

## Cold, warm, temperate and brackish: Bivalve biodiversity in a complex oceanographic scenario (Uruguay, southwestern Atlantic)\*

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**Abstract:** The temperate zone of the southwestern Atlantic Ocean (23–42°S), which includes the Patagonian Shelf Large Marine Ecosystem and the Subtropical Convergence Zone, is one of the most productive areas of the Southern Hemisphere. Key features of this region are a wide continental shelf, the convergence of cold and warm currents, and continental freshwater input of the La Plata River. The Uruguayan marine and estuarine waters are at the core of this zone. The marine and estuarine bivalve fauna of Uruguay has received good attention since the publication of the *Voyage* of Alcide d’Orbigny (1834–1846). Here we provide an overview of taxonomic, faunistic and biogeographic issues, identifying knowledge gaps and highlighting priorities for future research. The main threats for that fauna are discussed, with emphasis on species of current or potential socioeconomic interest. Of the 231 species reported from the area, only four species are strictly estuarine: *Erodona mactroides* Bosc, 1801, *Tagelus plebeius* (Lightfoot, 1786), *Brachidontes darwinianus* (d’Orbigny, 1842) and *Mytella charruana* (d’Orbigny, 1842). All of these have large biomasses, as is also the case for the marine euhaline *Macra isabelleana* d’Orbigny, 1846. A total of 112 deep-sea species (*i.e.*, living deeper than 200 m) are recorded for the region, including almost every known group occurring elsewhere in deep-sea basins, with the exception of sunken wood associated species. Of these, 38 have been recorded only from the Argentine Basin. Some new records are preliminarily reported and discussed, including *Acharax* Dall, 1908 (Solemyidae), *Lucinoma* Dall, 1901, *Graecina* Cosel, 2006 (Lucinidae), and *Callogonia* Dall, 1889 (Vesicomidae), all from the continental slope. A total of 19 warm and warm/temperate bivalve species have their southern distribution boundary in Uruguayan waters associated to warm waters of/or derived from the Brazil Current, including species distributed from the U.S.A. to Uruguay or from southeast Brazil to Uruguay. On the other hand, at least eight exclusively cold-water bivalves exhibit their northernmost distribution boundary off La Plata River; their occurrence there is associated with offshore sub-Antarctic waters. Uruguayan waters represent a critical biogeographical and ecological crossroads because of the complex interaction of currents and water masses. This region is thus particularly well suited as a system for the study of processes underlying biodiversity patterns. Pending challenges in taxonomic and biogeographic research will be successfully addressed only if multinational collaborative initiatives are undertaken in a framework of integrative taxonomy.

**Keywords:** La Plata River, estuary, shelf, deep-sea, biogeography

The temperate zone of the Southwestern Atlantic Ocean (23–42°S), which includes the Patagonian Shelf Large Marine Ecosystem and the Subtropical Convergence Zone, is one of

the most productive areas of the Southern Hemisphere. Key features of this region are a wide continental shelf, the convergence of cold and warm currents, and the continental

\* From the Symposium “Bivalvia of the Americas” presented at the 79th Annual Meeting of the American Malacological Society, in conjunction with the Society of Malacology of Mexico, the Latinoamerican Society of Malacology, and the Western Society of Malacologists on June 24–25, 2014 in Mexico City, Mexico. Symposium manuscripts were reviewed and accepted by the Symposium Co-Organizer and Guest Editor, Dr. Diego Zelaya.

freshwater input of the La Plata River (e.g., Bisbal 1995, Acha *et al.* 2004, Piola 2008). Their interaction during millions of years, at least since the Miocene, shaped the biogeography of a region that includes endemic temperate components as well as elements of tropical, subtropical and subantarctic origins (e.g., Carranza *et al.* 2008). The core of this zone (ca. 34°–36° S) has been the center stage of that scenario and matches the Uruguayan marine and estuarine waters (e.g., Palacio 1982 and references therein). Bivalves are major, yet understudied players, well exemplified by large stocks of mytilids, pectinids, mactroideans and venerids (e.g., Penchaszadeh 1979, Orensanz 1986, Walossek 1991, McLachlan *et al.* 1996, Gutiérrez and Defeo 2003, F. Scarabino *et al.* 2006, Morsan 2007, Carranza *et al.* 2009 and references therein). However, most of the information about this fauna, especially when considering non-edible species, remains scarcely documented (e.g., F. Scarabino 2006 and Miloslavich *et al.* 2011).

The marine and estuarine bivalve fauna of Uruguay has received attention since the times of the *Voyage dans l'Amérique Méridionale* (d'Orbigny, 1834–1847). Other outstanding malacologists such as E. A. Smith (1885), H. A. Pilsbry (1897), H. von Ihering (1907), W. H. Dall (1916) and W. H. Marshall (1928), contributed the basis of the current faunistic knowledge. Many of those studies benefitted from the collaboration of the local naturalist F. Felippone. Subsequently, the Argentinean malacologists A. Carcelles (1939, 1941, 1947) and M. Doello-Jurado (1949, 1951) described and discussed several species collected in Uruguayan waters. Almost with the only exception of the catalogue compiled by A. Formica-Corsi (1900–1901), which represents the earliest effort in a Latin-American country to catalogue the entire molluscan fauna, “native” malacology started in the 1950s. Since then, the Uruguayan malacologists L. P. Barattini, M. A. Klappenbach and A. Figueiras (sometimes in collaboration with E. H. Ureta, O. E. Sicardi and V. Scarabino) reported many other species (e.g., Barattini 1951, Barattini and Ureta 1961, Klappenbach 1967, 1968, 1970a, Figueiras 1962, Figueiras and Sicardi 1969, 1980). Klappenbach described several new species (e.g., Klappenbach 1963, 1970b, Klappenbach and V. Scarabino 1969), all still valid. Figueiras and Sicardi (1980) listed most species known to that date from Uruguayan waters, while F. Scarabino (2003) listed all the bivalve species recorded from Uruguayan waters. F. Scarabino *et al.* (2006) provided an updated synthesis on bivalve diversity from the coastline and the inner shelf (down to 50 m depth) and F. Scarabino and Zaffaroni (2004) discussed several species previously reported for that area. To date, there is not a synthesis of the bivalve fauna from the Uruguayan outer shelf (50–200 m). More recently, several Brazilian and Argentinean authors started the revision of southwestern Atlantic bivalves, including material from Uruguayan waters (e.g., Signorelli and Pastorino 2012, Pimenta and Oliveira 2013).

In a series of publications initiated in 1973, J. A. Allen and co-workers (Sanders and Allen 1973, 1977, 1985, Allen and Turner 1974, Oliver and Allen 1980, Allen and Morgan 1981, Allen and Sanders 1982, Allen and Hannah 1989, Payne and Allen 1991, Rhind and Allen 1992, Allen *et al.* 1995, Allen 1998, 2000a, 2000b, 2001, 2004) studied the bivalves collected in deep waters off Uruguay (200 to 5,500 m depth, slope and Argentine Basin) by the R/V *Atlantis II* (1971). Results from those studies were synthesized by Allen and Sanders (1997) and Allen (2008), which also included preliminary records of some previously untreated groups.

This review synthesizes published and unpublished data on marine and estuarine bivalves of Uruguay. Some new records are preliminarily reported and discussed. The current or potential socioeconomic interest of bivalve resources is briefly reviewed. Finally, priorities for future research are identified and highlighted.

## MATERIALS AND METHODS

### Study Area

The area considered includes [i] the Uruguayan coastline influenced by marine waters (Fig. 1), [ii] territorial waters of the La Plata River and inner shelf, [iii] and the Uruguayan Economic Exclusive Zone (UEEZ, Figs. 1 and 2), that extends 200 nautical miles off the Uruguayan coastline. One sampling site that falls some miles outside this zone (station 242 from Cruise 60 of the R/V *Atlantis II*) is included considering the forthcoming enlargement of the UEEZ.

The Uruguayan marine and estuarine coastlines (ca. 500 km, between ca. 33°40'S and 35°S) include sandy beaches interrupted by streams and coastal lagoons (without mangroves) and rocky (mainly metamorphic and igneous) outcrops forming capes. Besides the Port of Montevideo, which is situated in the estuary of the La Plata River and is the largest in the country, a couple of smaller harbors (Punta del Este, La Paloma) are located on the marine coast (Jackson 1988; Fig. 1).

An extended inner shelf (ca. 60 nautical miles wide, Fig. 2) is sedimentologically heterogeneous, with mostly muddy and sandy/shelly deposits and a few, poorly known, rocky outcrops. The outer shelf (> 50 m depth) includes mainly sandy and muddy sand bottoms with very scattered and poorly known rocky outcrops and mounds, which constitute the substrate for colonies of the scleractinian *Lophelia pertusa* (Martins and Corrêa 1996, Carranza *et al.* 2012). The latter occurs mostly in the upper slope, where terraces with muddy deposits and canyons with coarse materials are also observed (Franco-Fraguas *et al.* 2014). Bottoms of the lower slope and abyssal plain of the Argentine Basin are typically composed of mud deposits (Petschik *et al.* 1996).



**Figure 1.** Uruguayan coastline. Marine intrusion can reach up to San José coast. Stars indicates the Port of Montevideo and the Port of La Paloma.

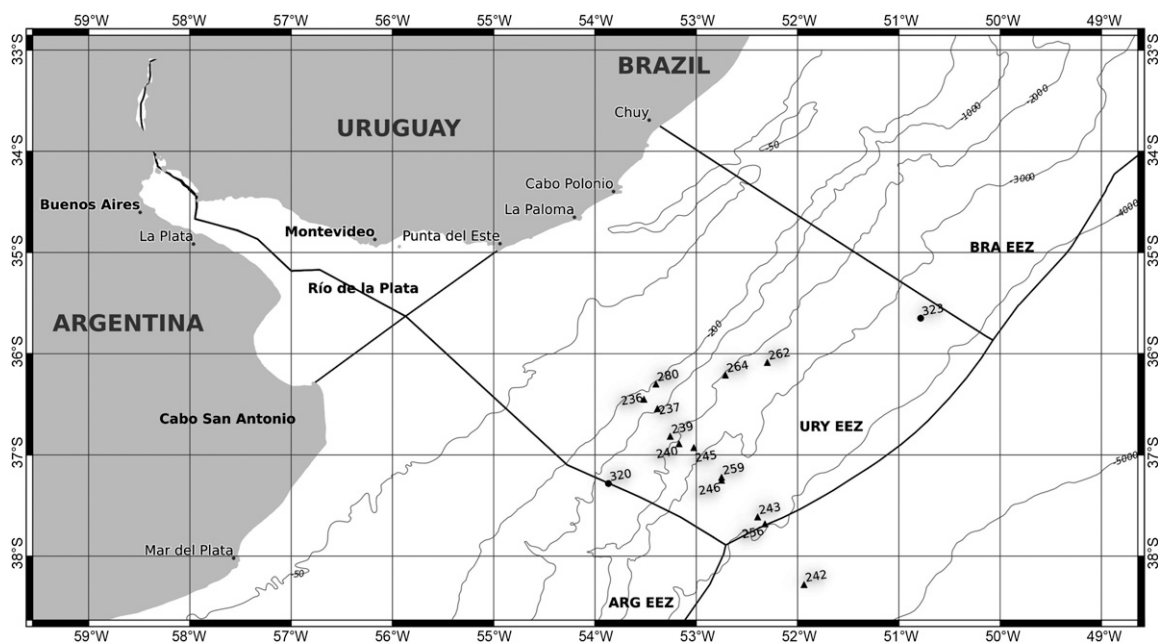
Circulation is complex due to the confluence of warm and cold marine currents, and the freshwater input from the La Plata River estuary (Fig. 3). The warm waters of the Brazil Current (formed by Tropical and South Atlantic Central Waters) flows southwards along the Brazilian and Uruguayan shelf up to 33–36°S, where it turns eastward and converges at about 38°S with the cold northward-flowing Malvinas Current that transports Subantarctic Waters at surface (Saraceno *et al.* 2004), originating the Convergence Zone (Gordon and Greengrove 1986) (Fig. 3). The whole area is characterized by steep fronts in upper waters (< 500 m) (Acha *et al.* 2004, Ortega and Martínez 2007), also influenced by the bottom topography (Franco-Fraguas *et al.* 2014). One of these fronts is formed when Subantarctic Shelf Water and Subtropical Shelf Water converge, generating the Subtropical Shelf Front that can be regarded as an extension of the Malvinas-Brazil Confluence over the shelf (Piola *et al.* 2000) (Fig. 3).

The seasonal cycle of the local wind regime, continental freshwater discharge (mainly from the La Plata River; Ciotti *et al.* 1995, Lima *et al.* 1996, Guerrero *et al.* 1997, Garcia 1998), and migration of the Convergence Zone (Ciotti *et al.* 1995) determine a predominance of cold waters derived from the Malvinas Current during (roughly) winter and warm waters from the Brazil Current during (roughly) the summer

(Lima *et al.* 1996, Garcia 1998, Ortega and Martínez 2007). Although there is a distinct seasonality in the temperature regime in Uruguayan waters, the E and NE areas (depth > 100 m, between ca. 34°30'S–36°S) are influenced by warm waters from Brazil Current permanently (Guerrero *et al.* 2010) (Fig. 3, grey circle).

Diluted waters (salinity < 33.2) dominate the shallow coastal area (< 50 m) but can also be transported offshore and produce a buoyant freshwater layer under extreme continental discharge conditions (Franco-Fraguas *et al.* 2014). This is related to annual changes in the precipitation regime, generally associated with El Niño Southern Oscillation (ENSO) (Cazes-Boezio *et al.* 2003) that modulate interannual variations in precipitation and freshwater discharge.

The upper layer (0–500 m), including the outer continental shelf and slope, is characterized by the occurrence of Tropical Water, Subantarctic Water and South Atlantic Central Water (Ortega and Martínez 2007) (Fig. 4). Temperature of the upper layer can exceed 20 °C (Tropical Water; Emilson 1961, Thomsen 1962) at the surface, and be close to 4 °C near the bottom over the shelf and slope, down ca. 500 m (Subantarctic Water; Thomsen 1962) while the South Atlantic Central Water register temperatures between 18 and 5°C (Emery 2001). Between ca. 500–1,500 m cold waters (2–6 °C) correspond to Antarctic Intermediate Water



**Figure 2.** Uruguayan Economic Exclusive Zone (URY EEZ), indicating the position of the stations sampled by the HMS *Challenger* (circle) and R/V *Atlantis II* (triangle).

(Tomczak and Godfrey 1994). From 1500 m to the abyssal plain, deep and near-bottom waters include Upper Circumpolar Deep Water; North Atlantic Deep Water, Lower Circumpolar Deep Water (Stramma and England 1999, Piola and Matano 2001) and Antarctic Bottom Water (Tomczak and Godfrey 1994) (Fig. 4), where temperature ranges between 1.7 and -0.9 °C (Emery 2001).

### Sources of Information

Sources of information for this study come from new samples obtained from the study area and a compilation of all available literature. Samples collected from 1997 to 2014 on board of the R/V *Aldebaran* (DINARA, Dirección Nacional de Recursos Acuáticos) include more than 200 dredgings (several sizes and types of Piccard and Spatangue dredges, epibenthic sledge and Agassiz trawl) and more than 250 otter-trawl hauls (Engel trawl for fisheries assessment, see Carranza *et al.* 2009) made between 3 and 250 m depth. Samples obtained by the R/V *Miguel Oliver* during a joint Spain-Uruguay campaign in 2010 consisted of 16 dredgings made between 200 and 1,000 m depth, on the Uruguayan slope using a Warén (rock) dredge. Material from these surveys is deposited in the Museo Nacional de Historia Natural (MNHNM), Montevideo, Uruguay. Many microbivalve samples have not been analyzed yet. The museum's collection harbors also abundant materials from shore collections made by members of the Sociedad Malacológica del Uruguay

between 1955 and 1980, and those obtained by us between 1993 and 2014.

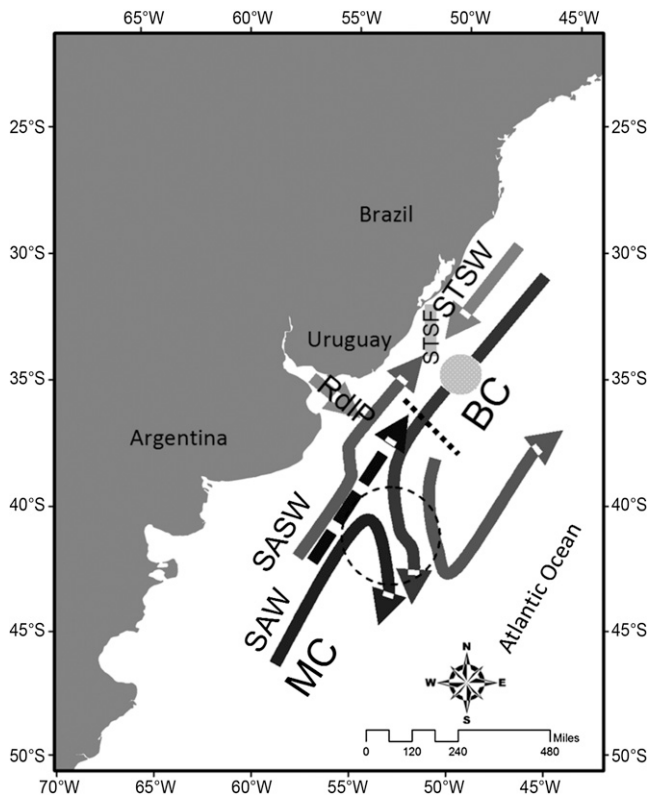
## RESULTS

### Biodiversity by major habitats or ecosystems

Based on the updated and revised published records, and the new findings reported here, the Uruguayan marine and estuarine bivalve fauna is represented by a total of 231 species, including five cryptogenic and one non-native species (Supplementary material, SM2; doi: 10.4003/006.033.0205.s1). Species only found in association with floating objects, for which there is no evidence of recruitment in Uruguayan waters, are not considered in that account. Freshwater species such as *Limnoperna fortunei* (Dunker, 1857) (Mytilidae) and *Corbicula fluminea* (Müller, 1774) (Cyrenidae), occurring in a part of the estuarine coast (part of the coast of San José and Montevideo) are also not considered. Below we consider bivalve biodiversity by major habitats or ecosystems, focusing on species that are either abundant or specially related with some depth, current or type of sediment when referring to the marine habitats.

#### Estuarine environments

Only four species are strictly estuarine: *Erodona mactroides*, *Tagelus plebeius*, *Brachidontes darwinianus* and *Mytella*



**Figure 3.** Regional circulation patterns in the Southwestern Atlantic continental shelf, slope and oceanic region, adapted from Matano *et al.* (2010) and Piola *et al.* (2000). The dotted straight line corresponds to the location of the hydrological profile showed in Figure 4. The gray circle depicts the area permanently influenced by warm water, and the dotted circle corresponds to the Malvinas-Brazil Convergence Zone; Malvinas Current (MC); Brazil Current (BC); Subantarctic Water (SAW); Subantarctic Shelf Water (SASW); Río de la Plata (RdIP); Subtropical Shelf Front (STSF); Subtropical Shelf Water (STSW).

*charruana*, while several others are marine eurihaline, as exemplified by *Mactra isabelleana*, *Pitar patagonicus* (d'Orbigny, 1842) [= *Pitar rostratus* (Koch in Philippi, 1844)], *Psammacoma uruguayensis* (E. A. Smith, 1885), *Petricolaria stellae* (Narchi, 1975), *Brachidontes rodriguezii* (d'Orbigny, 1842) and species of *Mytilus* Linnaeus, 1758 (F. Scarabino *et al.* 2006). Coastal lagoons and small estuaries are inhabited by dense populations of the brackish species *E. mactroides* and *T. plebeius*. *Erodona mactroides* also occurs in large subtidal areas of the La Plata River where the eurihaline *Mactra isabelleana* is also present in large concentrations. *Mytella charruana* and *Brachidontes darwinianus* form extensive beds in the subtidal rocky bottoms of the La Plata River estuary (F. Scarabino *et al.* 2006).

#### Coastal and shelf areas- unconsolidated substrates

Marine sandy beaches harbor intertidal populations of *Mesodesma mactroides* Reeve, 1854 and *Donax hanleyanus* Philippi, 1847, and in some cases subtidal populations of *Solen tehuelchus* Hanley, 1842, *Tivela zonaria* (Lamarck, 1818), *Amiantis purpurata* (Lamarck, 1818), *Mactra marplatensis* Doello-Jurado, 1949 and *Mactra isabelleana*. The subtidal *Donax gemmula* Morrison, 1971 only occurs during particularly warm/dry oceanographic/climatic events (Defeo *et al.* 1992, F. Scarabino *et al.* 2006 and references therein).

Inner shelf muddy bottoms are characterized by large concentrations of *Corbula patagonica* (d'Orbigny, 1845), *Pitar patagonicus* and *Ennucula uruguayensis* (E. A. Smith, 1880), but also by the recurrent presence of *Nuculana decora* (A. Adams, 1856), *Malletia subaequalis* (G. B. Sowerby II, 1870), *Psammacoma uruguayensis* and *Periploma compressum* d'Orbigny, 1846 (Cachés 1980, Layerle and V. Scarabino 1984, F. Scarabino *et al.* 2006).

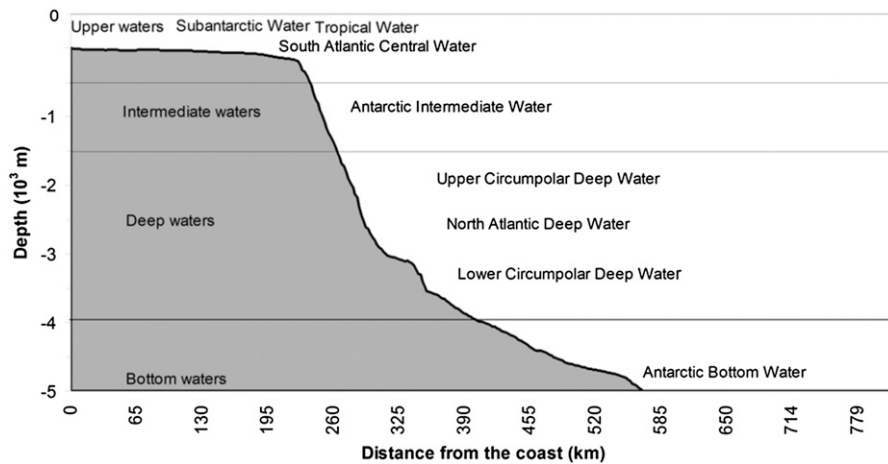
Shelly-coarse sand inner shelf bottoms are typically inhabited by *Glycymeris longior* (G. B. Sowerby I, 1833), *Semele casali* Doello-Jurado, 1949, *Eutivela isabelleana* (d'Orbigny, 1846), *Transenpitar americanus* Doello-Jurado, 1951, *Felaniella vilardeboana* (d'Orbigny, 1846), *Psammotreta brevifrons* (Say, 1834), *Corbula lyoni* Pilsbry, 1897 and *Ennucula puelcha* (d'Orbigny, 1842) (F. Scarabino *et al.* 2006 and references therein).

