al. 1966a, b; Penchaszadeh 1973) showed a zonation pattern unusual in temperate coasts: the absence of a barnacle belt. In hard substrates, whether sheltered or exposed, the small

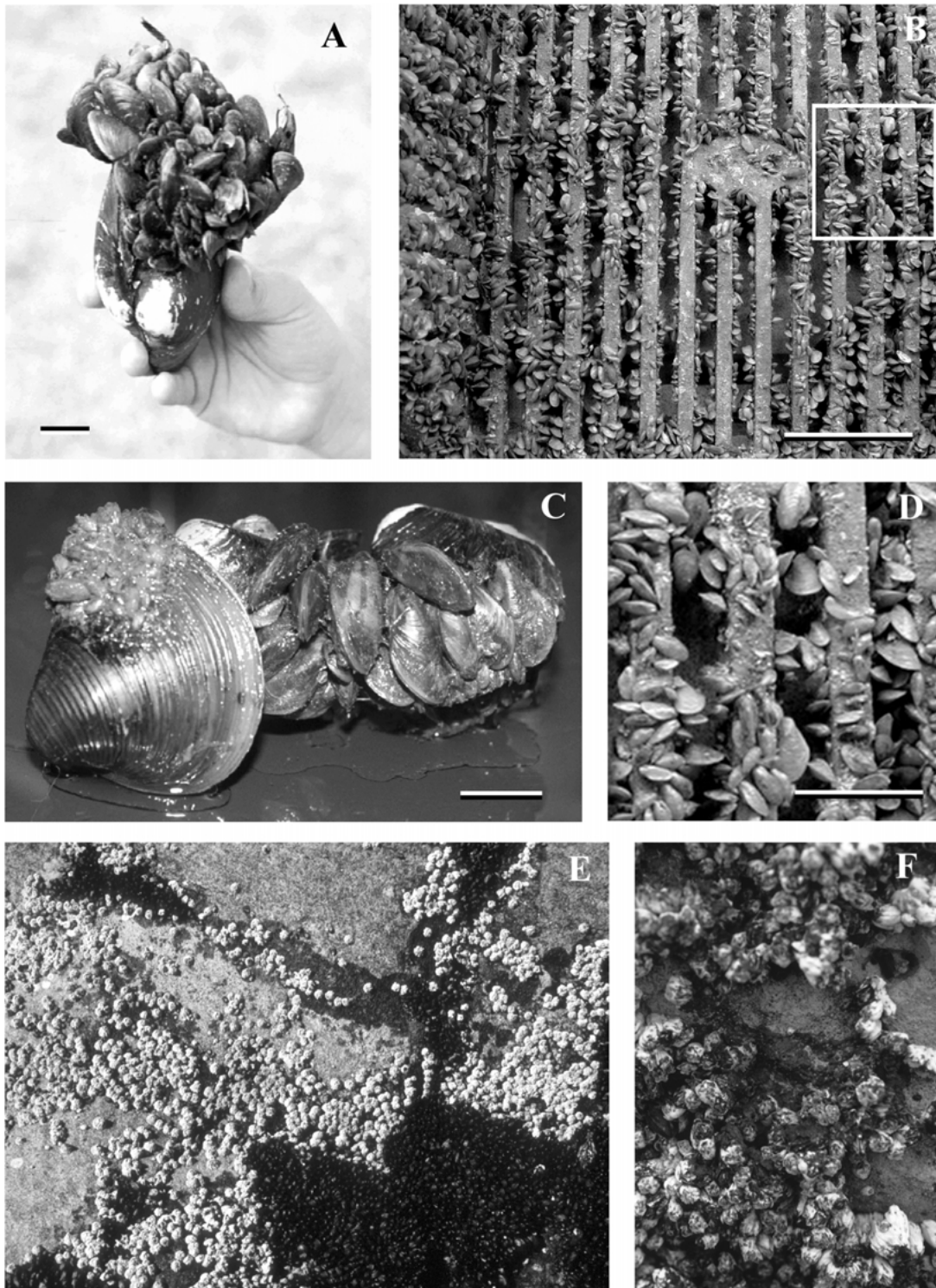


Figure 4. A–D: *Limnoperna fortunei* in La Plata River. A: mussels overgrowing a native clam *Anodontites trapesialis* (scale bar: 1 cm). B: mussels clogging a macrofouling sampler (scale bar: 5 cm). C: mussels overgrowing *Corbicula fluminea* (scale bar: 1 cm). D: Same as B, close up (scale bar: 2 cm). E–F: Belt of the barnacle *Balanus glandula* on the rocky shore of Mar del Plata. A: general view, B: detail of the contact zone with *Brachidontes rodriguezii*.

mytilids *Brachidontes rodriguezii* and *Perumytilus purpuratus* Lamarck (1819) (the first, predominant towards the northern part of the region, the second towards the south) monopolized space in most of the intertidal zone.

During the 1960s, an invasion by *Balanus amphitrite* Darwin (1854), was observed in the harbor of Mar del Plata (Bastida 1971, Figure 1), where it became dominant in the intertidal zone, alternating with degraded patches of the *B. rodriguezii*-dominated native community. By the end of the decade a second immigrant barnacle species, *Balanus glandula*, was detected on experimental plates within the harbor of Mar del Plata (Spivak and L'Hoste 1976; Bastida et al. 1980) and on adjacent rocky shores (Figures 4E–F). This second invader is native to the northeast Pacific, from Baja California to Alaska (Foster et al. 1991), where it is a prominent member of the high intertidal community along rocky shores.

In the southwestern Atlantic, *B. glandula* is now well established along all rocky shores between 37° S and 47° S. A record from Rio de Janeiro by Newman and Ross (1976), based on a personal communication by E. Spivak is incorrect; the communication referred instead to Mar del Plata. The interaction between *B. glandula* and the native intertidal mytilids appears to be complex, differing between sheltered and exposed habitats. In the latter, it tends to occupy the high intertidal zone (above the natural limit of the mussel belt; Figures 4E–F) and areas physically disturbed by episodic storms or sediment transport. The spread of this species may have been favored by winter reproduction allowing the occupation of bare substrate created by autumn-winter storms, and by the absence of invertebrate predators in the intertidal zone (at least towards the northern part of its new range) (Vallarino and Elías 1997; Elías and Vallarino 2001). Whatever the details of the pattern or the mechanisms involved, the rocky shores of the southwestern Atlantic now exhibit a well-developed barnacle belt over a range of ten degrees of latitude.

Undaria pinnatifida (Harvey) Suringar (1872)

Undaria pinnatifida is a laminarian kelp native to temperate coasts of Japan, Korea and parts of China (Akiyama and Kurogi 1982). It is an invasive species in France (Perez et al. 1981), the Mediterranean (Boudouresque et al. 1985), New Zealand (Hay and Luckens 1987), on the east coast of Tasmania (Sanderson 1990), Galicia and Asturias

(Santiago Caamaño et al. 1990; Salinas et al. 1996), northern Argentine Patagonia (Piriz and Casas 1994), the Venice lagoon (Curiel et al. 1994), the south coast of England (Fletcher and Manfredi 1995), Australia (Campbell and Burridge 1998), Belgium and The Netherlands (Dumoulin and De Blauwe 1999; Stegenga 1999).

It was recorded for the first time in Argentina in December 1992 (Piriz and Casas 1994). The first plants were found attached to wharf piles in Puerto Madryn (Figure 1), suggesting that the most likely vector of introduction was the ballast water or fouling of cargo ships or fishing vessels arriving to Nuevo Gulf from Japan or Korea. About eight years later, its range has expanded 20 km to the north and 18 km to the south of the introduction site, occupying both artificial and natural substrates. *Undaria pinnatifida* is the only Laminarian kelp there; the indigenous phytobenthos is composed of comparatively small seaweeds, like *Codium*, *Dictyota*, *Ulva*, *Anotrichium* and *Ceramium*.

Although sporophytes are present all year round, they are most abundant and become fertile by the end of winter. In spring, when they attain their maximal development, they can exceed a meter in height. The crowded sporophytes are anchored by their conspicuous holdfasts, which overlap and entangle with each other, covering the original vegetation; their wide blades form a canopy that produces significant shading on the bottom. The seascape in those sites has changed dramatically; a situation that will reoccur in other places where *Undaria* populations develop. *Undaria pinnatifida* is now regularly found among seaweeds cast ashore along the beaches of Puerto Madryn city. Large dislodged thalli are pulled by the tides disturbing the bottom and benthic communities along their track. *Undaria* also constitutes a new potential food source for local grazers, like the gastropod *Tegula patagonica* d'Orbigny (1835) and the sea urchins *Arbacia dufresnii* Blainville (1825) and *Pseudechinus magellanicus* Philippi (1857).

