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Review

Medusae (Scyphozoa and Cubozoa) from southwestern Atlantic and Subantarctic region (32-60°S, 34-70°W): species composition, spatial distribution and life history traits

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ABSTRACT. In this study, we reported the species composition and spatial distribution of Scyphomedusae and Cubomedusae from the southwestern Atlantic and Subantarctic region and reviewed the available knowledge of life history traits of these species. We gathered the literature records and presented new information collected from oceanographic and fishery surveys carried out between 1981 and 2017, encompassing an area of approximately 6,7 million km^2 (32-60°S, 34-70°W). We confirmed the occurrence of 15 scyphozoans and 1 cubozoan species previously reported in the region. *Lychnorhiza lucerna* and *Chrysaora lactea* were the most numerous species, reaching the highest abundances/biomasses during summer/autumn period. *Desmonema gaudichaudi*, *Chrysaora plocamia*, and *Periphylla periphylla* were frequently observed in low abundances, reaching high numbers only occasionally. *Phacellophora camtschatica*, *Aurelia* sp., *Drymonema gorgo*, *Atolla chuni*, *Stygiomedusa gigantea* and *Pelagia cf. noctiluca* were observed always in low numbers. *Atolla wyvillei*, *Stomolophus meleagris*, *Desmonema comatum* and *Tamoya haplonema* were reported just a few times and mostly individually. Although new species/reports can be found as surveys are undertaken, these results are considered to be the reliable baseline for further ecological studies seeking to understand the ecological role that these jellyfish play in marine ecosystems.

Keywords: jellyfish, Scyphomedusae, gelatinous zooplankton, Argentina, Uruguay, south Atlantic Ocean.

INTRODUCTION

Scyphomedusae and Cubomedusae (hereafter, the medusae stage of a polyp/medusa or medusa-only scypho- or cubozoan life cycle) include most of the largest solitary marine invertebrates. Most of them exhibit seasonal population outbreaks as a natural part of their life cycles and can reach high densities frequently named as “blooms” (Arai, 1997; Pitt & Lucas, 2014). Interest in these species has risen during the last three decades mainly due to the increasing reports of the negative socio-economical effects related to their mass occurrences (*e.g.*, fisheries, tourism, aquaculture; see Purcell *et al*., 2007; Richardson *et al*., 2009), the acknowledge from fishery scientists of the importance of including these species in ecosystem models (Pauly *et al*., 2009), and the expansion of the jellyfish fisheries from its origin in Asia abroad (Brotz & Pauly, 2017; Brotz *et al*., 2017). As a whole, these concerns highlight the need to better understand the factors controlling medusae abundance and the role of these species in the marine environment. Given the potential impacts of Scypho- and Cubomedusae on these valuable ecosystem services, baseline information on medusa composition and distribution is crucial.

Recent studies of gelatinous zooplankton in the world´s oceans revealed that the Southwestern Atlantic is one of the least studied regions (Condon *et al*., 2012;

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Lucas *et al*., 2014). Herein we present the current status of knowledge of the ecology of the scypho- and cubomedusae fauna from the southwestern Atlantic and Subantarctic region, encompassing Uruguayan and Argentine shelves and their adjacent oceanic waters between 32-60°S, 34-70°W (Fig. 1). We gathered historical data from the literature and added new data from different sources collected between 1981 and 2017. We also compiled the information about biological and ecological traits of each species and their interaction with human enterprise in the region. Finally, we described the spatial distribution patterns in relation to the traditional biogeographical schemes.

Records of species composition and spatial distribution in this region are characterized by a marked space-time discontinuity. The earliest data came from large plankton expeditions that occurred during the 19th and 20th century (Lesson, 1830; Haeckel, 1880, 1882; Browne, 1908; Vanhöffen, 1908; Stiasny, 1934). The reports from these expeditions were the only sources of knowledge about scyphomedusae until mid-20th century and several valid species were described from them (Fig. 2).

After a gap of about 30 years, a few more sporadic records were published (Vannucci & Tundisi, 1962; Goy, 1979) (Fig. 2). Then, Larson (1986) accomplished the first study covering a wide spatial range reporting the highest number of findings from Antarctic seas up to 30°S but based mainly on the inhabitants of the outer continental shelf and oceanic environments. A few years later, Mianzan published the first systematics and biogeographic account of these taxa, including for the first time neritic species from the Uruguayan and Argentine continental shelves (Mianzan, 1986, 1989a, 1989b; Mianzan *et al*., 1988). Ten years later, Mianzan & Cornelius (1999) provided the first literature review about the taxonomy and biogeography of these species, including maps of their spatial distribution. More recently, a few isolated studies have been published, two revisions made on particular species or restricted geographical areas, and a compilation of all faunistic data on medusozoans available for South American marine waters but with no information on spatial distribution (Table 1).

Biogeographic domains

The study area was divided into different biogeographic domains based on Boltovskoy *et al*. (1999). Coastal (neritic) domains were defined as the regions where oceanic circulation is significantly modified by the interaction with coastal topography and the coastal wind regime (Mittelstaedt, 1991). Thus, the coastal boundary domain is defined by the shelf-break front which latitudinally overlaps with the 200 m isobaths forming a wide continental shelf of *ca*. 200 nm along the Argentine coastline. Over the continental shelf, the northern area *i.e.*, the Transitional Neritic Domain is dominated by the Brazil Current (BC) flowing southwards and carrying subtropical plankters and higher temperatures (Fig. 1). The southern area *i.e.*, the Sub Antarctic Neritic Domain, is dominated by the northwards flowing Malvinas Current (MC) carrying subantarctic plankters (Fig. 1). In between, a Transitional Zone (sub-Antarctic) dominated by mixed subtropical-subantarctic assemblages is defined over the continental shelf (Fig. 1). Over oceanic waters (eastwards the continental shelf break), the Transitional Oceanic, the Sub Antarctic Oceanic, and the Antarctic Oceanic Domains are located from lower to higher latitudes (Fig. 1). The borders of these domains are seasonally variable and are still under discussion depending on the authors and the parameters utilized to define them.

Collection of new data and literature review

The boundaries of the study area were defined by the availability of records of macro medusae (>5 cm bell diameter) belonging to the classes Scyphozoa and Cubozoa. Thus, 3749 demersal and pelagic trawls at different geographical positions were examined resulting in 726 new records of scypho- and cubomedusae from neritic and oceanic environments (0 to 2500 m depth) gathered between 32-60°S and 34-70°W, encompassing an area of *ca*. 1.9 million nm^2 (~6.7 million km^2) and a 36-year period (1981-2017) (Fig. 1).

Most of the data were obtained from fishery and oceanographic research cruises. Although the main goal of these surveys was to collect data on fish stock assessment, the bycatch of non-targeted species provided the opportunity to assemble information about macromedusae over the broadest spatial scale ever studied in the region. Data were also collected through research programs performed (at smaller spatial scales) onboard small boats, or collecting specimens stranded on the beach in the scope of different research programs from Argentina and Uruguay. A small proportion of these new records also came from reports from citizen-science programs recently started at different tourist spots in Argentina. The proportion of data coming from these sources and the methodology applied in each case is detailed in Table 2.

The best representatives (well-preserved specimens) of most species reported as new records in this study were deposited in the medusozoan collection of the Marine Biological Station of the National University of Mar del Plata (Estación Costera Nágera, Mar del Plata, Argentina), and the Colección de Zoología de Invertebrados de la Facultad de Ciencias (Universidad de la

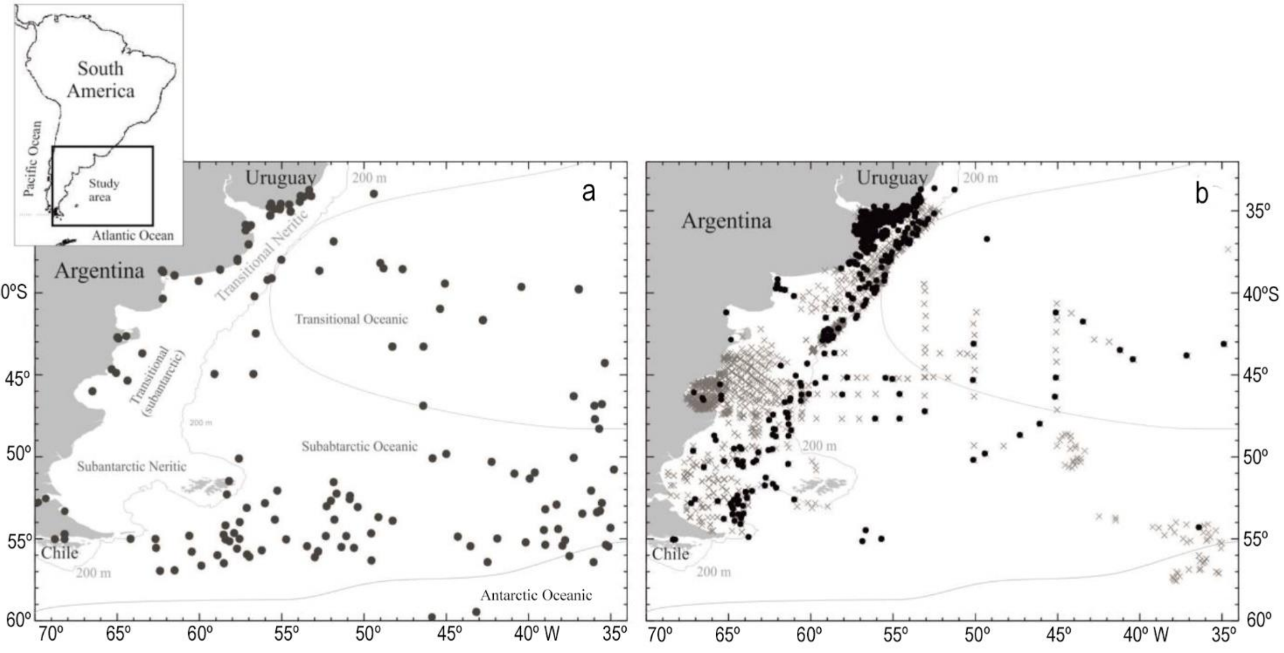

Figure 1. Map of the study area showing the location of the records of Scyphomedusae and Cubomedusae. a) Records present in the literature (period: 1880-2017, n = 215); b) location of the samples examined in the present study (crosses) (period: 1981-2017, n_{total} = 3749). New records of Scypho- and Cubomedusae presented in this study are represented by circles (n = 726). Biogeographic domains were based on Boltovskoy *et al.* (1999).

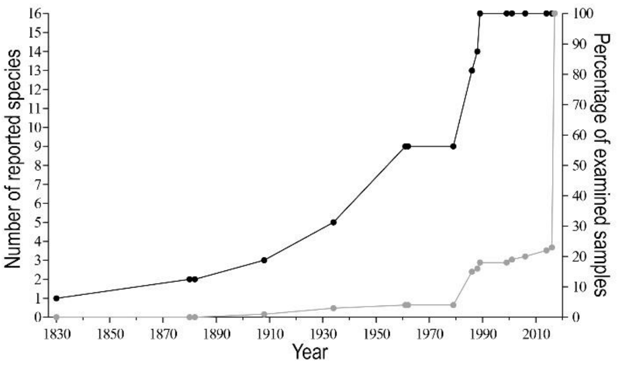

Figure 2. Scyphozoa and Cubozoa from the southwestern Atlantic and Subantarctic region (32-60°S, 34-70°W). The accumulated number of reported species (left axis, black dots) and percentage of examined samples over time (right axis, grey dots).

República, Montevideo, Uruguay). Freshly collected specimens were preserved in 4-10% formaldehyde solution in seawater (depending on the bell diameter). When possible, bell diameters were recorded using rulers (cm ± 0.5). In the few cases where the identification was achieved through the analysis of pictures taken at the sampling location, only confirmed species were included. The identification and classification broadly followed that presented by Oliveira *et al.* (2016). In addition to these new records, information available in the literature was reviewed including peer-reviewed papers, Spanish-written technical reports, and unpublished thesis.

We calculated the frequency of occurrence as the number of geographical positions (*i.e.*, sampling stations) from where each species was observed. The number of specimens observed/collected in each position were classified into one of the following categories: 0) record of the occurrence without further abundance data; 1) only one medusa was observed/ collected; 2) 2-20 medusae were observed/collected; 3) >20 medusae were observed/collected. In most cases, the information required for a proper classification of these phenomena was not available or was non-existent (see Box 2.2 in Lucas & Dawson, 2014). Therefore, the term ‘accumulation’ was used to refer the observations classified as 3 in our dataset without implying a cause. Only in the particular cases where the authors were confident about the magnitude of the accumulations, or the reasons causing it, specific terms were utilized.

Biases within the data set

Given the utilized sampling methodologies (gears and operational modes), relatively small species or specimens (*i.e.*, juvenile individuals) are likely misrepresented in the samples. Therefore, species composition and abundances may be underestimated.

Table 1. Peer-reviewed papers reporting new records of scypho- and cubomedusae from the southwestern Atlantic and Subantarctic region (32-60°S, 34-70°W). [1]Reported as *Phacellophora ornata*; [2]Reported as *Desmonema chierchianum* and *D. gaudichaudi* as two different species or only as *D. chierchianum*; [3]Reported as *Chrysaora hysoscella*; [4]Reported as *Aurelia aurita*; [5]Reported as *Catostylus cruciatus*; [6]Some specimens identified as *Chrysaora hysoscella*; [7]One specimen of *L. lucerna* reported as *Stomolophus meleagris*; [8]Reported as *Chrysaora gaudichaudi*; [9]Reported as *Chrysaora* sp.

	Lesson (1830)	Haeckel (1880)	Haeckel (1882)	Browne (1908)	Vanhöffen (1908)	Stiasny (1934)	Brattini & Ureta (1961)	Vannucci & Tundisi (1962)	Goy (1979)	Larson (1986)	Mianzan *et al.* (1988)	Mianzan (1989a)	Mianzan (1989b)	Mianzan & Cornelius (1999)	Pastorino (2001)	Faillia Siquier (2006)	Mianzan *et al.* (2014)	Stampar *et al.* (2016)	Leoni *et al.* (2016)	Dutto *et al.* (2017)	Present study
Chrysaora lactea								X	X^{6}		X^{6}	X	X			X^{6}				X	X
Chrysaora plocamia					X^{9}			X^{3}		X^{9}			X^{3}				X	X			X
Phacellophora camtschatica				X^{1}									X								X
Aurelia sp.											X^{4}	X^{4}	X^{4}			X^{4}				X^{4}	X
Drymonema gorgo												X	X							X	X
Desmonema comatum								X		X											
Desmonema gaudichaudi	X^{8}			X^{2}	X^{2}	X^{2}		X^{2}		X			X^{2}								X
Stygiomedusa gigantea										X				X							X
Poralia rufescens										X											
Lychnorhiza lucerna								X	X^{5}		X		X			X^{7}					X
Stomolophus meleagris													X								
Atolla wyvillei		X	X			X				X											X
Atolla chuni						X				X				X							X
Atolla gigantea										X											
Periphylla periphylla						X				X			X	X							X
Tamoya haplonema							X		X						X	X			X		X

Moreover, as samples came from the top 550 m of the water column, only the epipelagic and upper portions of the mesopelagic environments were considered. The deeper layers may contain other species which may inhabit surface waters at seasons or times of day that were not sampled mostly because of the diel vertical migrations. Therefore, the frequency of occurrence and abundance of bathypelagic species (*e.g.*, coronate medusae) may also be underestimated. The spatio-temporal heterogeneity of the sampling did hinder our ability to study population dynamics of these species; thereby, these parameters were pooled as a first approach into the study of the potential ecological, biogeographical and societal importance of these species in the region.

Species composition

The analysis of the literature and the surveys presented in this study yielded 15 unique species (*i.e.*, diagnosed as different species) and 1 morphotype corresponding to the genus *Aurelia*. *Aurelia aurita* was the species previously reported for the study area; however, we recorded it as *Aurelia* sp. in the present contribution (see below). The species belong to 2 classes, 4 orders, 10 families, and 12 genera. New records *i.e.*, geographical positions of 11 scyphomedusae and 1 cubomedusa species are presented in the present review but in all cases corresponded to species previously reported for the study region in spite of the large number of samples examined.

Although members of the Class Cubozoa are found south of 35°S in Australia and New Zealand (Southcott, 1956, 1958; Kramp, 1961, 1970), they were rare at the same latitudes in the southwestern Atlantic. Leoni *et al.* (2016) stated that attention will have to be paid due to the potential expansion of *Tamoya haplonema* southwards and its potential impact on tourism and general public health. However, the current evidence (*i.e.*, only sporadic findings) indicates that this species is so far rare in this region. In contrast, scyphozoan taxa (particularly Semaeostomeae) are well represented in both neritic and oceanic environments across the latitudinal range covered in this study.

From the total of *ca.* 200 scyphozoan species worldwide (Daly *et al.*, 2007), 15 (7.5%) have been recorded within the study area. It is likely that this relatively low number of species is due to the paucity of research rather than species impoverishment. For the Scyphozoa, in particular, the number of species is likely to rise as a result of an increased research effort

Table 2. Number of records of scypho- and cubomedusae from the southwestern Atlantic and Subantarctic region (32-60°S, 34-70°W), including the information source and method of collection. [1]INIDEP: National Institute for Fishery Research and Development, Mar del Plata, Argentina (www.inidep.edu.ar). [2]Collections or observations by specialists funded by different research grants, [3]Observations reported by citizens. Identification of specimens based on pictures, dates, and locations. Only accurate species ID were included.

Source	Sampling gear	Number of records
INIDEP[1] Fishery Research Cruises	Demersal trawling	475
	Pelagic trawling (midwater nets: IKMT, RMT, METHOT)	2
	Planktonic devices (Bongo, Nackthai, Motoda, Multinet)	47
	Benthic devices (dredge) Demersal trawling	4
		5
Oceanographic Research cruises performed by other institutions	Pelagic trawling (midwater nets: IKMT, RMT, METHOT)	36
	Planktonic devices (Bongo, Multinet)	12
Research Programs[2]	Strandings on the beach	127
Citizen Science[3]	Strandings on the beach	18
Total number of new records (1981-2017)		726
Number of records from literature (1880-2017)		215
Number of total records		941

(Appeltans *et al*., 2012), particularly on molecular analyses (Dawson, 2004; Chiaverano *et al*., 2016; Gómez-Daglio & Dawson, 2017). However, our results suggest that the current number of scyphozoan species might remain stable at least those inhabiting the upper 500 m of the water column. It is remarkable that the current number of species registered for the study area has been reached in 1989, after examining only the 18% of the currently available information (166/941 reports of scyphozoan species) (Fig. 2). Nowadays, in spite of having increased the number of records nearly six times in relation to the information available in the literature, the number of species did not increase (Fig. 2), at least based only on taxonomic criteria. In this regard, molecular techniques are likely to give new information on the number of species occurring within the area of study, as previous studies have shown genetic diversity without morphological differentiation (*e.g.* Dawson, 2003; Chiaverano *et al*., 2016).

PHYLUM CNIDARIA Verrill, 1865

SUBPHYLUM MEDUSOZOA Petersen, 1979

CLASS SCYPHOZOA Goette, 1887

ORDER CORONATAE Vanhöffen, 1892

FAMILY ATOLLIDAE Haeckel, 1880

1. *Atolla chuni* Vanhöffen, 1902
2. *Atolla wyvillei* Haeckel, 1880
3. *Atolla gigantea* Maas,1897

FAMILY PERIPHYLLIDAE Haeckel, 1880

4. *Periphylla periphylla* (Péron & Lesueur, 1810)

ORDER RHIZOSTOMEAE Cuvier, 1800

FAMILY LYCHNORHIZIDAE Haeckel, 1880

5. *Lychnorhiza lucerna* Haeckel, 1880

FAMILY STOMOLOPHIDAE Haeckel, 1880

6. *Stomolophus meleagris* L. Agassiz, 1860

ORDER SEMAEOSTOMEAE L. Agassiz, 1862

FAMILY CYANEIDAE L. Agassiz, 1862

7. *Desmonema gaudichaudi* (Lesson, 1830)
8. *Desmonema comatum* Larson, 1986

FAMILY DRYMONEMATIDAE Haeckel, 1880

9. *Drymonema gorgo* Müller, 1883

FAMILY PELAGIIDAE Gegenbaur, 1856b

10. *Chrysaora lactea* Eschscholtz, 1829
11. *Chrysaora plocamia* (Lesson, 1830)

FAMILY PHACELLOPHORIDAE Straehler-Pohl, Widmer & Morandini, 2011

12. *Phacellophora camtschatica* Haeckel, 1880

FAMILY ULMARIDAE Haeckel, 1880

13. *Aurelia* sp. Péron & Lesueur 1810
14. *Stygiomedusa gigantea* (Browne, 1910)
15. *Poralia rufescens* Vanhöffen 1902

CLASS CUBOZOA Werner, 1973

ORDER CUBOMEDUSAE Haeckel, 1880

FAMILY TAMOYIDAE Haeckel, 1880

16. *Tamoya haplonema* Müller, 1859

The occurrence of *Stomolophus meleagris*, reported in the literature in different occasions (Table 1), is based on the finding of one specimen (Fig. 3c). Sensu Mianzan (1986), this finding consists in one medusa (13.8 cm bell diameter) collected from Mar del Plata (Buenos Aires, Argentina) in September 1925 (preserved and at the MACN; collection #22807). Hence, Mianzan (1986) and Mianzan *et al*. (1989b) suggested that the occurrence *S. meleagris* in the study region is likely due to accidental occurrence rather than endemism. Our results support Mianzan's hypothesis and confirm that the occurrence of *S. meleagris* in Argentina has been an isolated episode. Given the spatial distribution of this species in the Atlantic coasts of South America (Oliveira *et al*., 2016), its presence in the study area is expected to be limited to the northern region in the Transitional Neritic Domain. Because the northern part of the study area has been intensively studied (Fig. 1b), it would be reasonable to expect *S. meleagris* to occur more frequently. Given the fact that it is not the case, we conclude that *S. meleagris* is not endemic of the study area and naturally inhabits lower-latitude, subtropical or tropical environments.

The other three species that were not found in the present study (*Poralia rufescens, Desmonema comatum, Atolla gigantea*) have been reported only by Larson (1986). Except for one record of *D. comatum* (Fig. 3g) found in the Transitional Neritic Domain, the other geographical positions were located in the Subantarctic Oceanic Domain, close to the Polar Front near the border of the Antarctic Domain (Fig. 4). This is a poorly studied area from which information is scarce. Therefore, in contrast to what has been observed for *S. meleagris*, it is likely that the number of reports of these species would increase with further research cruises in that particular area. On the other hand, *P. rufescens* and *A. gigantea* (Fig. 3) seem to be more frequent southwards of our study area in the Antarctic Oceanic Domain (Larson, 1986).

The frequent problems related to the identification of *Aurelia* species could also affect the number of scyphozoan species presented in the study region. Based on morphological features all the *Aurelia* specimens in this study corresponded to *Aurelia aurita*. However, we have found *Aurelia* medusae in two widely distant geographical areas. Whereas the majority of the specimens have been found in the Transitional Neritic Domain, eight specimens have been found off Ushuaia (55°S, Argentina) thousands of kilometers southwards in the Subantarctic Neritic Domain (Fig. 4). This major geographical separation posed the question that whether *Aurelia* is represented in the study region by two populations of the same species or by two different species. Although samples for genetic studies have been taken from the southern specimens (A.C. Morandini, *unpubl. data*), those corresponding to the northern findings have still to be collected.

Spatial distribution, frequency of occurrence, relative abundance, and life history traits

The spatial distribution of the different species identified in the study area is shown in Figure 4.

Lychnorhiza lucerna

The spatial distribution of *L. lucerna* (Fig. 3b) in the study region was derived from information provided in five previous studies collating 16 geographical positions over the coasts of Argentina and Uruguay (Table 1, Fig. 4). In the present paper, we report 255 new geographical positions confirming and extending the previous knowledge about the distribution of this species. The medusae of this species is limited to the northern region and occur along the Uruguayan coasts, drifting southwards over the surface salinity front of Río de la Plata Estuary and reaching the Buenos Aires Province coasts (Mianzan *et al*., 2001; Schiariti, 2008), always within the Transitional Neritic Domain (Fig. 4). Our data extended the southernmost limit of the spatial distribution from 37° to 38°S (Mar del Plata, Argentina). However, although *L. lucerna* is found south of 37°S, it occurred sporadically and always in low numbers (Fig. 4).

This species is one of the two most frequent and abundant scyphomedusae in the study region. In the 33% of the samples *L. lucerna* has formed accumulations (Table 3). These medusae have been found in estuarine and marine waters (rarely deeper than 40-50 m) during summer and autumn (December to early May) with few specimens found during winter (June-July) (Schiariti, 2008). However, their accumulations and mass occurrences have been reported almost exclusively between January and March. Specimens ranging from 5 to 48 cm always had mature gonads (Schiariti, 2008; Schiariti *et al*., 2012).

Lychnorhiza lucerna presents a metagenetic life cycle (Schiariti *et al*., 2008) but its polyps and ephyrae have never been found in their natural habitat (Schiariti, 2008). The diet of *L. lucerna* has been poorly studied. However, laboratory observations indicate that this species can consume ephyrae of other species (Carrizo *et al*., 2016). The only study describing feeding mechanisms and diet of *L. lucerna* included specimens collected from southeastern Brazil (Nagata, 2015; Nagata *et al*., 2016). The common accumulations of this species in the Río de la Plata Estuary attract sea turtles *Dermochelys coriacea* and *Chelonia mydas* that

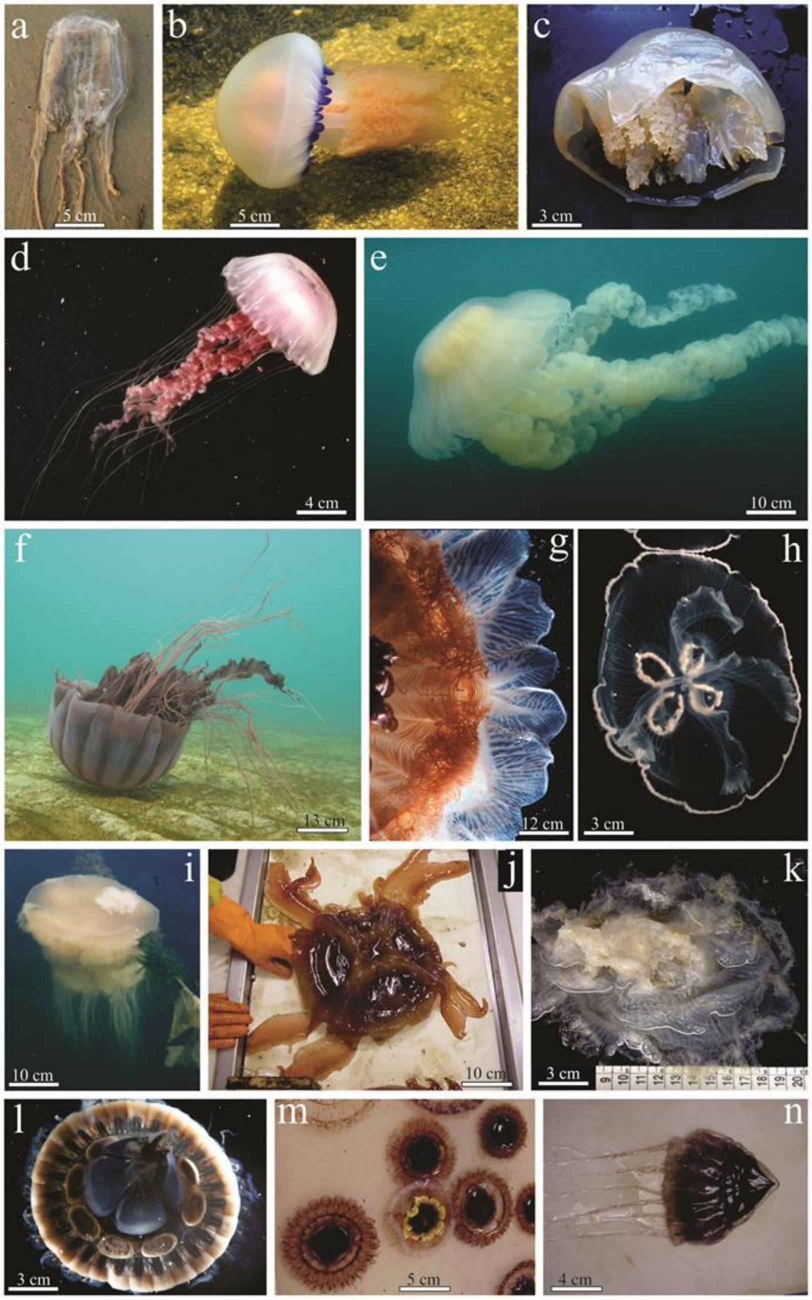

Figure 3. Scyphomedusae and Cubomedusae from southwestern Atlantic and Subantarctic region. a) *Tamoya haplonema* (photo S. García), b) *Lychnorhiza lucerna* (photo F. Montenegro), c) *Stomolophus meleagris* (photo A. Schiariti), d) *Chrysaora lactea* (photo L. Giberto), e) *Chrysaora plocamia* (photo M.S. Rodríguez, Beagle Secretos del Mar), f) *Desmonema gaudichaudi* (photo M.S. Rodríguez, Beagle Secretos del Mar), g) *Desmonema comatum* (photo R. Larson), h) *Aurelia* sp. (photo A.E. Migotto), i) *Drymonema gorgo* (photo H. Mianzan), j) *Stygiomedusa gigantea* (photo H. Mianzan), k) *Phacellophora camtschatica* (photo A.C. Morandini), l) *Atolla gigantea* (photo R. Larson), m) *Atolla wyvillei* (photo H. Mianzan), n) *Periphylla periphylla* (photo H. Mianzan).

prey on them (Estrades *et al*., 2007; González-Carman *et al*., 2014). In addition to trophic interactions, different interspecific associations have been described between *L. lucerna* and other taxa including crabs, cestodes, digenean parasites, and fishes (Vannucci-Mendes, 1944; Zamponi, 2002; Morandini, 2003; Morandini *et al*., 2005; Nogueira Jr. & Haddad, 2005; Sal Moyano *et al*., 2012; Schiariti *et al*., 2012). The

Figure 4. The geographical position of Scyphomedusae and Cubomedusae and from southwestern Atlantic and Subantarctic region. Circle size is proportional to the number of specimens collected. 0: information about the number of observed/collected specimens not available; 1: one single specimen observed/collected; 2: between 2 and 20 specimens observed/collected; 3: more than 20 specimens observed/collected. Records from literature are indicated by stars.

presence of the most vulnerable life stages of crabs (larvae, juveniles, and soft-shell individuals) within the gastric cavity of *L. lucerna* indicates that this medusa constitutes one of the few available structures in the pelagic realm of the Río de la Plata Estuary probably providing protection against predation (Schiariti *et al*., 2012).

The large accumulations of *L. lucerna* during summer and autumn interfere with tourism and fisheries in the region (Schiariti, 2008; Nagata *et al*., 2009). Although *L. lucerna* is not a stinging species, its large accumulations frequently strand on beaches and rapidly decompose, generating nuisance for the different recreational activities in these areas (summer tourism, recreational fishing, surf, kite-surfing, sailing, etc.). On the other hand, the development of a jellyfish fishery based on *L. lucerna* is currently under investigation in Argentina (Schiariti, 2008; Schiariti & Mianzan, 2013; Brotz *et al*., 2017). The potential extraction of collagen is an ongoing project as well in Brazil and Argentina.

Chrysaora lactea

Chrysaora lactea (Fig. 3d) has been reported in eight previous studies achieving a total of 18 locations in the Río de la Plata Estuary (Argentina-Uruguay) and Buenos Aires Province (Argentina) (Table 1, Fig. 4). Here, we report 239 new geographical positions where this species has been observed, confirming and extending the previously known spatial distribution. The distribution of *C. lactea* resembled that of *L. lucerna* occurring all over the Río de la Plata Estuary at the Transitional Neritic Domain. However, *C. lactea* reaches higher latitudes along the Buenos Aires Province coast. Our data extended southwesterly the spatial distribution range of this species from Bahía San Blas (40ºS, 62ºW) to Las Grutas (41°S, 65ºW) (Fig. 4). In addition, this species has been sporadically found deeper over the continental shelf up to the shelf break front but always within the Transitional Neritic Domain (Fig. 4).

Chrysaora lactea is also one of the most frequent and abundant species from the region. In the 31% of the cases, this species has been found forming accumulations (Table 3). High abundances of adult medusae have been observed throughout their range. However, these phenomena are more common and intense near the coast and at the outer region of the Río de la Plata (Fig. 4).

Adults of *C. lactea* have been observed mostly from December to May with sporadic specimens found in August, and accumulations were found between January and April. Bell diameters ranged between 4 and 21 cm. Specimens larger than 9 cm have mature gonads. This species presents a metagenetic life cycle (Morandini *et al*., 2004). Despite of being previously reported (Table 2 in Duarte *et al*., 2012), polyps of *C. lactea* have been never found in their natural habitat. Although Mianzan (1989a) specifically stated that polyps have not been found in the wild, the presence of ephyrae suggests they should be located nearby at the Bahía Blanca harbor. Interestingly, ephyrae were frequently found only in the Bahía Blanca Estuary and neighboring areas (from October to January; Dutto *et al*., 2017) but never in the Río de la Plata Estuary (Fig. 4) despite numerous plankton samples examined in this later area (>3500; Schiariti, 2008).

In contrast to *L. lucerna*, the presence of *C. lactea* ephyrae suggests that this species may complete its life cycle in Argentina, off southern Buenos Aires Province. However, further studies are needed in the region to corroborate this hypothesis. Mianzan (1986) presented the only estimations of growth rate for this species, reporting specimens from 1.8 to 2.9 mm from Bahía Blanca reached between 3.5 and 91 mm during December-January and between 36.0 and 146 mm by February-March. Although no information about the number of medusae examined is available, Mianzan (1986) reported an average growth rate of 0.66 mm d^{-1} (based on mean monthly numbers).

Very little is known about the diet of *C. lactea* in the region. Mianzan (1986) reported unidentified gelatinous fragments (likely ctenophores) and one hydromedusa specimen (*Phialella falklandica*) and a juvenile fish (*Scynosion striatus*) within the gastric cavity, and calanoid copepods and tintinnids in the tentacles.

Other interspecific interactions observed in *C. lactea* medusae from Argentina and Uruguay include several unidentified fish species swimming around their conspicuous oral arms. In addition, a few studies have reported parasitic associations between *C. lactea* and the isopods *Cymothoa catarinensis* and *Synidotea marplatensis* (Nogueira Jr. & Silva, 2005), as well as the larvae of the anemone *Peachia* sp. (A. Puente, *pers. comm.*).

Chrysaora lactea has been described as a stinging species in Brazil (Marques *et al*., 2014). Although no formal studies have been performed in Argentina and Uruguay, reliable identifications made by lifeguards indicate that these species do sting (Dutto *et al*., 2017), and that could be troublesome if their accumulations overlap with the several touristic hotspots over the Buenos Aires province (Argentina) and Uruguayan coasts.

Desmonema gaudichaudi

Desmonema gaudichaudi (Fig. 3f) has been reported in seven studies, occasionally as *D. chierchianum*, achieving a total of 11 geographical positions in suban-

Table 3. Frequency of occurrence (*i.e.*, number of records of each species), and number of specimens captured/observed in each case. 0: number of sampling stations with no information about the number of observed/collected specimens; 1: number of reports with one single specimen observed/collected, 2: number of reports with 2-20 specimens observed/collected, 3: number of reports with >20 specimens observed/collected.

Species	Frequency of occurrence			Relative abundance			
	Literature	Present study	Total	0	1	2	3
Lychnorhiza lucerna	16	255	271	130	25(18%)	69(49%)	47(33%)
Chrysaora lactea	18	239	257	57	47(23%)	92(46%)	61(31%)
Desmonema gaudichaudi	11	137	148	25	68(55%)	39(32%)	16(13%)
Periphylla periphylla	38	33	71	36	33(94%)	2(6%)	0
Aurelia sp.	6	38	44	18	5(19%)	15(58%)	6(23%)
Atolla wyvillei	35	1	36	36	0	0	0
Atolla chuni	27	1	28	26	2(100%)	0	0
Tamoya haplonema	22	3	25	1	22(92%)	2(8%)	0
Chrysaora plocamia	13	9	22	10	7(77%)	0	4(23%)
Drymonema gorgo	5	6	11	1	8(80%)	2(20%)	0
Stygiomedusa gigantea	4	3	7	3	4(100%)	0	0
Phacellophora camtschatica	2	4	6	1	2(40%)	3(60%)	0
Poralia rufescens	8	0	8	8	0	0	0
Desmonema comatum	3	0	3	3	0	0	0
Atolla gigantea	3	0	3	3	0	0	0
Stomolophus meleagris	1	0	1	0	1(100%)	0	0

tarctic waters (Table 1, Fig. 4). In the present review, we add 137 new geographical positions, extending its range of spatial distribution northwards, from 50° to 35°S (Fig. 4). Thus, our new data show that the distribution of *D. gaudichaudi* is not restricted to subantarctic waters but extends northwards from the Subantarctic Neritic and the Subantarctic Oceanic Domains, and northwards by the MC along the shelf-break front *i.e.*, the border between the Transitional Oceanic and Transitional Neritic Domains (Fig. 4).

Desmonema gaudichaudi is the third most common species in the region (Table 3). However, their accumulations were found only in the 13% of the samples. This species represents one of the most common by-catch items (in terms of biomass) of demersal trawls performed by commercial fishing vessels over the continental shelf break (200-1000 m depth) between 40 and 55ºS (A. Schiariti, *pers. obs.*). Medusae of *D. gaudichaudi* have been also reported stranded at different locations in southern Patagonian coasts (Fig. 4) but so far at relatively low numbers (Table 3). These results posed the question whether the apparently low occurrence of these accumulations correspond to natural cycles or sampling bias related to 1) the seasonality of its population dynamics, or 2) the fact that this species has been frequently caught in deep waters (from 200 to 3000 m) by using sampling gears that covered only the upper layers (sporadically deeper than 400-500 m).

Knowledge about this species is almost restricted to taxonomic and morphological descriptions. Large (20-100 cm bell diameter) and sexually mature medusae have been recorded throughout their range of distribution. However, the paucity of the observations prevented us from identifying temporal patterns. The life cycle of *D. gaudichaudi* has not yet been described. Assuming that metagenesis is typical among the Semaeostomeae species (18 metagenetic life cycles over 20 descriptions of semaeostome species; Jarms, 2010; Morandini *et al.*, 2013), this species is likely to have a metagenetic life cycle. If this is the case, why sexually mature medusae are frequently found over such a wide latitudinal range, where the chances for the planulae to access substrate to settle and metamorphose into polyps are minimal because of the deep depths? A plausible answer to this question may be found in the concept of "sources and sinks populations", proposed for habitats differing in quality (Dias, 1996). Thus, the medusae occurring in the neritic environment surrounding Tierra del Fuego and Malvinas (= Falkland) Islands would constitute a source population where the proximity to the coasts (*i.e.*, available substrates) would allow the completion of the metagenetic life cycle. On the other hand, the medusae drifting northwards over the continental shelf-break would constitute the exported demographic surplus that could form the "sink populations". Further studies are needed to test this hypothesis.

One previous study reports the presence of hyperiid amphipods (likely *Hyperia galba*; up to 50 individuals per medusa host) infesting the radial canals of *D. gaudichaudi* (identified as *D. chierchianum*; Mianzan, 1986). No stinging events or injuries to humans have been reported. However, the large diameters commonly found in combination with the large accumulations of this species do generate problems for commercial fishing operations (A. Schiariti, *unpubl. data*).

Periphylla periphylla

Periphylla periphylla (Fig. 3n) has been reported from 71 geographical positions, 38 from the literature and 33 from our new dataset (Table 1, Fig. 4). In the southwestern Atlantic, this species has been always found inhabiting oceanic environments (see references in Table 1), along almost the entire latitudinal range covered in this review (south of 35°S) and eastwards of the shelf-break front at the border between the continental shelf and the oceanic deep-waters (Fig. 4). All new geographical records included in this paper are within the previously described geographical distribution, but they fill in some spatial gaps (Fig. 4). The occurrence of *P. periphylla* was restricted to the Subantarctic and Transitional Oceanic domains. Although documented in all the expeditions performed in oceanic environments within the boundaries of the study area, this species has been always found in low numbers (mostly one single specimen) (Table 3), which may be attributed to the sampling gear does not reach depths deeper than 500 m. Therefore, subsequent exploration of deeper waters may result in higher estimations of *P. periphylla* abundances/biomasses in the region.

This species has a holopelagic life cycle (Jarms *et al*., 1999) but the life history and population dynamics of *P. periphylla* in the southwestern Atlantic and Subantarctic region remains unknown. The only available information to date consists of bell diameter of two specimens (3 and 8 cm) collected at 55ºS-57ºW with the larger individual carrying developed gonads. A few specimens were also observed northwards of the study area, along the coast of Brazil (Morandini, 2003).

Chrysaora plocamia

Chrysaora plocamia (Fig. 3e) has been reported at 22 geographical positions in five studies including the present paper. This species has been previously reported as *Chrysaora* sp. and *C. hysoscella*; however, all these records have been confirmed to be *C. plocamia* by Morandini & Marques (2010) (Table 1, Fig. 4). The nine new records presented here confirmed the previously described range of the species, except for one finding located *ca*. 200 nm offshore over the shelf-break front (200 m depth) (Fig. 4). All the geographical records of this species are within the mixed zone in between the Transitional Neritic and Subantarctic Neritic, known as Transitional (Subantarctic) at depths lower than 50 m (Fig. 4). The occurrence of large and sexually mature specimens (25-40 cm bell diameter) is relatively common along the northern Patagonian coasts between 42° and 46°S, becoming rare northerly (Fig. 4). Smaller specimens (9-20 cm) have been found in relatively low abundances (Mianzan, 1986). Accumulations of *C. plocamia* are common off Peru and northern Chile, but much rarer in the studied area, with only three reports in northern Patagonia (Mianzan *et al*., 2014; present study), where this species mostly occurs in low numbers or even individually (Table 3). The connectivity between the Pacific and Atlantic populations can be partially explained by the circulation of the MC interacting with the Patagonian current flowing northwards (Acha *et al*., 2004 for oceanographic descriptions). The same explanation could also be given for the two isolated findings of *C. plocamia* at the shelf break front (*ca*. 42°S, 59°W, present study) and the Uruguayan coast (Stampar *et al*., 2016) in the Transitional Neritic Domain (Fig. 4).

Chrysaora plocamia has a metagenetic life cycle (Riascos *et al*., 2013) but the location of polyps in their natural habitat is unknown. Post-ephyrae and juvenile stages have been reported as *C. plocamia* by Mianzan (1986, 1989a) occurring in spring. The few sexually mature medusae were found in Patagonia during austral summer-autumn. In this area, a few senescent medusae have been observed with damaged and decomposed tentacles and oral arms over the seabed in late autumn (see Fig. 10.3 in Mianzan *et al*., 2014). In addition to their potential role in biogeochemical cycles transporting the energy obtained in the pelagic realm to the bottom, some schools of stromateid juvenile fishes have been observed probably looking for shelter and food around large *C. plocamia* medusae (see Fig. 10.5 in Mianzan *et al*., 2014). A large proportion of specimens of this medusa has been found infected by the sea anemone *Peachia hastata*; between 1 and 11 larvae were found attached to different body parts of the medusae (oral arms, tentacles, gastric cavity) (Mianzan, 1986). Due to its impact on different human enterprises in the Pacific *C. plocamia* has been identified as a troublesome species (Mianzan *et al*., 2014). However, little reliable evidence has been found in Argentina.

Aurelia sp.

Aurelia sp. medusae (Fig. 3h) have been reported at six geographical positions, three of them near the Uruguayan coast of the Río de la Plata (*ca*. 35°S) and the other three off Bahía Blanca (39°S) and Bahía San Blas (40°S, Buenos Aires, Argentina) (Table 1, Fig. 4). In the present paper, we found 35 new records at the Río de la Plata Estuary and along the Buenos Aires Province coasts, filling spatial gaps in between these two areas and confirming the previously reported locations within the Transitional Neritic Domain (Fig. 4). We also have found *Aurelia* sp. at three new geographical locations off Ushuaia (Tierra del Fuego, Argentina), in the Subantarctic Neritic Domain (Fig. 4).

In contrast to the frequent and intense blooms of *Aurelia* species in other regions (Lucas, 2001), in Argentina and Uruguay, this species occurred at intermediate frequencies and mostly at low numbers (Table 3), with one accumulation of *Aurelia* sp. being reported so far (Mianzan, 1989a). Ephyrae, juveniles, and adults have been observed along their distributional range (Mianzan, 1986, 1989a, 1989b; Mianzan *et al*., 1988; Faillia-Siquier, 2006; Dutto *et al*., 2017). In the Bahía Blanca Estuary, ephyrae were captured from November to December (2.6-3.0 mm), and juveniles and adults have been found between January (55-350 mm) and May (180-219 mm), with growth rates estimated at 0.62 mm d^{-1} (Mianzan, 1986). