



Hydromedusae (Cnidaria: Hydrozoa) from the temperate southwestern Atlantic Ocean: a review

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Abstract

Hydromedusae are one of the best-represented planktonic groups in waters of the South Atlantic Ocean in terms of species richness. Nevertheless, medusae of the region are inadequately known because earlier studies have been limited and restricted to few areas. During the last two decades, almost 2000 samples from 54 research cruises have been collected, mostly within the continental shelf of Argentina and Uruguay (33 – 55° S). These samples provide an opportunity to significantly augment knowledge of the richness of the medusa fauna in the southwest Atlantic. Forty species of hydromedusae (six of them new records for the area), including 15 of Anthomedusae, 14 of Leptomedusae, three of Limnomedusae, four of Narcomedusae, and four of Trachymedusae, were identified. Our results indicate that previous lists overestimated species richness of hydromedusae in the area. When misidentifications, updated species synonymies, and doubtful records are taken into account, 71 valid species are recognized here from the study area. Based upon this corrected inventory list, the data suggest that the number of species of hydromedusae decreases markedly with increasing latitude, corresponding with that observed in other planktonic groups of invertebrates.

Key words: Hydrozoa, hydromedusae, southwestern Atlantic Ocean, biodiversity, checklist, plankton

Introduction

Hydromedusae, the planktonic adult stage (medusa) of the Hydrozoa exclusive of siphonophores, constitute one of the best-represented planktonic groups in the South Atlantic Ocean in numbers of species, with 197 species reported from the region (Bouillon 1999). Only Copepoda, with more than 400 species (Bradford-Grieve *et al.* 1999), are known to be more diverse. Notwithstanding the relative importance of the group in terms of species numbers, the medusa fauna of the South Atlantic Ocean remains inadequately known. This is because earlier studies have been relatively few and restricted to few geographic areas.

Knowledge on species composition and distribution of hydromedusae from the southwestern Atlantic Ocean is characterized by a marked space-time discontinuity (see fig. 1a). The earliest records came from a few scattered reports appearing almost exclusively over the first half of the 20th century. These studies were restricted mainly to Subantarctic Islands and in a lesser degree to southern Patagonia, with occasional reports from the coast of Uruguay (see mainly Browne 1902; Thiel 1938; Browne and Kramp 1939; Kramp 1957). After an interval of nearly 30 years without any reports, a few sporadic studies on medusae were undertaken along the coast of Buenos Aires and in neighbouring areas (see mainly Goy 1979; Ramirez and Zamponi 1980; Zamponi 1983a, b, 1984).

Ramirez and Zamponi (1981) provided the first species inventory of hydromedusae from the southwestern Atlantic Ocean based on a compilation of literature, mainly from Kramp, (1959), whose inventory list for this region was also based on earlier published records. More recently, Bouillon (1999) presented an extensive literature revision of the hydromedusae of the entire South Atlantic. In it he reported 197 species, with 135 of them recorded from the southwestern Atlantic. A similar number, 131 species, was reported by Migotto *et al.* (2002) for tropical and subtropical waters of the region (Brazilian coast). However, biodiversity and distribution of hydromedusae from large sectors of temperate waters of the southwestern Atlantic (Argentina and Uruguay), remain poorly known. The lack of specimen-based revisions, the scarcity of collections, and the absence of faunistic studies over vast areas of the continental shelf leave a significant gap in knowledge of hydromedusae from this region.

During the last two decades, almost 2000 samples from 54 research cruises (see Materials and Methods, and Fig. 1b) were collected, mostly from the continental shelf of Argentina and Uruguay (33 – 55°). The geographic coverage of the surveys was larger than any previous study and included unexplored sectors. Given the effort involved, an increment in the number of known species might be expected. For instance, in the Mediterranean Sea the number of known hydrozoan species doubled in recent decades (see Boero *et al.* 1997; Bouillon *et al.* 2004); in Papua New-Guinea the number of known meroplanktonic medusae tripled (see Bouillon 1986), and in the Red Sea the number increased seven times (Schmidt 1973).

The goals of this study were to analyze and update information on biodiversity of the five subclasses of hydromedusae (Anthomedusae, Leptomedusae, Limnomedusae, Narcomedusae, and Trachymedusae) found in the southwestern Atlantic Ocean.

Study area. The study region comprises the continental shelf of the southwestern Atlantic Ocean (SWA) from Chuí, Uruguay-Brazil (~33°S) to Burdwood Bank, Argentina (~55°S). This area basically corresponds to the Subantarctic Biogeographical Region, which includes the Bonaerensian (or Argentina) and Magellanic subregions (Balech 1957; Stuardo 1964). A recent review on its water masses can be found in Guerrero and Piola (1997). This region is relatively narrow at its northern end but widens progressively to the south, reaching a maximum width of 850 km near Burdwood Bank (off southern Patagonia). From Río de la Plata to Tierra del Fuego, there are several major coastal embayments (Blanca Bay and the Gulfs of San Matias, San Jorge and Nuevo), and the headland of Peninsula Valdes.

The extension of the continental shelf off Argentina (ca. 1,000,000 km²) produces an exceptionally large Neritic Province. Within this region marine fronts are abundant, covering several scales of space and time. Winds, tides, freshwater discharges, and oceanic currents are their main forcing (Acha *et al.* 2004). The general circulation over this vast region consists of a northward flow of cold and fresh Subantarctic waters in the south (Brandhorst and Castello 1971, Krepper 1977; Bakun and Parrish 1991), and a southward flow of warm and salty waters of tropical and subtropical origin in the north (Castro and Miranda 1998). These distinct water masses meet near 33°S, generating a frontal region known as the Subtropical Shelf Front (Piola *et al.* 2000). The dominant feature of offshore circulation is the opposing flows, and confluence, of the Brazil and Malvinas (Falkland) currents. The Malvinas (Falkland) Current is a swift, barotropic, and narrow branch of the Antarctic Circumpolar Current that flows along the continental slope of Argentina. The Brazil Current is a highly baroclinic western boundary that flows poleward along the continental margins of Brazil, Uruguay and Argentina. The collision of these two currents occurs near 36 °S (Olson *et al.* 1988; Piola and Matano 2001) and it is considered one of the most energetic regions of the world ocean (Chelton *et al.* 1990). This collision occurs off Rio de la Plata. This river comprises one of the largest estuarine systems of South America (about 38,000 km² in area of mixohaline waters), and is characterized by the occurrence of a quasi-permanent salt wedge regime. Fresher, and therefore lighter, water flows out of the estuary as a surface layer, and a deeper flow brings more saline water from the sea into the estuary (Mianzan *et al.* 2001). The effects of the river discharge over the shelf (23,300 m³ s⁻¹ on average) flows mostly towards the NNE, and can be traced throughout the year as far as southern Brazil (Piola *et al.* 2000).

Material and methods

The hydromedusae analyzed in this work were collected during 54 surveys, mostly during spring and summer (a period in which most medusa species would likely be present), covering most of the vast continental shelf off Argentina and Uruguay and neighbouring areas (33°–55°S). A total of 1992 plankton samples were collected, mostly using Hensen and Bongo plankton nets. In addition, Nackthai, Calvet, Biomoc, and Multired nets were occasionally used (see Wiebe and Benfield 2003 for description of each of the nets employed). Several specimens were also collected directly by means of SCUBA or by manual plankton net. Nearly 49,000 specimens of hydromedusae were sorted and analyzed from the samples. Identifications were based mainly on the work by Bouillon (1999).

All specimens were preserved in a 5% formaldehyde solution, and have been deposited in collections of the first two authors (Departamento de Ciencias Marinas, FCEyN – UNMdP and INIDEP).

Results and discussion

A total of 48,763 specimens of hydromedusae were examined. Forty species were identified, including 15 species of Anthomedusae, 14 of Leptomedusae, three of Limnomedusae, four of Narcomedusae, and four of Trachymedusae (see taxonomic list below). As in other regions of the world (see Bouillon 1999), species richness of Anthomedusae was higher than Leptomedusae (37.5 % and 35.0 % respectively). Proportionally, species numbers of Limnomedusae (7.5 %) and Narcomedusae (10.0 %) was higher than in other areas of the world.

Subclass Anthomedusae

Order Filifera

Suborder Margelina

Fam. Bougainvilliidae

Bougainvillia macloviana (Lesson, 1830)

Bougainvillia muscus Allman, 1863

Fam. Oceaniidae

Turritopsis nutricula McCrady, 1857

Fam. Pandeidae

Amphinema dinema (Péron and Lesueur, 1809)

Halitholus intermedius (Browne, 1902)

Leuckartiara octona (Fleming, 1823)

Fam. Proboscidactylidae

Proboscidactyla mutabilis (Browne, 1902)

Order Capitata

Fam. Corynidae

Dipurena reesi Vannucci, 1956

Coryne eximia Allman, 1859

Coryne gracilis (Browne, 1902)

Fam. Euphysidae

Euphysa aurata Forbes, 1848

Fam. Tubulariidae

Hybocodon unicus (Browne, 1902)

Hybocodon prolifer L. Agassiz, 1862

Fam. Porpitidae

Porpita porpita (Linnaeus, 1758)

Veleva veleva (Linnaeus, 1758)

Subclass Leptomedusae

Order Conica

Fam. Aequoreidae

Aequorea coerulea (Brandt, 1835)

Aequorea forskalea Péron and Lesueur, 1810

Rhacostoma atlanticum L. Agassiz, 1850

Fam. Blackfordiidae

Blackfordia virginica Mayer, 1910

Fam. Eirenidae

Eutonina scintillans (Bigelow, 1909)

Fam. Eucheilotidae

Eucheilota ventricularis McCrady, 1859

Fam. Laodiceidae

Laodicea undulata (Forbes and Goodsir, 1851)

Fam. Mitrocomidae

Halopsis ocellata A. Agassiz, 1863

Mitrocomella brownei (Kramp, 1930)

Mitrocomella frigida (Browne, 1910)

Order Proboscoida

Fam. Campanulariidae

Clytia gracilis (M. Sars, 1851)

Clytia loma (Torrey, 1909)

Clytia simplex (Browne, 1902)

Obelia longissima (Pallas, 1776)

Subclass Limnomedusae

Fam. Olindiidae

Aglauropsis kawari Moreira and Yamashita, 1972

Gossea brachymera Bigelow, 1909

Olindias sambaquiensis Müller, 1861

Subclass Narcomedusae

Fam. Aeginidae

Solmundella bitentaculata (Quoy and Gaimard, 1833)

Fam. Cuninidae

Cunina frugifera Kramp, 1948

Cunina octonaria McCrady, 1859

Fam. Solmarisidae

Pegantha laevis H. B. Bigelow, 1909

Subclass Trachymedusae

Fam. Geryoniidae

Liriope tetraphylla (Chamisso and Eysenhardt, 1821)

Fam. Rhopalonematidae

Amphogona apsteini (Vanhöffen, 1902)

Crossota brunnea Vanhöffen, 1902

Rhopalonema velatum Gegenbaur, 1857

The most frequent and abundant species were the trachymedusa *Liriope tetraphylla* and the leptomedusa *Eucheilota ventricularis* (41.0 and 30.7% of the total specimens, respectively). Several other species were less numerous although frequent in different plankton samples, e.g., *Proboscidactyla mutabilis* and *Bougainvillia macloviana* (Anthomedusae); *Blackfordia virginica*, *Laodicea undulata*, *Mitrocomella frigida*, *Obelia longissima* (Leptomedusae); and *Rhopalonema velatum* (Trachymedusae). The remaining species were represented by few and only occasional specimens (Table 1).

TABLE 1. Percentage abundances of 40 species (from a total of 48,763 specimens) identified here (A), and their percentage presences (P) in a total of 1992 plankton samples, of hydromedusae collected during 54 surveys conducted in the southwestern Atlantic Ocean (33° S– 55°S).

Species	A	P
<i>Liriope tetraphylla</i>	41.0	19.0
<i>Eucheilota ventricularis</i>	30.7	7.0
<i>Blackfordia virginica</i>	20.5	0.20
<i>Obelia longissima</i>	5.67	0.50
<i>Proboscidactyla mutabilis</i>	0.63	3.76
<i>Mitrocomella frigida</i>	0.61	2.60
<i>Laodicea undulata</i>	0.20	0.85
<i>Bougainvillia macloviana</i>	0.14	0.30
<i>Rhopalonema velatum</i>	0.07	0.90
<i>Aequorea coerulescens</i>	0.06	0.85
<i>Gossea brachymera</i>	0.05	0.25
<i>Olindias sambaquiensis</i>	0.05	0.20
<i>Coryne eximia</i>	0.04	0.25
<i>Amphogona apsteini</i>	0.02	0.35
<i>Clytia simplex</i>	0.02	0.30
<i>Leuckartiara octona</i>	0.02	0.25
<i>Veella veella</i>	0.02	0.25
<i>Cunina octonaria</i>	0.016	0.35
<i>Turritopsis nutricula</i>	0.01	0.10
<i>Halitholus intermedius</i>	0.01	0.35
<i>Hybocodon prolifer</i>	0.01	0.10
<i>Aequorea forskalea</i>	0.01	0.35
<i>Clytia lomae</i>	0.01	0.30
<i>Aglauropsis kawari</i>	0.01	0.15
<i>Amphinema dinema</i>	0.008	0.01
<i>Coryne gracilis</i>	0.008	0.05
<i>Clytia gracilis</i>	0.008	0.10
<i>Mitrocomella browni</i>	0.008	0.05
<i>Solmundella bitentaculata</i>	0.006	0.15
<i>Euphysa aurata</i>	0.004	0.10
<i>Hybocodon unicus</i>	0.004	0.10

to be continued.

TABLE 2. (continued)

Species	A	P
<i>Eutonina scintillans</i>	0.004	0.10
<i>Bougainvillia muscus</i>	0.002	0.05
<i>Dipurena reesi</i>	0.002	0.05
<i>Porpita porpita</i>	0.002	0.05
<i>Rhacostoma atlanticum</i>	0.002	0.05
<i>Halopsis ocellata</i>	0.002	0.05
<i>Cunina frugifera</i>	0.002	0.05
<i>Pegantha laevis</i>	0.002	0.05
<i>Crossota brunnea</i>	0.002	0.05

Most species of hydromedusae found in the study region (~ 66 %) are cosmopolitan or have a wide distribution in all oceans. A smaller number of species (~ 16 %) are restricted to the Southern Hemisphere, while even fewer (~ 8 %) are reported from both the northwestern and southwestern Atlantic. Only four species (~ 10 %) are endemic to the southwestern Atlantic: *Proboscoidactyla mutabilis*, *Olindias sambaquiensis*, *Mitrocomella frigida*, and *Coryne gracilis* (see remarks, Table 2).

The region is characterized by warm waters of tropical and subtropical origin in the north, and by cold subantarctic waters in the south. Fourteen species were found exclusively in the northern sector (33°– 42°S) and only three in the southern sector (42° – 60°S), while 23 species were found in both zones.

The collision of the Brazil and Malvinas (Falkland) currents occurs off the mouth of the La Plata River. We found 21 of the 40 species collected (52.5%) in this area; moreover, the highest density values were observed of the most frequent species, *Liriope tetraphylla* and *Eucheilota ventricularis* (which usually exceeded 350 and 160 ind m⁻³ respectively). Remarkably, many Anthomedusae are represented only by their medusa stages in this frontal area; possibly these medusae are released from polyps in neighbouring areas and transported here by currents. This explanation is supported by their occasional presence only, usually during summer, together with the absence of any records of their polyps from the area (Genzano and Zamponi 1997).

Students of Hydrozoa often specialize in the study of either the hydroid or medusa stages, and two systems of classification and nomenclature have frequently been used in the classification of Hydrozoa, one for hydropolyps and another for hydromedusae. However, this matter does not constitute a significant problem in this study. The link between hydroid and medusa is questionable in only two species: *Phialella chilensis* (Hartlaub, 1905) is thought to be the polyp stage of the medusa *Phialella falklandica* (see Rees and Thursfield 1965, Blanco *et al.* 2000), while *Stegopoma fastigiatum* (Alder, 1860) is considered the polyp stage of the medusa *Modeeria rotunda* (see Millard 1975, Blanco *et al.* 2000).

The link between polyp and medusa stages of the various species of *Obelia* is difficult to ascertain due to the absence of characters in distinguishing the medusa stages, which are usually identified simply as *Obelia* sp. In the case of *Clytia* sp., very few medusae species are clearly identified as well. We found medusae of *C. simplex*, *C. lomae* and *C. gracilis*, but presumably the medusa stage of *C. hemisphaerica* (Linnaeus 1767) is also present in the area since Genzano (1995) reported its hydroid colonies there.

Changes in biodiversity, in terms of species numbers, are best determined by taxonomic specialists. As noted above, the number of known hydrozoan species in the Mediterranean Sea increased twofold in the last thirty years as a consequence of studies conducted by specialists (457 species, including hydropolyps, hydromedusae, and siphonophores; see Boero *et al.* 1997; Bouillon *et al.* 2004). In the Insular Pacific, extensive studies in Papua New Guinea (see Kramp 1961, Bouillon 1986) elevated the number of known meroplanktonic species of medusae from 59 to 176. In the Red Sea, Schmidt (1973) increased the number of known medusae species from 10 to 73.

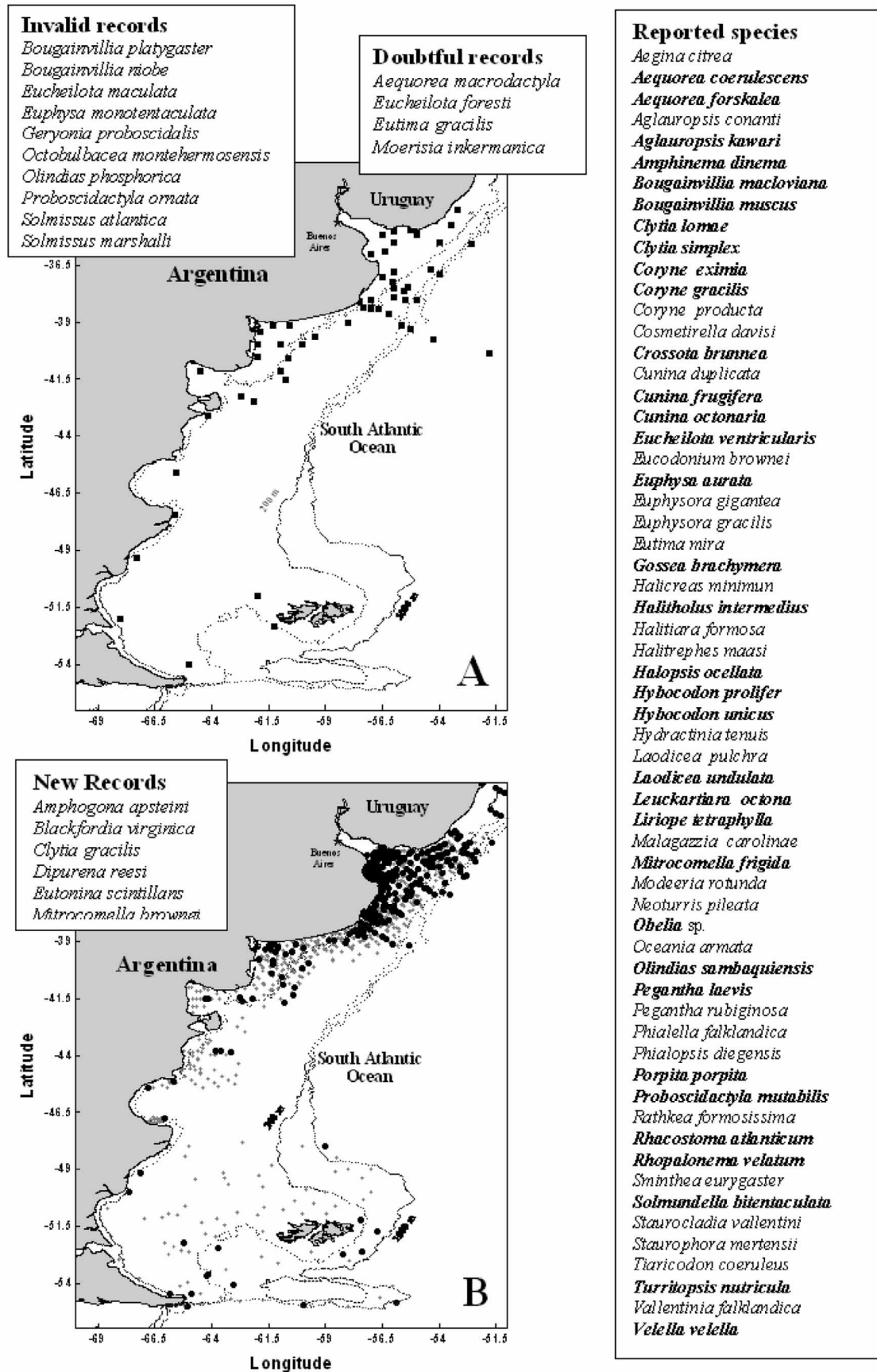


FIGURE 1. A: Geographic distributions of species recorded in the literature on hydromedusae from 1830–1994 (■). B: Station locations of samples examined during this study (●). Samples containing hydromedusae (●).

TABLE 2. Annotated check list of species of hydromedusae reported from the southeastern Atlantic Ocean (33–60°S).

Species	Record between the 33 – 60°S
Subclass Anthomedusae	
Order Filifera	
Fam. Bougainvilliidae	
<i>Bougainvillia macloviana</i> (Lesson, 1830)	Medusa of species reported near Malvinas (Falkland) Islands by Vanhöffen, 1910 (as <i>Hippocrene macloviana</i>), Buenos Aires coast (Vannucci and Tundisi 1962) and 41°42'S – 60°57'W (Zamponi, 1983b).
Material examined: 69 medusa specimens from 38° 08' S – 57° 31' W and between 51°15'–53°68'S and 64°16'–64°58'W.	
<i>Bougainvillia platygaster</i> (Haeckel, 1879)	Specimens reported by Zamponi (1983b) from 52°27' S – 61°12'W as <i>B. platygaster</i> were considered here to be medusae of <i>B. macloviana</i> (see text).
<i>Bougainvillia muscus</i> Allman, 1863	Medusa stage reported at 37°08'S–57°31'W and between 41°08'S–42°19'S and 60°57'W–62°51'W (Ramírez and Zamponi 1980; Zamponi 1983a).
Material examined: one mature medusa, Mar del Plata, 38°08'S – 57°31'W.	
<i>Bougainvillia niobe</i> Mayer, 1894	Species reported in error from the study area (see text).
Fam. Oceaniidae	
<i>Oceania armata</i> Kölliker, 1853	Medusae reported by Ramirez and Zamponi (1980) and Zamponi (1983b) at 40°05'S – 64°00'W; 40°51'S – 61°30'W and 41°55'S – 64° 25'W.
<i>Turritopsis nutricula</i> McCrady, 1857	Species recorded from Buenos Aires coast, Argentina (Ramirez and Zamponi 1980; Zamponi and Suarez 1991). Distribution of <i>T. nutricula</i> is difficult to establish because many specimens described under this name have recently been included in the synonymy of other species of <i>Turritopsis</i> (Schuchert 2004).
Material examined: five medusae, 35°09'S – 52°45'W; 35°21'S – 52°30'W and 39°08'S – 62°00'W.	
Fam. Eucodoniidae	
<i>Eucodonium brownei</i> Hartlaub, 1907	Medusa reported by Zamponi (1983a) between 38°30' to 49°20'S and 57°27' to 67°20'W.
Fam. Hydractiniidae	
<i>Hydractinia tenuis</i> (Browne, 1902)	Malvinas (Falkland) Islands (Browne 1902; Browne and Kramp 1939; as <i>Podocoryne tenuis</i>).
Fam. Rathkeidae	
<i>Rathkea formosissima</i> (Browne, 1902)	Malvinas (Falkland) Islands (Browne 1902; Browne and Kramp 1939).
Suborder Tiarida	
Fam. Pandeidae	
<i>Amphinema dinema</i> (Péron and Lesueur, 1809)	Species previously reported between 40°52' to 45°55'S and 60°28' to 60°45'W (Zamponi 1983a).
Material examined: four medusae, 38°33'S – 57°20'W.	
<i>Halitholus intermedius</i> (Browne, 1902)	Previous records correspond to Malvinas (Falkland) Islands; Cape of Good Hope (Browne and Kramp 1939; Kramp 1959) and between 37° 11' to 43°00'S and 54°08' to 63°54'W (Zamponi 1983a, 1985).
Material examined: eight medusae, 34°48'S – 52°50'W; 35° 40'S – 54°16'W; 36°03'S – 55°07'W and 36°09'S – 56°10'W.	
<i>Leuckartiara octona</i> (Fleming, 1823)	Reported from 39°52' to 46°28'S and 55°23' to 66°27'W (Zamponi, 1983b).
Material examined: nine medusae, 36°06'S – 56°24'W; 37°06'S – 56°25'W; 38°05'S – 56°29'W; 45°22'S – 64°27'W and 45°24'S – 66°47'W.	
<i>Neoturris pileata</i> (Førsskal, 1775)	Reported in the Strait of Magellan (Vanhöffen 1913).
Fam. Proboscidactylidae	