By late 1999, it was found in Caleta Malaspina (Figure 1), about 500 km from Puerto Madryn. Here it poses a serious threat, as it could compete with native seaweeds of economical significance, like *Gracilaria gracilis* (Stakhouse) Steentoft, Irvine and Farnham (1995), *Gigartina skottsbergi* Setchell and Gardner (1937), and *Macrocystis pyrifera* (Linnaeus) C. Agardh (1820).

Ships leaving Puerto Madryn transport ballast water in their empty holds. Even though legislation to prevent

bioinvasions via ballast water does exist in Argentina, it is seldom enforced. Seawater temperatures in many Argentine coastal locations match those reported as optimal for its development well, thus creating a scenario that may facilitate its spread. Recreational and artisanal fishing boats often commute between the Nuevo and San José Gulfs. The latter being a marine park of great ecological and economic significance, strict controls and education of the public are urgently needed to prevent an impending ecological disaster. Once established, eradication of populations seems impracticable: if just the large sporophytes (the most visible stage) were targeted, only half of the problem would be attacked. *Undaria* constitutes a potential economic resource as human food, and so commercial harvesting could have some merit as part of a control strategy.

To our best knowledge, this is the only documented case of exotic macroalgae introduction in the southwestern Atlantic.

Spartina anglica Hubbard (1968)

The origins of this species are convoluted. After the accidental introduction of *S. alterniflora* Loisel. (1807), to England (with ship ballast), the latter naturally crossed with the native *S. maritima* (Curtis) Fernald (1916) (the only species of the genus that is not found in the Americas), generating the vigorous hybrid *S. × townsendii* H. and J. Groves (1881). *Spartina anglica* (a name that seems to be strictly invalid but widely accepted to identify this organism; Gray et al. 1990) is a fertile organism originating from chromosomal doubling of the sterile hybrid *S. × townsendii* (Gray et al. 1990; Briggs and Walters 1997). It has vigorous vegetative growth contrasting with poor seed production. Like many other C4 grasses, *S. anglica* does not commence canopy development until air temperature exceeds 9°C. As suggested for northwestern Europe (Marks and Mullins 1990), this fact could be the reason why its growing season is shortened in comparison with several native C3 perennial grass species.

Spartina anglica, showing high inter- and intra-population phenotypic variation, can be a pioneer species in exposed tidal flats, as well as an established one in the middle and high marsh. Highly competitive and tolerant to submergence, it can invade mudflats replacing native seagrasses and mangrove communities, eventually altering the entire native faunistic and floristic composition of a marsh (Chung 1990;

Goss-Custard and Moser 1993). In England and The Netherlands, for example, it can give origin to a dense monospecific sward by rapid lateral tussock growth, in combination with high shoot density and slow rate of establishment of the other species (Scholten and Rozema 1990). Nowadays, *S. alterniflora* is virtually extinct in England, while *S. × townsendii* is largely confined to the upper marsh zone because of competition with *S. anglica* (Gray et al. 1990; Adam 1993). However, it appears that its competitive ability is less effective on cobble beaches (Hacker et al. 2001) and sandy substrates than on finely textured ones, depending on physical variables (e.g. salinity, temperature; Davy and Costa 1992). In fact, the chances for eradication of this species seem to be modulated by the interplay between habitat physical conditions and species interactions (Hacker et al. 2001).

Spartina anglica was not included in major lists of South American *Spartina* species, starting with Brongniart (1829). It was first reported for Tierra del Fuego (Argentina, Figure 1) in 1959 as *S. × townsendii* (Parodi 1959, cited by Nicora 1978), but the date of its introduction is unknown (Nicora 1978). For many years, *S. anglica* was not included in *Spartina* species lists due to its cryptic similitude with *S. × townsendii* (e.g. Moberley 1956; Lambert 1964), this being the reason for its introduction often going unnoticed. Based on the descriptions by Parodi (1959, cited by Nicora 1978) of samples from Tierra del Fuego, Nicora (1978) revised these records, identifying the species as *S. anglica*. No other record has been reported for Argentina, Uruguay or Brazil, where at least three other *Spartina* species (*S. alterniflora*, *S. ciliata* Brongn. (1829), and *S. densiflora* Brongn. (1829)) and a hybrid (*S. longispica* Hauman and Parodi et St. Yves (1932); but see Parodi 1937) are known to occur (West 1977; Cabrera and Zardini 1978; Costa and Davy 1992). The most recent catalogue of the Poaceae of Argentina (Zuloaga et al. 1994) does not include *S. anglica*.

Considering its area of origin (i.e. UK), it is possible that *S. anglica* were intentionally introduced to the SW Atlantic in the Malvinas (Falklands) Islands (Figure 1), later dispersing into Tierra del Fuego (southern Argentina). It was planted and sporadically cultivated to favor coastline stabilization in Tierra del Fuego (Nicora 1978). Worldwide, the ecological consequences of its spread have been significant (e.g. Gray et al. 1990, Hacker et al. 2001), and control as well as

eradication, rather than further planting, have been the concern of managing authorities in recent years (Adam 1993, Hacker et al. 2001). Despite the dramatic ecological impact that this species could have in the short term within native saltmarshes, little to no attention has been directed to confirm its present distribution in the SW Atlantic.

Overview

Earlier we discussed the six exotic species that are most significant in terms of their present or future ecological impact in the southwestern Atlantic (Figure 2). Given the scarcity of local studies pertaining to their ecological effects, it is difficult to predict their future impacts. Yet, *Crassostrea gigas*, *Balanus glandula*, *Undaria pinnatifida* and *Limnoperna fortunei* are likely to continue spreading along the coast, modifying the local benthic communities at an even larger scale. The knowledge of the ecological effects of *Spartina anglica* is poor and no field surveys were done in order to study its biology. *Ficopomatus enigmaticus* is the best-studied case. Even though this species is not currently spreading its range along the coast, their reefs chronically alter the sedimentary dynamics and ecological interactions in a unique environment, designated by UNESCO as a MAB site. Could any of these invasions have been predicted? Ecologists that described patterns of ecological zonation in the rocky intertidal of the region during the 1960s noticed the absence of a barnacle belt (Olivier et al. 1966a, b), a common feature along other temperate coasts of the World. They could have hypothesized about the likelihood of a barnacle invasion. In retrospect, the expansion of *Crassostrea* in Bahia San Blas, once introduced, was also a reasonable prediction, based on experience from other regions. In these and other cases, some knowledge of the pre-invasion conditions is required to generate workable hypotheses. Our review points in that direction.

Summary and conclusions

Our survey of recorded invasions of the southwestern Atlantic by exotic species, the first of its nature for this region, had results unexpected to us at the onset of the project. Most coastal ecosystems between the La Plata River estuary and Golfo Nuevo (Figure 2) have already been modified, or are expected to be so in the short term. A barnacle (*Balanus glandula*) belt has developed on

all rocky shores where none was present 30 years ago, a macro-fouler (*Limnoperna fortunei*) and a reef-builder (*Ficopomatus enigmaticus*) have strongly modified estuarine ecosystems, Pacific oyster (*Crassostrea gigas*) reefs are expanding in shallow bays at a fast rate, and kelp (*Undaria pinnatifida*) is rapidly modifying nearshore benthic communities along the coasts of central Patagonia. At this point, it is uncertain how many of the cordgrasses (*Spartina* spp.) found in coastal salt marshes correspond to exotic forms. Only exposed sandy beaches appear to be free from the pervasive ecological impact of invasion by exotic species.

Besides, a substantial list of exotics was compiled (Table 1) and there are many more candidates for that status (Table 2). If we considered that our survey included a wide latitudinal range (ca. 20°), the abundance of exotic species in our coastal systems ($n = 31$) is relatively low if compared to other well-studied areas. As an example, the highly invaded San Francisco Bay estuary has 150 exotic species in saltwater (excluding fishes and protozoans; Cohen and Carlton 1998), while the Chesapeake Bay has 180 exotic species (excluding fishes, birds and mammals; Ruiz et al. 1999) and within North America, 255 (Ruiz et al. 2000). This contrast could reflect the fact that the southwestern Atlantic has been little studied, or simply that it has been less exposed to invasions due to the lower intensity of maritime transportation. Attending to the geographic distribution of references (Introduction, Figure 1), and taking frequencies in our sample of 344 references as an index, the ratio of introduced species to references in the sample is 31/1 (31) for the southwestern Atlantic. The respective ratios for the West, East and Gulf coasts of North America (counts of non-indigenous species from Ruiz et al. 2000, p. 494) are 187/89 (2.1), 108/59 (1.8) and 7/10 (0.7). The higher the value of the ratio, the lesser the attention given to non-indigenous species. While the three figures for North American coasts are commensurate among them (ca. 2 on average), the value for the southwest Atlantic is 15-fold larger. This is strongly indicative of bias.

Even if the number of documented exotics is comparatively small, the biodiversity tapestry of the region has been strongly altered. In many cases, it may be very difficult to ascertain the real status of a species. More consequential, it is becoming increasingly difficult to establish what the pristine condition of coastal communities was. The paucity of good descriptive,

pre-impact work aggravates this problem; the few existing antecedents (Olivier et al. 1966a, b; 1972a, b; Penchaszadeh 1973) highlight the significance of that type of studies.

The results of the survey reveal some patterns of general interest. All of the four invading animal species that have already had a significant ecological impact tend to concentrate in crowded patches and have pelagic larvae. This combination may provide conditions favorable for the rapid spread of an invading species, even if initially 'inoculated' as a small but dense clutch of reproductive individuals (this was the case for the Pacific oyster).

There are numerous ways in which exotic marine and freshwater species are introduced, generally associated with human activity. Ships are the main source of species introduction (via ballast water or fouling; Ruiz et al. 2000), but intentional translocations of species for aquaculture, food and sport activities are also important. Among the exotic species established in the southwestern Atlantic, only one (the Pacific oyster) was intentionally introduced, and two (the Pacific oyster and *Spartina anglica*) have been artificially propagated after their introduction. Most introductions were accidental, most likely associated with fouled objects or ballast water discharges. Although Argentina has regulations regarding the latter, they are not strictly enforced. It is still not well understood that once awareness has been raised, what were accidents in the past, in fact become choices in the future. We hope that our compilation will assist in the implementation of more proactive policies. Reactive policies are of little use, as the invasion by a marine exotic is an asymmetric process: once established, its extirpation is, as a rule, impossible. Yet, introduced species may be manageable in some cases. The development of markets of potentially usable species (for example, *Undaria* or the Pacific oyster) may be part of control strategies.

Prevention and control are particularly important in the case of ecologically sensitive areas. The best regional example is San José Gulf, north of Valdés Peninsula, a major calving ground for southern right whales and the first marine protected area of the Argentine coast, recently classified by UNESCO as part of the World's Heritage. Preserving it in its pristine condition is a well-established societal goal. Yet, coastal rocky shores have already been invaded by *Balanus glandula*, and the arrival of *Undaria* is most likely just a matter of time. Opposite to the better understood problem of chemical contamination, 'species

contamination' does not gradually vanish following a contamination event, rather, it tends to increase and propagate as time passes (Westbrooks 2000).

As a closing recommendation, it is important that scientists and scientific agencies in the region understand the urgency of research on systematics and biogeography. The biodiversity of the southwestern Atlantic (particularly its warm-temperate sector) is among the least known in the world. Given that circumstance, the detection, prevention and control of biological invasions by exotic species may become virtually impossible: no one will be able to even read the winning combinations in the 'biological roulette' (Carlton and Geller 1993). If there is a general lesson to be learned from our scrutiny of introduced species in the southwestern Atlantic, it is that many areas of the World currently perceived as relatively pristine may be already altered by biological invasions.

Acknowledgements

The authors thank the following institutions and programs for support during the development of this project: Pew Marine Conservation Collaborative Project (Lobo Orensanz); CIC (Buenos Aires, Argentina), and Fundacion Antorchas scholarship program (Evan Schwindt); Fundación Antorchas, CONICET (Argentina) and the Andrew Mellon Foundation (Alejandro Bortolus); CONICET (Juan López Gappa); Dirección Nacional de Recursos Acuáticos (ex INAPE), Uruguay (Fabrizio Scarabino). We thank the organizers of the 4th Jornadas Argentinas de Ciencias del Mar (Puerto Madryn, 11–15 September 2000) for providing the context that made possible the inception of this collaborative project. Comments made by D. Vázquez, J. T. Carlton and three anonymous reviewers greatly improved the manuscript. Finally, we thank D. Vázquez, R. Aragón and J. T. Carlton for inviting us to participate in this special issue of the journal.

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