Fine-medium sandy inner shelf bottoms are mainly inhabited by *Tellina gibber* Ihering, 1907 and *Mactra marplatensis* Doello-Jurado, 1949, while a small to large content of mud in sandy bottoms seems to be a key factor for the presence of a more diverse community of bivalves, in some cases found in sheltered zones (bays), e.g., *Adrana patagonica* (d'Orbigny, 1845), *Raeta plicatella* (Lamarck, 1818), *Macrella janeiroensis* (E. A. Smith, 1915), *Periploma ovatum* d'Orbigny, 1846, *Phycidderma semiaspera* (Philippi, 1836), *Panopea abbreviata* Valenciennes, 1839 and *Trachycardium manueli* (Prado, 1993) (F. Scarabino *et al.* 2006).

Large beds of *Mytilus* sp. develop on muddy sand bottoms, mostly between 35 and 50 m depth, but also occur in shallower and deeper environments (Juanicó and Rodríguez-Moyano 1976, F. Scarabino *et al.* 2006; F. Scarabino pers. obs.).

*Ostrea puelchana* d'Orbigny, 1842 is widely distributed in the inner shelf, developing on small hard microsubstrates both on sandy and muddy sand bottoms (Ranson 1967, F. Scarabino *et al.* 2006, F. Scarabino, pers. obs.).

*Ptereria colymbus* (Röding, 1798) is widely distributed in the outer shelf (although not restricted there), commonly attached to one or several objects/organisms such as polychaete tubes, colonial ascidians and other bivalves (Doello-Jurado 1938, Olivier and V. Scarabino 1972, F. Scarabino *et al.* 2006, Signorelli *et al.* 2013, F. Scarabino, pers. obs.).



**Figure 4.** Hydrographic profile (dotted straight line in Figure 3) and simplified bathymetric location of different water masses present in outer continental shelf, slope and oceanic region of the Uruguayan Economic Exclusive Zone.

Species with high biomasses in the southern part of the outer shelf area are best represented by *Zygochlamys patagonica* (King, 1832) and “*Tindariopsis*” *sulculata* (King, 1832), where *Pandora braziliensis* G. B. Sowerby II, 1874 and *Cyclocardia velutina* (E. A. Smith, 1881) are also recurrent species, although displaying a low biomass (Roux and Bremec 1996, Gutiérrez and Defeo 2003, F. Scarabino pers. obs.). Species with recurrently low biomass occurring in the northern region of the outer Uruguayan shelf include *Nuculana larranagai* Klappenbach and V. Scarabino, 1969, *Dulcina* cf. *lens* (Verrill and Smith [in Verrill]), 1880, *Poromya cymata* Dall, 1890 and *Crassatella uruguayensis* E. A. Smith, 1880 (F. Scarabino pers. obs.).

#### Coastal and shelf areas- epilithic species on consolidated substrates

*Brachidontes rodriguezii* and *Mytilus* sp. form dense banks in the more saline area of the La Plata River estuary, particularly the intertidal zone. Along the Atlantic shores, *Mytilus* sp. occurs mostly subtidally, although some intertidal exposed zones are also dominated by this species (F. Scarabino *et al.* 2006; Orensanz and F. Scarabino, pers. obs.).

*Perna perna* (Linnaeus, 1758), a cryptogenic species in the southwestern Atlantic, forms large subtidal banks along the easternmost Uruguayan coast, but low abundances have been reported as south as Punta del Este. The Uruguayan coast was massively colonized by this species in the late 1950s. Afterwards, *P. perna* almost vanished between the 1970s and 1997, when there was a resurgence of new populations (Orensanz *et al.* 2002, F. Scarabino *et al.* 2006).

Other epilithics include a guild of “nesting” species such as *Sheldonella bisulcata* (Lamarck, 1809), *Paraleptopecten bavayi* (Dautzenberg, 1900), *Hiatella* sp., *Sphenia fragilis*

(H. and A. Adams, 1854), *Musculus viator* (d’Orbigny, 1842), *Entodesma patagonicum* (d’Orbigny, 1846) and, occasionally, *Modiolus carvalhoi* Klappenbach, 1966 (associated with other mytilids) (F. Scarabino *et al.* 2006, Pastorino and Bagur 2011, F. Scarabino pers. obs.).

#### Endolithic species

Mechanical borers are represented by *Petricola dactylus* G. B. Sowerby I, 1823, *Petricolaria stellae* (Petricolinae), *Cyrtopleura lanceolata* (d’Orbigny, 1841), *Pholas campechiensis* Gmelin, 1791, *Barnea lamellosa* (d’Orbigny, 1841) and *Netastoma darwinii* (G. B. Sowerby II, 1849) (Pholadidae), which live mostly in the shallow subtidal zone.

*Petricolaria stellae* is a euryhaline species, with significant populations in the outer estuarine zone of La Plata River (F. Scarabino *et al.* 2006 and references therein).

Chemical borers include *Petricola* cf. *lapicida* (Gmelin, 1791) (Petricolinae, Huber, 2010), *Lithophaga patagonica* (d’Orbigny, 1842) (Mytilidae) and *Lamychaena* cf. *hians* (Gmelin, 1791) (Gastrochaenidae) (F. Scarabino *et al.* 2006 and references therein, see also Simone *et al.* 2015).

#### Wood-borers

Wood-borers were extensively dispersed by vessels since the earliest human ocean expeditions (Carlton 1996). Wood-boring bivalves were intensively studied during the first half of the 20<sup>th</sup> century, mainly by Turner (1966), who deployed test panels around the world<sup>1</sup>. There are few studies dealing with wood borers in the southwestern Atlantic. Six species were identified in Uruguay; however, the taxonomic assignment of some of them is still uncertain. *Teredo navalis* Linnaeus, 1758 is the only species that can be clearly categorized as introduced to Uruguay. It has been observed in ship hulls, on flotsam, or in harbor test panels placed in estuarine and marine areas (Barattini 1951, V. Scarabino and Maytía 1968, Calvo 1984). Other isolated records include cryptogenic species such as *Teredo bartschi* Clapp, 1923 (Calvo 1984, in test panels), *Nausitora fusticulus* (Jeffreys, 1860) (Barattini 1951, as *Bankia brasiliensis* Bartsch, 1922, found in naval constructions), *Bankia fimbriatula* Moll and Roch, 1931 (collected in Montevideo in 1969, MCZ # 356530), and *Bankia*

<sup>1</sup> Unpublished records of species from Uruguay arising from this work are here mentioned, indicating vouchers in Museum of Comparative Zoology (MCZ), Harvard University, Massachusetts, USA.

(*Bankiella gouldi* (Bartsch, 1908) (V. Scarabino and Maytía 1968, on a floating wood; test panels in Montevideo: MCZ # 280028). *Martesia fragilis* Verrill and Bush, 1898 has only been occasionally registered on stranded floating wood (Klappenbach 1967, F. Scarabino and Zaffaroni, pers. obs.).

#### Deep-sea

There are 112 deep-sea species recorded for the study region, including almost every known group occurring elsewhere in deep-sea basins, with the exception of sunken wood associated species (SM 1; doi: 10.4003/006.033.0205.s1). Of these, 38 have been recorded only from the Argentine Basin.

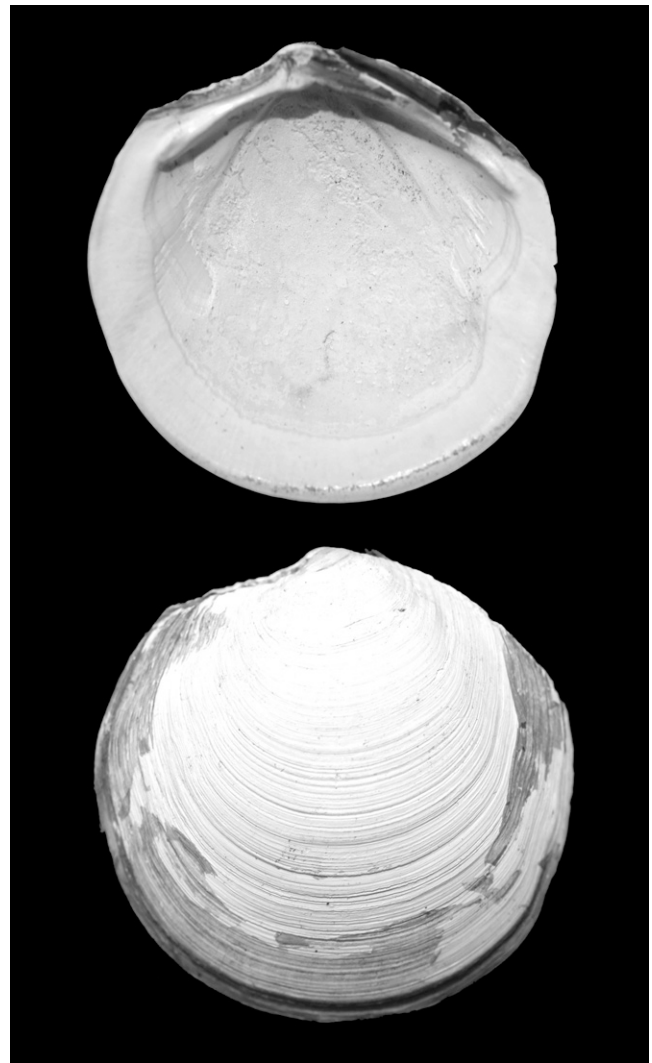
Allen and Sanders (1997) and Allen (2008) suggested a high degree of endemism for the deep-sea bivalves of the Argentine Basin. However, almost none of the described species have been compared with their Magellanic or Antarctic counterparts. This is a significant issue considering the incidence of cold sub-Antarctic and Antarctic waters off La Plata River. In fact, the only comparison along those lines, showed that *Silicula mcalesteri* Sanders and Allen, 1973 and *Silicula patagonica* (Dall, 1908) appear to be synonyms (Sanders and Allen 1973, Dell 1990, Huber 2010).

Among the materials recently collected in a locality with *Lophelia*-reefs and gas seeps, *Callogonia birmani* (Domaneschi and Lopes, 1990) (Vesicomidae) and *Graecina* sp. (Lucinidae) constitute novel additions. The first is missing from most recent assessments of vesicomids (although discussed by Huber 2010), and until now was known only from its type locality, off Paraná (25°40'S), Brazil, 400 m depth (Domaneschi and Lopes 1990).

*Graecina* sp. (Fig. 5) is recorded for the first time from the southwestern Atlantic; the genus is otherwise known from the West coast of Africa (off Angola, 360–367 m depth; *G. karinae* Cosel 2006) and the Caribbean Sea (off Colombia, 366 m depth; *G. colombiensis* Taylor and Glover, 2009) (Cosel 2006, Taylor and Glover 2009). The West African record comes from a habitat similar to the one for which Uruguayan specimens were collected.

*Lucinoma* sp. is widely distributed along the Uruguayan upper slope and, therefore, its presence in the Argentinean and southernmost Brazilian slope is almost certain. Determining the correspondence with other species known from the Magellanic region, *i.e.*, *Lucinoma lamellatum* (E. A. Smith, 1881) (Holmes *et al.* 2005) is difficult due to the great phenotypic variability among members of this genus.

*Acharax* sp. has been found in the lower slope; empty but fresh valves were recovered from the stomach content of the holocephalan *Hydrologus* sp. and entangled in the traps used for the capture of the Patagonian toothfish (*Dissostichus eleginoides*). Previous records of “*Solemya patagonica* E. A. Smith, 1885”, a species of *Acharax* (Barattini 1951, Figueiras and Sicardi 1969) from Uruguayan actually correspond to



**Figure 5.** *Graecina* sp. Uruguayan slope, R/V “Miguel Oliver” cruise URU 01/10, station 1, 35°01’S–52°16’W, 289–277 m, January 17 2010. Length: 30 mm.

*Solemya notialis* Simone, 2009 (F. Scarabino and Zaffaroni, pers. obs.).

#### Patterns of geographic distribution

A number of bivalve species have either their northernmost or southernmost distribution boundary in the Uruguayan coastline or shelf (Table 1). This accounts for the 22.5% (27 species) of the total species recorded from the shelf (120 species). This was early noticed and discussed by Doello-Jurado (1938), Olivier and V. Scarabino (1972), V. Scarabino (1977) and Maytía and V. Scarabino (1979). A total of 19 warm and warm/temperate bivalve species have their southernmost distribution boundary in Uruguayan waters, including

**Table 1.** Species that display the southernmost (S) or northernmost (N) distributional end point in Uruguayan waters. (\*): Species reported here that represent the first record; IS: inner shelf; OS: (northern/southern) outer shelf.

Species	Geographical distribution and bathymetric range	Main references for area/material/occurrence
<i>Ameghinomya antiqua</i> (King, 1832) (Veneridae)	N (Uruguay-Chile), IS and OS	F. Scarabino <i>et al.</i> (2006, isolated localities of the coast); common in areas of the southern sector of the outer shelf; MNHNM
<i>Amygdalum sagittatum</i> (Rehder, 1935) (Mytilidae)	S (U.S.A.-Uruguay), OS	Klappenbach (1975); MNHNM. Rare records from outer shelf sandy bottom.
<i>Antarctolima pygmaea</i> (Philippi, 1845) (Limidae)	N (Uruguay-Chile), OS	Living-collected material at MNHNM: infrequent in the southern sector of the outer shelf. Carcelles (1947), without indication of living/dead status; coastal record of Figueiras and Sicardi (1968) and part of the material in their collections belong to <i>Limatula cf. hendersoni</i> Olsson and McGinty, 1958. Records from southernmost Brazil (Rios 1975) either belong to odd-valves of <i>A. pygmaea</i> or living-collected specimens of <i>Limatula</i> spp. (FS, pers. obs.).
<i>Crassatella uruguayensis</i> E. A. Smith, 1880 (*) (Crassatellidae)	S (Brazil-Uruguay), OS	MNHNM (previous citations unsubstantiated, type locality in South Brazil). Infrequent in the northeastern most outer shelf.
<i>Parvilucina pectinella</i> (C. B. Adams, 1852) (Lucinidae)	S (U.S.A.-Uruguay), IS	F. Scarabino <i>et al.</i> (2006); MNHNM. Rare findings of living specimens, valves common along the Atlantic coast.
<i>Cyclocardia moniliata</i> (Dall, 1903) (Carditidae)	S (Brazil-Uruguay), OS	Güller and Zelaya (2013); MNHNM. See also under <i>C. velutina</i> . Frequent in the northeastern most outer shelf.
<i>Cyclocardia velutina</i> (E. A. Smith, 1881) (*) (Carditidae)	N (Uruguay-Chile), OS	MNHNM, frequent in the southern sector of the outer shelf. Previous report belongs to <i>C. moniliata</i> , Güller and Zelaya (2013).
<i>Donax gemmula</i> Morrison, 1971 (Donacidae)	S (Brazil-Uruguay), IS	F. Scarabino <i>et al.</i> (2006); MNHNM. Only present during particular (warm/dry) oceanographic/climatic events.
<i>Dulcina cf. lens</i> (Verrill and Smith <i>in</i> Verrill, 1880) (*) (Lucinidae)	S (U.S.A.-Uruguay), OS	Figueiras and Sicardi (1980, as <i>Myrtea</i> sp.); MNHNM. Frequent in the northeastern most outer shelf.
" <i>Epicodakia</i> " <i>falklandica</i> Dell, 1964 (Lucinidae)	N (Uruguay-Argentina), OS	Common in areas of the southern sector of the outer shelf; MNHNM
<i>Limopsis hirtella</i> Rochebrune and Mabilie, 1889 (*) (Limopsidae)	N (Uruguay-Chile), OS	MNHNM. Infrequent in the southern sector of the outer shelf.
<i>Lunarca ovalis</i> (Bruguère, 1789) (Arcidae)	S (U.S.A.-Uruguay), IS	F. Scarabino <i>et al.</i> (2006); MNHNM. Isolated specimens in the easternmost coast (Rocha).
<i>Modiolus carvalhoi</i> Klappenbach, 1966 (Mytilidae)	S (Brazil-Uruguay), IS	Zaffaroni (2000), F. Scarabino <i>et al.</i> (2006), Carranza and Borthagaray (2009). Isolated specimens in the easternmost coast (Rocha).
<i>Nuculana larranagai</i> Klappenbach and V. Scarabino, 1969 (Nuculanidae)	S (Brazil-Uruguay), OS	Klappenbach and V. Scarabino (1969); MNHNM. Common in the northeastern most outer shelf.
<i>Paraleptopecten bavayi</i> (Dautzenberg, 1900) (Pectinidae)	S (Caribbean-Uruguay), IS	Klappenbach (1970a), F. Scarabino <i>et al.</i> (2006); MNHNM. Infrequent species in subtidal rocky substrata along the Atlantic coast (Maldonado and Rocha).
<i>Perna perna</i> (Linnaeus, 1758) (Mytilidae)	S (Brazil-Uruguay), IS	Amaro-Padilla (1965), Orensanz <i>et al.</i> (2002), F. Scarabino <i>et al.</i> (2006), Carranza and Borthagaray (2009); MNHNM. Common species in subtidal rocky substrata all along the Atlantic coast (Maldonado and Rocha) but especially in the easternmost part (Rocha).
<i>Pholas campechiensis</i> Gmelin, 1791 (Pholadidae)	S, (U.S.A.-Uruguay), IS	Klappenbach (1967), F. Scarabino <i>et al.</i> (2006); MNHNM. Frequent along the Atlantic coast down to Maldonado Bay.



**Table 1.** (Continued)

Species	Geographical distribution and bathymetric range	Main references for area/material/occurrence
<i>Poromya cymata</i> Dall, 1890(*) (Poromyidae)	S (Brazil-Uruguay), OS	Figueiras and Sicardi (1980, as <i>Poromya</i> sp.); MNHNM. Frequent in the northeastern most outer shelf.
<i>Retrotapes exalbida</i> (Dillwyn, 1817) (Veneridae)	N (Uruguay-Chile), OS	Figueiras and Sicardi (1980). Frequent odd isolated valves with ligament (only a small paired valves) in areas of the southern sector of the outer shelf; MNHNM
<i>Scissula sandix</i> (Boss, 1968)	S (Caribbean-Uruguay), IS	F. Scarabino <i>et al.</i> (2006); MNHNM. Infrequent in the easternmost coast (Rocha).
<i>Semele martinii</i> (Reeve, 1853)	S (Brazil-Uruguay), IS	Klappenbach (1968), F. Scarabino <i>et al.</i> (2006); MNHNM. Isolated worn valves and unique findings of fresh valve/living specimen.
<i>Sheldonella bisulcata</i> (Lamarck, 1819)	S (U.S.A.-Uruguay), IS	F. Scarabino <i>et al.</i> (2006); MNHNM. Common species in subtidal rocky substrata along the Atlantic coast (Maldonado and Rocha).
“ <i>Tindariopsis</i> ” <i>sulculata</i> (Gould, 1852)	N (Uruguay-Chile), OS	Roux and Bremec (1996); MNHNM. Material from Rio Grande do Sul (Brazil) consists in eroded valves (FS, pers. obs.). Dominant species in wide areas of the southern sector of the outer shelf.
<i>Tivela zonaria</i> (Lamarck, 1818)	S (Brazil-Uruguay), IS	F. Scarabino <i>et al.</i> (2006); MNHNM. Common in the easternmost coast (Rocha).
<i>Warrana besnardi</i> (Klappenbach, 1963)	S (Brazil-Uruguay), IS	Layerle and V. Scarabino (1984), F. Scarabino <i>et al.</i> (2006); MNHNM. Valves and living records in the easternmost coast (Rocha).
<i>Zygochlamys patagonica</i> (King, 1832)	N (Uruguay-Chile), OS	Lasta and Zampati (1981), Walossek (1991), Defeo and Brazeiro (1995), Gutiérrez and Defeo (2003), MNHNM. Dominant species in wide areas of the southern sector of the outer shelf.

species distributed from the U.S.A., the Caribbean or from southern Brazil to Uruguay (Table 1). On the other hand, at least eight exclusively cold-water bivalves (including *e.g.*, *Zygochlamys patagonica*, “*Tindariopsis*” *sulculata*, *Cyclocardia velutina* and *Limopsis hirtella* Rochebrune and Mabilie, 1889) exhibit their northernmost distribution boundary off La Plata River; their occurrence there is associated with offshore sub-Antarctic waters. The submergence of these and other Magellanic species off Buenos Aires Province (Argentina) and Uruguay has been documented; some of them being observed in bathyal depths off Uruguay (*e.g.*, Doello-Jurado 1918, C. Monniot and F. Monniot 1983, Carranza *et al.* 2007, 2008, F. Scarabino, pers. obs.).

Several authors have suggested that low salinity and sedimentary input from the La Plata River estuary impose a biogeographic barrier to the distribution of warm, warm/temperate and cold water species (*e.g.*, V. Scarabino 1977, Escofet *et al.* 1979, Maytía and V. Scarabino 1979, Walossek 1991). However, the bottom salinity off La Plata River is not significantly affected even during periods of extreme outflow, *e.g.*, during the El Niño Southern Oscillation warm phase.

Even then, when a buoyant subsuperficial plume of low salinity water could be observed even near the shelf break, near-bottom salinity remains unaffected (Ortega and Martínez 2007, Franco-Fraguas *et al.* 2014). Moreover, the flow of the La Plata River is considerably lowered during dry seasons/periods, which often match with a stronger influence of oceanic warm waters in the coastal zone, allowing/enhancing the sporadic recruitment of warm and warm/temperate species south of the La Plata River (Orensanz *et al.* 2002 and references therein). On the other hand, exceptionally cold oceanographic events also allow northwards dispersion (and even recruitment) of cold water species, as reported by F. Scarabino and Ortega (2004) for *Aulacomya atra* (Molina, 1782).

In a well-documented case, Gutiérrez *et al.* (2008, and references therein) concluded that the northernmost distribution boundary of *Zygochlamys patagonica* (off La Plata River) could be explained by a combination of environmental factors that include: 1) temperatures higher than 9°C (above species tolerance limit, associated with the influence of the Subtropical Water in the Brazil-Malvinas/Falklands Confluence), and 2) food availability (reflected by low

concentrations of chlorophyll). Such environmental windows are likely to constrain the range of other bivalves as well. The prevailing, stressful environmental conditions at the northern edge of the Patagonian scallop range of distribution caused poor and irregular recruitment, low growth rate and high natural mortality, thus suggesting that scallop beds in Uruguayan waters are disjoint “sink” subpopulations (*sensu* Orensanz and Jamieson 1998), connected through pelagic larvae dispersal within a larger metapopulation extending to the south (Gutiérrez and Defeo 2003).

Several warm and warm/temperate species occur along the coast and inner shelf from the U.S.A. or the Caribbean to Golfo San Matías (*e.g.*, *Musculus viator*, *Plicatula gibbosa* Lamarck, 1801, *Pododesmus rudis* (Broderip, 1834) and *Semele proficua* (Pulteney, 1799)), while the distributional range of others stretches from Espírito Santo, Brazil (22°–23°S) to San Matías/Nuevo Gulfs, Argentina (42°–43°S) (*e.g.*, *Macra isabelleana*, *Lithophaga patagonica*, *Barnea lamellosa*). A very low number of cold/temperate species distributed through the coastal and inner shelf from Patagonia reach the southernmost Brazilian coast/Uruguay (*e.g.*, *Netastoma darwinii*, *Petricola dactylus*). Ihering (1907), who strongly influenced South American malacology, recognized the potential importance of the freshwater input of both Amazonas and La Plata River, but also suggested that it would not have a significant impact on the distribution of tropical species. On the contrary, he argued that most cold water species exhibited their distribution boundary at the empties of the Negro River (Gulf of San Matías) and La Plata River.

## DISCUSSION

### Knowledge gaps

#### Taxonomy

Problems concerning Uruguayan bivalve taxonomy are similar to those posed by the fauna from southern Brazil and northern Argentina, and the worldwide issues discussed by Bieler *et al.* (2013). Even the large sized or abundant species found in shallow waters of this region exhibit unaddressed alpha-taxonomy problems, and although some cases have been recently addressed (*e.g.*, Signorelli and F. Scarabino 2010; Trovant *et al.* 2013) these studies (at present) just cover a minor proportion of the total number of species. The clearest example is offered by *Mytilus*, well studied on the southeast Pacific (Chile) but not in the southwestern Atlantic (Uruguay and Argentina). While often referred to as *Mytilus edulis* Linnaeus, 1758 or *Mytilus edulis platensis* d'Orbigny, 1846, its taxonomic status and the eventual genetic correlates of well-differentiated phenotypes (F. Scarabino *et al.* 2006) are still unresolved.

Not a single species occurring in Uruguayan waters has been tested to detect possible cryptic species using molecular information (F. Scarabino *et al.* 2006). Additionally, the tendency to identify species from the South Hemisphere based on North Hemisphere criteria affects many identifications, *e.g.*, of members of *Pododesmus* Philippi, 1837, *Musculus* Röding, 1798, *Psammotreta* Dall, 1900, *Phlyctiderma* Dall, 1899 and *Semele* Schumacher, 1817, among others. In fact, we only formally maintain the local identification of many species, starting to be more conservative (see for instance identification and comments about *Dulcina* cf. *lens*) with new identifications implying species with large western Atlantic distributions.

Small-sized species (notably microbivalves) remain to be thoroughly studied. This applies not only to poorly known groups, such as the Galeommatoidea and Cyamioidea, but also to other less cryptic but morphologically variable species, such as members of *Hiattella* Bosc, 1801, *Abra* Lamarck, 1818 and the Corbulidae.

#### Geographic, bathymetric and habitat-related coverage

An extensive, deep-water sector of the northern UEEZ remains virtually unexplored (Calliari *et al.* 2003), with just one species, *Pristigloma nitens* (E. A. Smith, 1885), reported by the HMS *Challenger* Expedition from station 323. Hard bottoms located on the outer shelf and slope, remain under-sampled. All dredging performed until now has been hampered by the depth of the dredge cutting edge; dredges specially designed for deep penetration into the sediments have not been used to date.

The La Plata River is expected to contribute an important amount of sunken wood to the sea, but wood-boring bivalves have been only seldom sampled (*e.g.*, Calvo 1984). The presence of wood-associated bivalves (either epibenthic or borers) in bathyal and abyssal depths has not been reported for Uruguayan waters.

Associations between epibiotic bivalves and their potential hosts (as those engaging many galeommatoideans) have not been explored in the region. Large populations of the shallow subtidal stomatopod *Heterosquilla platensis* (Berg, 1900), as well as several species of ghost shrimps Callianassidae (Demicheli and F. Scarabino 2006, F. Scarabino pers. obs.), may represent suitable habitats for minute epibiotic bivalves.

#### Reliability of records

Inferred ranges of geographic or bathymetric distribution of shelly marine invertebrates are distorted by a series of problems, including: unresolved/non-reviewed taxonomy, living/dead status not specified in records, poor quality of data (*e.g.*, records from fishermen) and published information, lack of attention to the local literature, and taxonomic “provincialism”, defined by adherence to regional traditions.

Current biogeographical understanding of southwestern Atlantic bivalves is particularly affected by such problems. This has resulted, for example, in the inclusion in regional check-lists of extant fauna of species that no longer occur in Uruguayan waters. This is the case for the venerids *Anomalocardia flexuosa* (Linnaeus, 1767) (= *Venus brasiliana* Gmelin, 1791) and *Tawera elliptica* (Lamarck, 1818) (= *Venus gayi* Hupé, 1854) (F. Scarabino and Zaffaroni 2004, see Huber 2010). The former is common in Quaternary deposits along the La Plata River and Atlantic coasts of Uruguay (e.g., Martínez *et al.* 2001, F. Scarabino and Zaffaroni, pers. obs.), but isolated valves can be found far from those deposits. The southernmost living records of this species come from Santa Catarina State (Brazil), being absent from (at least) southern Rio Grande do Sul State (Brazil) (F. Scarabino and Zaffaroni, pers. obs.). Odd valves of *T. elliptica* can be found in the outer shelf of Uruguay and southern Brazil. Previous records from that region (both Recent and Quaternary) actually correspond to *Transenpitar americanus* and an unidentified species of *Transenella* (F. Scarabino and Zaffaroni 2004, F. Scarabino and Zaffaroni, pers. obs.).

A different problem relates to extra-littoral records of species that are recorded only occasionally along the coasts of Uruguay and southernmost Brazil, but are reported as residents or in unspecified condition. *Aulacomya atra* (Molina, 1782) and *Gaimardia trapesina* (Lamarck, 1819) constitute good examples. Those two species reach the Uruguayan waters on exceptional occasions, by rafting on kelp adrift, in some cases in the form of empty valves or juveniles (Figueiras 1963, Olivier and V. Scarabino 1972, V. Scarabino 1977, Rios 1975, 1985, F. Scarabino and Ortega 2004). This is also the case of *Brachidontes purpuratus* (Lamarck, 1818), cited by Figueiras and Sicardi (1980) and listed by F. Scarabino (2003). In this context, we highlight that the warm-water species *Martesia fragilis*, *Isognomon bicolor* (C. B. Adams, 1845) and *Pinctada imbricata* Röding, 1798 have only been found on floating objects on the Uruguayan coast (Breves *et al.* 2014; Marques and Breves, 2015; F. Scarabino and Zaffaroni, pers. obs.).

F. Scarabino and Zaffaroni (2004) discussed seven other littoral species that have been considered residents but whose occurrence is not confirmed: *Scapharca brasiliana* (Lamarck, 1819), *Scapharca chemnitzii* (Philippi, 1851), *Iphigenia brasiliana* (Lamarck, 1818), *Eurytellina trinitatis* (Tomlin, 1929), *Eurytellina angulosa* (Gmelin, 1791), *Tellina lineata* Turton, 1819 and *Sphenia hatcheri* Pilsbry, 1899.

Records of several Magellanic species reported by Rios (1975, 1985–basis for latter editions of his books) for Rio Grande do Sul (Brazil) are based on odd valves or specimens provided by fishers, which often constitute unreliable information. The relevance of gathering reliable ecological information supporting taxonomic records is highlighted by the

fact that bivalve diversification seems to be more related to ecological/physiological adaptation than to isolation by geographical barriers (Mikkelsen 2011).

### Threats to biodiversity

F. Scarabino (2004) stressed the difficulty of evaluating the conservation status of the marine and estuarine Uruguayan malacofauna given the paucity of studies on taxonomy, biology and ecology, and the lack of country-wide assessments of anthropic impacts on estuarine, shallow subtidal and rocky habitats. Here we summarize available information on exploited species, mass mortalities, biological invasions and habitat degradation threatening the native bivalve malacofauna.

#### Commercial and recreational extraction

The shallow-water stocks of the mussel *Mytilus* sp. (“mejillón”) and *Mesodesma mactroides* (“almeja amarilla”) have been historically (at least since the decade of 1950) the main bivalves extracted from Uruguayan waters (Amaro-Padilla 1967, Defeo 1989, Defeo *et al.* 1993, Defeo and Riestra 2000). These, together with *Perna perna* (“cholga”) and *Donax hanleyanus* (“berberecho”), are also extracted recreationally (F. Scarabino *et al.* 2006). The latter two are also of extracted for human consumption, but only at a small scale. *Erodona mactroides* (“berberecho de laguna”) is also sporadically extracted (Fabiano and Santana 2006), while *Tagelus plebeius* is mainly harvested and commercialized for bait (F. Scarabino *et al.* 2006).

Long-term, large-scale field experiments have demonstrated a predictable pattern of responses to bivalve extraction. Defeo (1996) showed that elevated harvesting rates applied on the yellow clam *Mesodesma mactroides* in Uruguayan sandy beaches significantly reduce recruitment to the exploitable stock and to the population as a whole, resulting in a declining spawning stock, a decreasing age/size at maturity and a decreasing proportion of older individuals in the catch.

The local industrial extraction of bivalves has been inconstant and directed to *Zygochlamys patagonica* (“vieira patagónica”), *Pitar patagonicus* (= *Pitar rostratus*) (“almeja blanca”) and the inner-shelf stocks of *Mytilus* sp. (“mejillón de profundidad”) (Gutiérrez and Defeo 2003, F. Scarabino *et al.* 2006). Clearly, there is a variety of bivalve resources, some still underexploited, including several sandy-bottom clams, such as *Amiantis purpurata*, *Macra isabelleana*, *Tivela zonaria*, *Eutivela isabelleana*, *Glycymeris longior* and *Solen tehuelchus*. Large stocks of *M. isabelleana* inhabiting the La Plata River remain untouched.

Chronic disturbances resulting from bottom trawling activities can cause large-scale and persistent impacts in bivalve populations, as well as in the habitat and in assemblages associated with bivalve beds. These issues have been

particularly studied in the Patagonian scallop *Zygochlamys patagonica* fishery, where the number of taxa (fish and invertebrates) that comprises the by-catch of the fishery is close to 200 species (Schejter *et al.* 2012). Detrimental effects of fishing can also be exacerbated when they are superimposed on environmental change, irrespective of whether such change is of anthropogenic origin, or not (Ortega *et al.* 2012). As harvesting not only affects the targeted species directly through fishing mortality, but it also has collateral impacts that can alter ecosystem structure and functioning, bivalve fisheries can have impacts disproportionate to their economic value.

#### *Biological invasions*

Biological invasions also may threaten some components of the estuarine bivalve fauna. The Rapa whelk (*Rapana venosa* (Valenciennes, 1846), Muricidae), a large predatory gastropod native of the Western Pacific, is one of the most unwelcome and conspicuous invading mollusks. It was found for the first time in the La Plata River estuary during the 1990s. Although previously reported from the mid portion of the estuary, the Rapa whelk is—as predicted—preying on the mussel beds in outer estuarine coast close to Punta del Este (F. Scarabino *et al.* 2006 and references therein; Carranza *et al.* 2008, 2010). This may further contribute to the ongoing decline of native mussel beds, which have been fully exploited since, at least, 1991. The combined effects of overexploitation and other human-induced impacts (*e.g.*, pollution) may have caused the decline of mussel beds in the area prior to the appearance of the Rapa whelk (Defeo and Riestra 2000).

Bivalves themselves include some of the most aggressive invaders among marine and estuarine organisms. It should not come as a surprise if future research indicated the presence of introduced mussels, eventually hybridizing with native ones.

#### *Habitat degradation*

Lercari and Defeo (2006) summarized the knowledge about the impact of the freshwater discharge coming from an artificial canal discharge (Canal Andreoni) at the sandy beach stretch extending between La Coronilla and Barra del Chuy. This freshwater effluent arising from human activities causes a broader deterioration in the quality of the surrounding habitat, with impacts at various levels of ecological organization, including populations of the bivalves *M. mactroides* and *D. hanleyanus*, which experienced reduced abundance, survival, growth and fecundity rates close to the freshwater discharge (Defeo and de Álava 1995).

#### *Climate variability*

In *Mesodesma mactroides*, mass mortalities sequentially occurred in a north-south direction since 1993 (southern

Brazil) to 2002 (Argentina), including Uruguay, where the most important episode occurred in 1994. These mortalities were mainly observed between late spring and early summer, when these cold-water clams are more sensitive to diseases (Fiori *et al.* 2004). The systematic increase in sea surface water temperature, associated with a southward migration of a critical warm isotherm, has exacerbated the negative influence of warm waters (Ortega *et al.* 2012, Defeo *et al.* 2013). In Uruguay, these mass mortalities have determined fishery closures for almost two decades, without evidence of a strong recovery of the harvestable stock (*i.e.*, adult clams), suggesting that effects of climate variability have swamped management measures directed to rebuild the resource.

#### **Final considerations**

The Uruguayan waters represent a critical biogeographical and ecological crossroad because of the complex interaction of currents and water masses. This region is particularly well-suited as a system for the study of processes underlying biodiversity patterns. The knowledge gaps discussed above constitute important issues for future study. Pending challenges in taxonomic and biogeographic research will be successfully addressed only if multinational collaborative initiatives are undertaken in a framework of integrative taxonomy.

#### **ACKNOWLEDGMENTS**

This work has been supported by the CURE, DINARA and MNHNM. FS is particularly grateful to R. Bird, E. Chiesa, E. Delfino, J. and M. Leguizamón, L. Paesch and P. Puig for their help during sampling carried on R/V *Aldebaran*. He is also grateful to the members of the NGOs *Karumbé* and *InvBiota* for collaboration on coastline fieldwork and laboratory work respectively. G. Lecuona was of great assistance at MNHNM. P. Meneses (formerly at DINARA) is acknowledged for the deep-sea material obtained as by-catch. G. López and S. Horta skillfully and generously produced Figures 1 and 2. The projects “*Ecología y sistemática de recursos pesqueros (invertebrados) en el Atlántico Sudoccidental (ASO; 34°–43°S)*” (MINCYT-MEC) and “*Caracterización del margen continental uruguayo*” (ANCAP-Facultad de Ciencias, UdelaR, Uruguay) contributed to the development of this work.

The bibliographic supply of papers by many colleagues along many years was decisive for our work. In that sense we are particularly grateful to J. A. Allen, R. Bieler, P. Bouchet, E. V. Coan, O. Domaneschi, P. M. Mikkelsen, G. Pastorino, E. C. Rios, and C. Salas. A. Sogaray (DINARA) also provided some important files. Along the years and among others, P. Bouchet, S. Gofas, J. H. Leal, M. G. Harasewych, G. Pastorino, E. C. Rios and K. Way offered valuable insights about several

molluscan issues and access to collections that we acknowledge and were eventually considered in this work.

Three anonymous reviewers and R. Bieler provided detailed revisions and comments that are deeply acknowledged as is the editorial work of C. M. Winters, F. Moretzsohn and P. Valentich-Scott.

Last but not least, FS is especially grateful to Inés Pereyra for her permanent support (¡Gracias linda!).

This work is dedicated by all his coauthors to Lobo Orensanz, a brilliant scientist who inspired many people through his passion in marine biology, with profound concerns in marine biodiversity and conservation. Lobo was an exceptional and generous human being who will be deeply missed by all his colleagues, students, friends and family. Lobo passed away when this manuscript was completed and benefited from his outstanding knowledge, generosity and work capacity.

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**Submitted:** 23 January 2015; **accepted:** 1 February 2015;  
**final revisions received:** 19 July 2015