- Proboscidactyla mutabilis* (Browne, 1902)
Material examined: 308 medusae found between 34°58' – 41°47'S and 52°51' – 62°50'W.
Proboscidactyla ornata (McCrary, 1859)
- Fam. Protiaridae
Halitiara formosa Fewkes, 1882
Order Capitata
Suborder Moerisiida
Fam. Moerisiidae
Moerisia inkermanica (Palschikowa-Ostroumova, 1925)
- Fam. Polyorchidae
Tiaricodon coeruleus Browne, 1902
Suborder Tubulariida
Fam. Corymorphidae
Euphysora gigantea Kramp, 1957
Euphysora gracilis (Brooks, 1882)
- Order Capitata
Fam. Corynidae
Dipurena reesi Vannucci, 1956
Material examined: mature colonies with scarce medusa buds, Las Grutas, San Antonio Oeste (40° 48' S – 65° 05' W), intertidal. One medusa, 41°50'S – 64°67'W.
Coryne eximia Allman, 1859
Material examined: 25 medusae, 37°50'S – 56°55'W, 38°08' S – 57°31'W and 42°50'S – 62°55'W.
Coryne gracilis (Browne, 1902)
Material examined: four mature medusae, 49°59' S – 67° 45'W.
Coryne producta (Wright, 1858)
- Fam. Eleutheriidae
Staurocladia vallentini (Browne, 1902)
- Fam. Euphysidae
- Reported from Malvinas (Falkland) Islands (Browne 1902, as *Willsia mutabilis*), Strait of Magellan, Patagonia, Puerto Madryn (Browne and Kramp 1939; Kramp 1961), Uruguay (Goy 1979), Buenos Aires coast (Zamponi 1983b, 1985).
Specimens reported as *P. ornata* by Zamponi (1983b) were considered conspecific with *P. mutabilis* (see text).
Reported at 38°08'S – 57°31'W (Zamponi 1992).
Zamponi (1983b) reported medusae of this species (as *Ostroumova inkermanica*) between 39°19' – 53°39'S and 60°36' – 62°09'W. *M. inkermanica* is considered native to the Black sea region; it is a well known invasive species, established in different estuarine areas of the world (Mills and Rees 2000). This is the only report of this species in southwestern Atlantic Ocean. Its presence needs to be confirmed.
Malvinas (Falkland) Islands and Puerto Desado, Santa Cruz (Patagonia) (Browne and Kramp 1939; Vannucci and Tundsini 1962).
Malvinas (Falkland) Islands (Kramp, 1957).
Medusae found at 34°30'S–53°–50'W; 35°00'S–56°–00'W and 35°10'S–53°–15'W by Ramirez and Zamponi (1980).
Previously recorded in Brazil (Vannucci 1956; Moreira *et al.* 1978; Grohmann *et al.* 1997). Ramirez and Zamponi (1981) assigned a tropical and subtropical distribution for this species but our record extends its distribution into sub-temperate waters and constituted the first record into the Argentinian Continental Shelf. Medusae were reported as *Sarsia eximia* (Ramirez and Zamponi 1981; Bouillon 1999).
Medusae reported in Malvinas (Falkland) Islands; type locality (Browne 1902; Browne and Kramp 1939; Schuchert 2001, as *Sarsia gracilis*). It is considered endemic to the southwestern Atlantic Ocean. However, Schuchert (1996) suggested that *C. gracilis* might be referable to *C. eximia*, but more study is needed before adopting that synonymy (Schuchert, 2001).
Reported by Zamponi (1983b) between 46°47'S – 65°08'W (as *Staurodiosarsia producta*).
Medusae reported in Malvinas (Falkland) Islands (Browne 1902; Browne and Kramp 1939).

- Euphysa aurata* Forbes, 1848
Material examined: two medusae, 38, 37° 54'S – 56°39'W and 38°05'S – 56°29'W.
- Euphysa monotentaculata* Zamponi, 1983
Fam. Margelopsidae
- Octobulbacea montehermosensis* Zamponi, 1983
Fam. Tubulariidae
- Hybocodon unicus* (Browne, 1902)
Material examined: two medusae, 38°58'S – 61°53'W and 38°59'S – 62°06'W.
- Hybocodon prolifer* L. Agassiz, 1862
Material examined: one mature medusa and five small juveniles from 38°08'S – 56°20'W and 39°20'S – 61°27'W, respectively.
Fam. Porpitidae
- Porpita porpita* (Linnaeus, 1758)
Material examined: one hydroid colony, 34°10'S – 53°00'W.
- Veleva veleva* (Linnaeus, 1758)
Material examined: 10 floating hydroid colonies, 34°10'S – 53°00'W; 37°54'S – 56°39'W, 45°59'S – 54°30'W, 46°01'S – 55°58'W and 46°00'S – 57°02'W.
Subclass Leptomedusae
Order Conica
Fam. Aequoreidae
- Aequorea coerulescens* (Brandt, 1938)
Material examined: 28 medusae, found on Buenos Aires coast between 35°59'S – 37°34'S and 53°45' – 56°40'W and North Patagonia between 43°49' – 44°25'S and 64°34' – 65°01'W.
- Aequorea forskalea* Péron and Lesueur, 1810
Material examined: 7 medusae, 37°40'S – 56°02'W; 43°31' – 43°34'S and 59°28' – 64°25'W; 46°28'S – 67°02'W and 52°31'S – 67°18'W.
- Aequorea macrodactyla* (Brandt, 1834)
- Rhacostoma atlanticum* L. Agassiz, 1850
Material examined: 3 medusae, 34°21'S – 53°30'W, 35°07'S – 56°44'W and 35°14'S – 56°42'.
Fam. Blackfordiidae
- Blackfordia virginica* Mayer, 1910
Material examined: 10,000 medusae, 36°06'S – 56°24'W, 36°14'S – 56°38'W 36°18'S – 56°44'W.
Fam. Eirenidae
- Eutima gracilis* (Forbes and Goodsir, 1851)
- Thiel (1938) reported medusae from the Patagonian Bank and Zamponi (1983a, 1985) at 45°52'S – 65°48'W and 38°21' – 57°00'W.
- Considered synonymous with *E. aurata* (see text).
- Not a valid species (see text).
- Reported at 45°52'S – 65°48'W (Girola 1985; Zamponi, 1983b) and Malvinas (Falkland) Islands (Browne and Kramp 1939).
- Reported at 38°20'S – 56°29'W (Zamponi 1984; Zamponi and Suarez, 1991).
- Hydroid colony previously reported at 34°42'S – 54°10'W (Mianzan and Girola 1990, as *Porpita umbella*). Medusae never recorded in South Atlantic Ocean.
- Hydroid colony previously reported in Uruguay and Argentina (Mianzan and Girola 1990). Medusae never recorded in South Atlantic Ocean.
- Reported in Malvinas (Falkland) Islands (Bigelow 1909; Kramp 1957).
- Reported by Kramp (1961) from Patagonia.
- Strait of Magellan (Kramp 1959). The presence of *A. macrodactyla* needs to be confirmed (see text).
- Reported from the coast off Buenos Aires, Argentina, between 35°44'S to 40°S (Ramirez and Zamponi 1980; Zamponi 1983b).
- This invasive medusa was recently detected in northern Argentina, constituting the first record in temperate waters of the southwestern Atlantic Ocean (Genzano *et al.* 2006).
- Reported by Zamponi and Suarez (1991) at 38°08'S – 57°31'W. Its occurrence in the study area needs to be confirmed (see text).

- Eutima mira* McCrady, 1859
Reported at 37°30'–55°28' and 38°08' S' –57°31' W (Zamponi 1983b; Zamponi and Suarez 1991).
- Eutonina scintillans* (Bigelow, 1909)
Material examined: 2 medusae, 38°54' S – 60°26' W.
This medusa was recently recorded from the Buenos Aires coast, extending its distribution toward temperate waters of southwestern Atlantic Ocean (Rodriguez *et al.* 2007).
- Phialopsis diegensis* Torrey, 1909
Fam. Eucheilotidae
Recorded by Kramp (1957) in Uruguay.
- Eucheilota foresti* Goy, 1979
Reported by Goy (1979) at 35°50' S – 56°19' W. Its validity needs to be confirmed (see text).
- Eucheilota ventricularis* McCrady, 1859
Material examined: 15,000 specimens found at 36°16' S – 57°50' W, 37°44' S – 57°18' W and 38°02' S – 57°31' W.
Reported in Uruguay, and along the entire Buenos Aires and Patagonian coast (Ramirez and Zamponi 1980; Zamponi 1983b; Zamponi and Suarez 1991; Girola *et al.* 1992; Zamponi and Genzano 1994; Rodriguez 2006).
- Eucheilota maculata* Hartlaub, 1894
Specimens from Uruguay reported by Goy (1979) as *E. maculata* were considered to be specimens of *E. ventricularis* instead (see text).
- Fam. Laodiceidae
Laodicea pulchra Browne, 1902
Malvinas (Falkland) Islands and 49°20' – 67°20' (Browne and Kramp 1939; Zamponi 1983a).
- Laodicea undulata* (Forbes and Goodsir, 1851)
Material examined: 98 medusae found between 34°38' to 49°08' S.
Reported in Tierra del Fuego and Patagonia (Mayer 1910; Thiel 1938) and Buenos Aires, 38°30' – 56°58' (Zamponi 1983b).
- Staurophora mertensii* Brandt, 1834
Fam. Malagazziidae
Malvinas (Falkland) Islands (Browne 1902, as *S. falklandica*).
- Malagazzia carolinae* (Mayer, 1900)
Widely reported from the Buenos Aires coast (Ramirez and Zamponi 1980; Zamponi 1983b; Zamponi 1985; Zamponi and Suarez 1991; all these reports as *Phialidium carolinae*).
- Fam. Mitrocomidae
Cosmetirella davisii (Browne, 1902)
Malvinas (Falkland) Islands and Patagonia (Browne and Kramp 1939; Kramp 1957) and 37°30' S–56°W, 37°50' S –56° (Ramirez and Zamponi 1980).
- Halopsis ocellata* A. Agassiz, 1863
Material examined: one specimen, 54°30' S – 64°52' W.
Reported from Malvinas (Falkland) Islands (Kramp 1957, 1961).
- Mitrocomella brownei* (Kramp, 1930)
Material examined: four mature specimens 39°20' S – 61°26' W. Two juvenile medusae, 40°30' S – 61°19' W.
In the southwestern Atlantic Ocean it has been reported in Brazil (Navas-Pereira 1981). This is the first record in temperate waters of the southwestern Atlantic.
- Mitrocomella frigida* (Browne, 1910)
Material examined: 300 specimens; Buenos Aires and north patagonian coast.
Species found north of Patagonian sector and from Buenos Aires coast, Argentina (Ramirez and Zamponi 1980; Zamponi 1983a, 1985; Zamponi and Suarez 1991; Zamponi and Genzano 1994; Rodríguez 2006).
- Fam. Phialellidae
Phialella falklandica Browne, 1902
Malvinas (Falkland) Islands Browne 1902; Mayer 1910 (as *Eucope falklandica*); Browne and Kramp 1939; Kramp 1957.
- Fam. Tiarannidae
Modeeria rotunda (Quoy and Gaimard, 1827)
Found in Patagonia by Hartlaub (1913) and Kramp (1957) (both as *Tiaranna rotunda*).

Order Proboscoida

Fam. Campanulariidae

Clytia gracilis (M. Sars, 1851)

Material examined: three medusae just released in aquarium. Four mature medusae from 38°08'S – 57°31'W.

Colonies of *C. gracilis* were reported along the entire Argentinian continental shelf from Buenos Aires to Tierra del Fuego (Blanco 1994; Genzano and Zamponi 1997, 2003), but this is the first record of the medusa stages in the study area.

Clytia lomae (Torrey, 1909)

Material examined: six medusae, 41°29'S – 64°18'W and 34°16'S – 53°30'W; 35°09'S – 52°45'W; 36°40'S – 56°35'W; 37°06'S – 56°39'W and 38°54'S – 56°21'W.

Reported from the Buenos Aires coast, Argentina (Zamponi 1992; Zamponi and Genzano 1994; as *Phialidium lomae*).

Clytia simplex (Browne, 1902)

Material examined: 11 medusae, 35°15'S – 54°59'W; 35°26'S – 54°25'W; 36°55'S – 55°23'W; 36°39'S – 54°38'W; 37°57'S – 56°45'W; 42°21'S – 62°40'W.

Reported from Malvinas (Falkland) Islands (Browne 1902; Browne and Kramp 1939) and Buenos Aires between 35°30' to 40° S and 58°00' – 64°10'W (Ramirez and Zamponi 1980; Zamponi and Suarez 1991; in all mentioned as *Phialidium simplex*).

Obelia longissima (Pallas, 1776)

Material examined: 300 medusae, 39°40'S – 61°38'W; 39°40'S – 61°51'W and 40°01'S – 61°00'W.

There are no characters to reliably identify medusa specimens of this genus to species level (usually identified as *Obelia* spp.). However; floating bits of *Obelia* hydroid colonies were found in some samples together their medusa stages. The comparison of these fragments with our reference collections permitted identification of these hydroids as *Obelia longissima*.

Subclass Limnomedusae

Fam. Olindiidae

Aglauropsis kawari Moreira and Yamashita, 1972

Material examined: 5 medusae, 35°59'S – 56°39'W; 38°44'S – 57°17'W and 39°23'S – 60°24'W.

Reported in Buenos Aires, Samborombon Bay (Girola *et al.* 1992; Zamponi 1992; Zamponi and Genzano 1994).

Aglauropsis conanti Browne, 1902

Malvinas (Falkland) Islands and South Patagonia (Browne, 1902).

Gossea brachymera Bigelow, 1909

Material examined: 24 medusae; 37°08'S – 57°10'W; 39°50'S – 61°10'W and Blanca Bay, between 38°45' to 39°20'S and 61°25' to 62°20'W.

Reported in the Strait of Magellan (Browne and Kramp 1939); south of Buenos Aires coast (Vannucci and Tundisi 1962) and Blanca Bay, Argentina (Mianzan 1986).

Olindias sambaquiensis Muller, 1861

Material examined: 11 specimens from 34°28'S – 53°43'W and 38°08'S – 57°31'W.

Olindias sambaquiensis is endemic to the temperate Atlantic coast of South America. It was reported from Cabo Frío (Brazil) to Valdés Península (see Mianzan 1989).

Olindias phosphorica (Delle Chiaje, 1841)

Specimens reported by Zamponi (1983b) at 47° 11' S – 65° 06' W were referred to *O. sambaquiensis* instead (see text).

Vallentinia falklandica Browne, 1902

Reported from Malvinas (Falkland) Islands (Browne 1902; Browne and Kramp 1939; Kramp 1959).

Subclass Narcomedusae

Fam. Aeginidae

Solmundella bitentaculata (Quoy and Gaimard, 1833)

Material examined: 3 specimens, 34°58'S – 52°57'W, 36°23'S – 53°45'W and 37°48'S – 55°38'W.

Reported from the Buenos Aires coast (Ramirez and Zamponi 1980) and between 44°22' – 51°27'S – 56°13' – 61°27'W (Zamponi 1983b).

Aegina citrea Eschscholtz, 1829

Reported from Uruguay (Thiel 1938; Goy 1979).

Fam. Cuninidae

<i>Cunina frugifera</i> Kramp, 1948 Material examined: one specimen, 54°59'S – 59°58'W.	Reported from Uruguay and Argentina, Buenos Aires and north Patagonian sectors (Kramp 1959; Zamponi 1983b; 1985).
<i>Cunina duplicata</i> Maas, 1893	Reported from the coast of South America as far south as about 53°S, and between Malvinas (Falkland) and South Georgia Islands (Kramp 1957, 1959, 1961).
<i>Cunina octonaria</i> McCrady, 1859 Material examined: eight medusae, 35°54'–36°51'S and 53°26'–56°35'W; and 38°02'S–57°31'W.	Reported from Buenos Aires and Patagonia (Ramirez and Zamponi 1980; Zamponi 1983b).
<i>Solmissus atlantica</i> Zamponi, 1983	Not a valid species (see text).
<i>Solmissus marshalli</i> Agassiz and Mayer, 1902 Fam. Solmarisidae	Species erroneously reported from the study area (see text).
<i>Pegantha laevis</i> Bigelow, 1909 Material examined: one specimen, 52°49'S – 63°50'W.	Patagonia and Malvinas (Falkland) Islands (Bigelow 1909).
<i>Pegantha rubiginosa</i> (Kölliker, 1853) Subclass Trachymedusae Fam. Geryoniidae	Reported by Zamponi (1983b) at 52°27'S – 61°12'W.
<i>Liriope tetraphylla</i> (Chamisso and Eysenhardt, 1821) Material examined: 20,000 specimens from 38°02'S – 57°31'W; 37°44'S – 57°18'W and 36°16'S – 57°50'W.	Reported from Buenos Aires, Río de la Plata and Blanca Bay estuaries, and Uruguay (Vannucci and Tundisi 1962; Zamponi and Genzano 1994, Gaitán 2004).
<i>Geryonia proboscidalis</i> (Forskäl, 1775) Fam. Halicreatidae	Specimens reported as <i>G. proboscidalis</i> by Zamponi and Genzano (1994) from the Buenos Aires coast were considered misidentified medusae of <i>L. tetraphylla</i> (see text).
<i>Halicreas minimum</i> Fewkes, 1882	Reported by Zamponi (1983b) at 44°01'S – 51°07'S and 60°57' – 67°53'W.
<i>Halitrephes maasi</i> Bigelow, 1909 Fam. Rhopalonematidae	Reported from the Buenos Aires coast, 35°44'–52°42'S and 52°46' and 67°34'W (Ramirez and Zamponi 1980; Zamponi 1983b).
<i>Amphogona apsteini</i> (Vanhöffen, 1902) Material examined: 11 medusae from 36°57'S–54°12'W, 52°15'S–65°12'W; 52°30'S–65°20'W; 53°50'S – 64°15'W and 55°03'S – 65°05'W.	Species frequently reported in Brazil (Vannucci 1963; Moreira 1973; Navas-Pereira 1981). It is the first record of this species in temperate waters of the southwestern Atlantic Ocean.
<i>Crossota brunnea</i> Vanhöffen, 1902 Material examined: 1 specimen, 37°39'S – 55°53'W.	Common in deep water in all oceans south of equator. Also reported at northwest of Gauss station, Antarctic (Kramp 1959, 1961).
<i>Rhopalonema velatum</i> Gegenbaur, 1857 Material examined: 32 medusae found between 35°54' to – 55°00'S.	Reported from the coast of Argentina (Ramirez and Zamponi 1980; Zamponi 1983b, 1985).
<i>Sminthea eurygaster</i> Gegenbaur, 1857	Found at 39°23'S – 55°11'W (Zamponi 1985).

From literature records (see Table 2), 75 species of hydromedusae are known from the neritic southwestern Atlantic Ocean (33 – 55°S, < 200 m depth). Bouillon (1999) had already excluded four taxa, two invalid species (*Clytia phosphoricum* and *Haliscera alba*) and two species erroneously reported from the region

(*Bougainvillia pyramidata* and *Heterotiara anonyma*). Our inventory also excluded a group of fourteen species which typically inhabit the pelagic zone, far from the study area: *Heterotiara minor* Vanhöffen, 1911, *Pandea conica* (Quoy and Gaimard, 1827), *Cunina peregrina* Bigelow, 1909, *Pegantha clara* Bigelow, 1909, *Pegantha martagon* Haeckel, 1879, *Pegantha triloba* Haeckel, 1879, *Botrynema brucei* Browne, 1908, *Halicera bigelowi* Kramp, 1947, *Aglaura hemistoma* Péron and Lesueur, 1810, *Aglantha digitale* (Müller, 1776), *Aglantha elata* (Haeckel, 1879), *Amphogona aplicata* Kramp, 1957, *Colobonema sericeum* Vanhöffen, 1902 and *Pantachogon haeckeli* Maas, 1893) (see Bouillon 1999; Kramp 1957, 1959, 1961; Pagès *et al.* 1992). These species are mainly Narco- and Trachymedusae, which are nearly all holopelagic and are usually oceanic in distribution.

We expected that this study would increase the number of species known from the southwestern Atlantic region (33 – 55°). Medusae from almost 2000 zooplankton samples were available to us from regular surveys conducted for nearly 20 years in different areas of coastal Argentina and Uruguay, covering a larger geographical area than any previous study. However, we identified only 40 species, including 34 of the 75 previously reported in the literature from the region. Six others constitute new records for the area: *Dipurena reesi*, *Blackfordia virginica*, *Mitrocomella brownei*, *Eutonina scintillans*, *Clytia gracilis*, and *Amphogona apsteini* (see figure 1, table 2 and references therein).

Many reasons can be given to account for a reduction of more than 45% between previously reported species numbers from the region and the present results.

Three of the reported taxa, *Solmissus atlantica*, *Euphysa monotentaculata*, and *Octobulbacea montehermosensis*, all described by Zamponi (1983a), are not considered valid species in this study. The poorly preserved specimen assigned to *S. atlantica* (Zamponi 1983a; pp. 176–178, Lam. 2) was probably a species referable to the family Aeginidae, while tentacles of *O. montehermosensis* (Zamponi 1983a; pp. 178–179, Lam. 2) resemble those of *Gossea brachymera*, and the specimen may be a juvenile of that species (in both, judging from Zamponi's figure; unfortunately all the types have been lost). The diagnostic characters of *E. monotentaculata* (Zamponi 1983a: pags.174 – 176, Lam. 1) are not clear enough to distinguish it from other species of *Euphysa*.

Another two species, *Bougainvillia niobe* and *Solmissus marshalli*, have been erroneously reported from the area. *Bougainvillia niobe* is widely reported in the northwestern Atlantic (Mayer 1910, p. 166; Kramp 1959, p.110, 1961, p. 79; Vannucci and Rees 1961, p. 77). Ramirez and Zamponi (1981, p. 452) erroneously reported this species in the South Atlantic. Bouillon (1999 p. 392 and 410) incorporated this mistake, but this species has never been reported in the southwestern Atlantic. *Solmissus marshalli*, reported in tropical and subtropical waters of Brazil (Kramp 1957, 1959, 1961), was mistakenly reported as occurring between 0° – 60°S by Ramirez and Zamponi (1981, p. 458).

We believe that records of five species from the study area are based on misidentifications. Although reference material was missing or unavailable for some, our conclusions are supported by evidence given below. Specimens reported by Zamponi (1983b) as *Bougainvillia platygaster* are considered here to have been medusae of *B. macloviana* because his specimens were found in the same location where we found abundant medusae of the latter species. In addition, *B. macloviana* polyps have been found in that area (Hartlaub 1905; as *Perigonimus repens*; Jäderholm 1910, 1917; Genzano unpublished data). Furthermore, *B. platygaster* is widely distributed in tropical and subtropical waters (Kramp 1961; Pagés *et al.* 1992; Bouillon 1999) but not in cold temperate waters. In the same way, specimens reported as *Proboscidactyla ornata* by Zamponi (1983b) are herein considered *P. mutabilis*, since we found abundant specimens of *P. mutabilis* during more than 12 years of continuous sampling in the same locations as Zamponi's record. Moreover, in the southwestern Atlantic Ocean *P. ornata* is a well-known species in tropical waters from Brazilian coast (Vannucci 1957, 1963; Moreira 1973; Navas-Pereira 1981), but not in temperate waters. Medusae reported as *Eucheilota maculata* by Goy (1979) are considered here to be *E. ventricularis*. Specimens reported by Goy did not have the characteristic black interradial pigments present in *E. maculata*, and her description of the medusae agreed

with our specimens of *E. ventricularis* from the same location. The later is a well-known species, frequent and abundant in the area (Rodríguez 2006). Specimens of *Olindias sambaquiensis* were assigned erroneously to *O. phosphorica* by Zamponi (1983b). *Olindias sambaquiensis* is an endemic medusa of the temperate Atlantic coast of South America, and it represents one of the most studied species of hydromedusae in the region due to its stinging capabilities that represent a nuisance for tourist activities on the coast of Buenos Aires (see Mianzan 1989; Chiaverano *et al.*, 2004). Small medusae with six radial canals and gonads, reported as *Geryonia proboscidalis* by Zamponi and Genzano (1994) from the Buenos Aires coast, were considered here to be anomalous specimens of *Liriope tetraphylla*.

Fourteen species have been reported two or three times from the area in the literature and another 18 species have been reported only once, but none of them were found in this study (see table 2). Most of those species are Anthomedusae and Leptomedusae with a short planktonic life, making them very difficult to collect. In addition, most of those previously reported species are from to Subantarctic Island areas, which still remain less studied (see fig. 1b). However, some of these records must be considered doubtful, such as the presence of *Moerisia inkermanica*, native to the Black sea region; it is a well known invasive species established in different estuarine areas of the world (Mills and Rees 2000). The species was reported by Zamponi (1983b) as *Ostroumovia inkermanica*, without any particulars on the collection site. Furthermore, the only record of *Eutima gracilis* (Zamponi and Suarez 1991), which was based on two damaged and poorly preserved specimens collected from Mar del Plata shoreline, need to be confirmed. Likewise, the presence of *Aequorea macrodactyla* reported in the Strait of Magellan (Kramp, 1959) seems doubtful since all medusae of *Aequorea* found in the study in South Patagonia corresponded to *A. forskalea*. Finally, the validity of *Eucheilota foresti* is also questioned. This new species was created by Goy (1979) based upon one medusa specimen found near the Uruguayan coast. These species were included in this inventory list (table 2), but further studies will be necessary to confirm the presence of these species in the region.

Consequently, excluding the three invalid species, the two species erroneously reported, the five misidentifications noted here, and considering the six new records mentioned above, the number of species of hydromedusae now known from the neritic region of the southwestern Atlantic Ocean (33°–55°S) is 71.

Based upon this corrected inventory list, the data suggest that hydromedusa species numbers decrease markedly with increases in latitude. The temperate area of the southwestern Atlantic Ocean supports fewer species than neighboring areas such as the tropical waters of the southwestern Atlantic (Brazilian coast) where 131 species were listed (Migotto *et al.*, 2002) (actually 129 species, since *Bougainvillia niobe* and *Heterotiara anonyma* were erroneously reported from the southwestern Atlantic [see above]). The emended species number for the temperate waters is therefore 71. The small number of studies conducted in the coldest regions of the southwestern Atlantic (Subantarctic islands and Antarctic sector) demonstrate the presence of even fewer species; about 12 based upon Browne (1902), Browne and Kramp (1939), and Kramp (1959, 1961); and 14 in the eastern part of the Weddell gyre (55°35'–66°53'S) (Pagés *et al.* 1992). This decline in the number of species of hydromedusae with increasing latitude, from 130 to less than 15, is in agreement with numbers of other planktonic invertebrate groups in the region (Boltovskoy *et al.* 1999).

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References

- Acha, E.M., Mianzan, H., Guerrero, R., Favero, M. & Bava, J. (2004) Marine fronts at the continental shelves of austral South America. Physical and ecological processes. *Journal of Marine Systems*, 44, 83–105.
- Bakun, A. & Parrish R.H. (1991) Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic. *Journal of Marine Sciences*, 48, 343–361.
- Ballech, E. (1957) Division zoogeográfica del litoral Sudamericano. *Revista de Biología Marina*, 4, 184–195.
- Bigelow, H.B. (1909) The Medusae. *Memoirs of Museum Comparative Zoology, Harvard*, 37, 1–243.
- Blanco, O. (1994) Enumeración sistemática y distribución geográfica preliminar de los Hydroida de la República Argentina. Suborden Athecata (Gymnoblastea, Anthomedusae), Thecata (Calyptoblastea, Leptomedusae) y Limnomedusae. *Revista del Museo de La Plata, Nueva Serie, Zoología*, 14 (161), 181–216.
- Blanco, O., Zamponi, M.O. & Genzano G.N. (2000) Campanuliniidae de la Argentina (Coelenterata; Hydrozoa). *Revista del Museo de La Plata, Nueva Serie, Zoología*, 14 (163), 267–278.
- Boero, F., Gravili, C., Denitto, F.M., Miglietta, P. & Bouillon, J. (1997) The rediscovery of *Condonorchis octaedrus* (Hyroidomedusae, Anthomedusae, Pandeidae), with an update of the Mediterranean hydroidomedusan biodiversity. *Italian Journal of Zoology*, 64, 359–365.
- Boltovskoy, D., Gibbons, M.J., Hatchings, L. & Binet, D. (1999) General biological features of the South Atlantic. In: Boltovskoy, D. (Ed.), *South Atlantic Zooplankton*, Backhuys Publishers, Leiden, 869–1098.
- Bouillon, J. (1986) Hydroméduses de la baie de Hansa (Mer de Bismarck; Papouasie Nouvelle-Guinée): répartition, conditions climatiques et hydrologiques. *Indo-Malayan Zoology*, 3, 105–152.
- Bouillon, J. (1999) Hydromedusae. In: Boltovskoy, D. (Ed.), *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, 385–465.
- Bouillon, J., Medel, M.D., Pagès, F., Gili, J.M., Boero, F. & Gravili, C. (2004) Fauna of the Mediterranean Hydrozoa. *Scientia Marina*, 68 (supplement 2), 5–438.
- Brandhorst, W. & Castello, J.P. (1971) *Evaluación de los recursos de anchoíta (Engraulis anchoita) frente a la Argentina y Uruguay. I. Las condiciones oceanográficas, sinopsis del conocimiento actual sobre la anchoíta y el plan para su evaluación*. Proyecto de Desarrollo Pesquero. Food and Agriculture Organization Publication 29, 63 pp.
- Bradford-Grieve, J., Markkaseva, E.L., Rocha, C.E.F. & Abialy, B. (1999) Copepoda. In: Boltovskoy, D. (Ed.), *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, 869–1098.
- Browne, E.T. (1902) A preliminary report on hydromedusae from the Falkland Islands. *Annals and Magazine of Natural History*, 7 (9), 272–284.
- Browne, E.T. & Kramp, P.L. (1939) Hydromedusae from the Falkland Islands. *Discovery Reports*, 18, 265–322.
- Castro, B.M. & Miranda, L.B. (1998) Physical oceanography of the western Atlantic continental shelf located between 4°N and 34°S. In: Robinson, A. R., Brink, K. H. (Eds.), *The Sea*. John Wiley & Sons, New York. 11, 209–252.
- Chelton, D.B., Schlax, M.G., Witter, D.L. & Richman, J.G. (1990) Geosat Altimeter Observations of the Surface Circulation of the Southern Ocean. *Journal of Geophysical Research*, 95(10), 17877–17903.
- Chiaverano L., Mianzan, H. & Ramirez, F. (2004) Gonad development and somatic growth patterns of *Olindias sambaquiensis* (Limnomedusae, Olindiidae). *Hydrobiologia*, 530/531, 373–381.
- Gaitán, E. (2004) *Distribución, abundancia y estacionalidad de Liriope tetraphylla (Hidromedusa) en el Océano Atlántico Sudoccidental y su rol ecológico en el estuario del Río de la Plata*. Master Science Thesis, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, 42 pp.
- Genzano, G.N. (1995) New records of hydropolyps (Cnidaria, Hydrozoa) from south western Atlantic Ocean. *Miscelánea Zoologica*, 18, 1–8.
- Genzano, G.N. & Zamponi, M.O. (1991) Ciclos biológicos de celenterados litorales.V. *Syncoryne sarsii* (Loven, 1836) (Anthomedusae; Corynidae). La no vigencia de su sinonimia. *Physis*, 49 (116–117), 1–6.
- Genzano, G.N. & Zamponi, M.O. (1997) Frequency of study and diversity of benthic Hydrozoa of the Argentine Continental Shelf. *Ciencias Marinas*, 23 (3), 285–302.
- Genzano, G.N. & Zamponi, M.O. (2003) Hydroid assemblages from Mar del Plata, Argentina, at depths between 0 – 500 m: distribution and biological substrata. *Oceanologica Acta* 25 (6), 303–313.
- Genzano, G.N., Mianzan, H., Acha, M. & Gaitán, E. (2006) First record of the invasive medusa *Blackfordia virginica* in the Río de la Plata estuary, Argentina-Uruguay. *Revista Chilena de Historia Natural*, 79, 257–261.
- Girola, C. (1985) *Variaciones Cualitativas y Cuantitativas de las Hydromedusas de la zona estuarial de bahía Blanca*. Master Science Thesis, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, 28 pp.

- Girola, C., Sardella, N. & Martorelli, S. (1992) Presencia de metacercarias de *Monascus filiformis* (Digenena, Fellodistomidae) en hidromedusas del océano Atlántico sur. *Revista Chilena de Historia Natural*, 65, 409–415.
- Goy, J. (1979) Méduses. *Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du Sud (1961 – 1962)*, 11, 263–295.
- Grohmann, P.A., Souza, M.M. & Nogueira, C.C. (1997) Hydroids from the vicinity of a large industrial area in Vitória, Espírito Santo, Brazil. *Proceedings of the VI International Conference on Coelenterate Biology, Leiden, The Netherlands*, 227–232.
- Guerrero, R. & Piola, A. (1997) Masas de agua en la Plataforma Continental. En: Boschi, E. (ed.), *El Mar Argentino y sus Recursos Pesqueros. Tomo 1: Antecedentes históricos de las exploraciones en el mar y las características ambientales*. Publicación Especial INIDEP, Mar del Plata, Argentina, 107–118.
- Hartlaub, C. (1905) Die hydroiden der Magalhaensischen Region und Chilenischen Kuste. *Zoologische Jahrbucher*, Supplement 6 (3), 497–714.
- Hartlaub, C. (1913) Craspedote Medusen. Teil I Leif. 3. Tiaridae. In *Nordisches Plankton Zoologischer Teil*. Vol. 6. Reprint by Acher, A. & Co, Amsterdam, 1964, 237–363
- Jäderholm, E. (1910) Ueber die Hydroiden welche Dr. C. Skottsberg in den Jahren 1907–1909 gesammelt, *Arkiven för Zoologischer*, 6 (14), 1 – 5.
- Jäderholm, E. (1917) Hydroids from the South Seas. *Redogorelse Norrkopings H. Allman. Laroverk Lasaret 1916 – 1917*, 1 – 25.
- Kramp, P.L. (1939) Medusae, Siphonophora and Ctenophora. *The Zoology of Iceland*, 2, 1–37.
- Kramp, P.L. (1957) Hydromedusae from the Discovery collections. *Discovery Reports*, 29, 1–128.
- Kramp, P.L. (1959) The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Reports*, 46, 1–283.
- Kramp, P.L. (1961) Synopsis of the medusae of the world. *Journal of Marine Biological Association of United Kingdom*, 40, 1–469.
- Krepper, C.M. (1977) Difusión del agua proveniente del Estrecho de Magallanes en las aguas de la plataforma continental. *Acta Oceanográfica Argentina*, 1, 49–65.
- Mayer, A.G. (1910) *Medusae of the world. Hydromedusae*. Vol. I and II: 1–498. Washington.
- Mianzan, H.W. (1986) *Estudio sistemático y bioecológico de algunas medusas Scyphozoa de la región subantártica*, Doctoral Thesis, Facultad de Ciencias Naturales y Museo de la Universidad Nacional de La Plata, 196 pp., 22 lám.
- Mianzan, H.W. (1989) Distribución de *Olindias sambaquiensis* Müller, 1861 (Hydrozoa; Limnomedusae) en el Atlántico Sudoccidental. *Iheringia, Série Zoologica*, 69, 155–157.
- Mianzan, H.W. & Girola, C. (1990) Los Celenteros Pleustónicos *Physalia physalis* (Linne, 1758), *Velevella velevella* (Linne, 1758) y *Porpita umbella* Muller, 1776 en el Atlántico Suroeste. *Investigaciones Marinas. Centro Interdisciplinario de Ciencias Marinas*, 5, 97–98.
- Mianzan, H., Lasta, C., Acha, M., Guerrero, R., Macchi, G. & Bremec, C. (2001) The Río de la Plata estuary, Argentina-Uruguay. In: Seeliger, U., de Lacerda, L. D. & Kjerfve, B. (eds.), *Coastal Marine Ecosystems of Latin América*. Springer-Verlag, Berlin, Ecological Studies 144, 13, 185–204.
- Migotto, A.E., Marques, A.C., Morandini, A.C. & Da Silveira, F.L. (2002) Checklist of the Medusozoa of Brazil. *Biota Neotropica*, 2 (1), 1–31.
- Millard, N.A.H. (1975). Monograph on the Hydroida of Southern Africa. *Annals of the South African Museum*, 68, 1–513.
- Mills, C. & Rees, J.T. (2000) New observation and corrections concerning the trio of invasive hydromedusae *Maeotias marginata* (= *M. inexpectata*), *Blackfordia virginica* and *Moerisia* sp. in the San Francisco Estuary. *Scientia Marina*, 64, 151–155.
- Moreira, G.S. (1973) On the diurnal vertical migration of hydromedusae off Santos, Brazil. *Publications of Seto Marine Biological Laboratory*, 20, 537–566.
- Moreira, G.S., Leite, L.R. & Nipper, M.G. (1978) Notes on *Dipurena reesi* Vannucci 1956 (Hydrozoa, Corynidae) with a description of an unusual method of asexual reproduction. *Boletim de Fisiologia Animal, Universidade de São Paulo*, 2, 159–164.
- Navas-Pereira, D. (1981) Distribuição das hidromedusas (Cnidaria, Hydrozoa) na região da plataforma continental do Rio Grande do Sul. *Seminários de Biologia Marinha, São Paulo. Rio de Janeiro, Academia Brasileira de Ciências*, 221–276.
- Olson, D.B., Podestá, G.P., Evans, R.H. & Brown O.B. (1988) Temporal variations in the separation of Brazil and Malvinas Currents. *Deep-Sea Research* 35, 1971– 1990.
- Pagès F., Gili, J.M. & Bouillon, J. (1992) Medusae (Hydrozoa, Scyphozoa, Cubozoa of the Benguala Current) Southeastern Atlantic. *Scientia Marina* 56, 1–64.
- Piola, A.R., Campos, E.J.D., Möller, O.O., Charo, M. & Martinez, C. (2000) Subtropical Shelf Front off eastern South America. *Journal of Geophysical Research*, 105 (3), 6565–6578.
- Piola A.R. & Matano, R.P. (2001) Brazil and Falklands (Malvinas) Currents., In: Steele, J. H., Thorpe, S.A., and Turekian, K.K. (Eds.), *Encyclopedia of Ocean Sciences*. London, United Kingdom, Academic Press, 340–349.

- Ramírez, F.C. & Zamponi, M.O. (1980) Medusas de la plataforma bonaerense y sectores adyacentes. *Physis*, Sección A, 39 (96), 33–48.
- Ramírez, F.C. & Zamponi, M.O. (1981) Hydromedusae. In: Boltovskoy, D. (Ed.), *Atlas del zooplancton del Atlántico sudoccidental y métodos de trabajo con el zooplancton marino*. INIDEP, Mar del Plata, Argentina, 443–469.
- Rees, W.J. & Thursfield, S. (1965) The hydroid collections of James Ritchie. *Proceedings of the Royal Society of Edinburgh Biology*, 69, 34–220.
- Rodríguez, C. (2006) *Distribución, abundancia y estacionalidad de Mitrocomella frigida y Eucheilota ventricularis (Hydrozoa, Leptomedusae) en el Atlántico Sudoccidental (33 – 55 °S)*. Master Science Thesis, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, 46 pp.
- Rodríguez, C., Mianzan, H. & Genzano, G.N. (2007) First record of *Eutonina scintillans* Bigelow, 1909 (Hydrozoa: Leptomedusae: Eirenidae) in temperate waters from the South Western Atlantic Ocean. *Investigaciones Marinas*, 35 (2), 135–138.
- Schmidt, H.E. (1973) Hydromedusae from the eastern Mediterranean Sea. *Israel Journal of Zoology*, 22, 151–167.
- Schuchert, P. (1996) The marine Fauna of New Zealand: Athecate hydroids and their medusae (Cnidaria: Hydrozoa). *New Zealand Oceanographic Institute, Memoir, Wellington*, 106, 157 pp.
- Schuchert, P. (2001) Survey of the family Corynidae (Cnidaria, Hydrozoa). *Revue suisse de Zoologie*, 108 (4), 739–877.
- Schuchert, P. (2004) Revision of the European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Families Oceanidae and Pachycordylidae. *Revue suisse de Zoologie*, 111, 315–369.
- Stuardo, J. (1964) Distribución de los moluscos marinos litorales en Latinoamérica. *Boletín del Instituto de Biología Marina, Mar del Plata*, 7, 79–91.
- Thiel, M.E. (1938) Die Bezielung der Südatlantischen Ocean mit Hydromedusen. *Deutschen Atlantische, Expedition 'Meteor'*, 12 (2), 32–100.
- Vanhöeffen, E. (1910) Die Hydroiden der deutschen sudpolar-Expedition 1901–1903. *Deutsche Sudpolar Expedition, Zoologie*, 3 (4), 269–340.
- Vanhöeffen, E. (1913) Die Craspedoten Medusen des "Vetor Pisani". *Zoologica*, 67, 1–34.
- Vannucci, M. (1956) Biological notes and description of a new species of *Dipurena* (Hydrozoa, Corynidae). *Proceedings of the Zoological Society of London*, 127, 479–487.
- Vannucci, M. (1957) On brazilian hydromedusae and their distribution in relation to different water masses. *Boletim do Instituto Oceanografico, São Paulo*, 8 (1–2), 23–109.
- Vannucci, M. (1963) On the ecology of Brazilian Medusae at 25° lat. S. *Boletim do Instituto Oceanografico, São Paulo*, 13(1), 143–184.
- Vannucci, M. & Rees, W.J. (1961) A revision of the genus *Bougainvillia* (Anthomedusae). *Boletim do Instituto Oceanografico, São Paulo*, 11(2), 57–100.
- Vannucci, M. & Tundisi, J. (1962) Las medusas existentes en los museos de La Plata y Buenos Aires. *Comunicaciones del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"*. *Ciencias Zoológicas* 3 (8), 211–215.
- Wiebe, P.H. & Benfield, M.C. (2003) From the Hensen net toward four-dimensional biological oceanography. *Progress in Oceanography*, 56, 7–136.
- Zamponi, M.O. (1983a) Nuevas adiciones a la medusofauna de la región subantártica. I. Anthomedusae y Narcomedusae (Coelenterata: Hydrozoa). *Neotrópica*, 29 (82), 173–181.
- Zamponi, M.O. (1983b) Ecología de las hidromedusas del Mar Epicontinental Argentino. *Neotrópica*, 29 (81), 65–81.
- Zamponi, M.O. (1984) Una nueva cita para la región Subantártica: *Hybocodon prolifer* Agassiz, 1862 (Anthomedusae: Tubulariidae). *Physis, Sección A*, 42 (103), 86.
- Zamponi, M.O. (1985) La alimentación de algunas especies de Hydromedusae. *Neotrópica* 31 (86): 155–162.
- Zamponi, M.O. (1992) New records of medusae from the La Plata River. *Plankton Newsletter*, 17: 57–58.
- Zamponi M. O. & Genzano, G.N. (1994) Seasonal distribution of zooplankton gelatinous (Hydromedusae) from Samborombon Bay (Bs. Aires province, Argentina). *Plankton Newsletter*, 19, 51–56.
- Zamponi M.O. & Suarez, E. (1991) Blooms of medusae on the shores of Mar del Plata (Argentina). *Plankton Newsletter*, 15, 19–20.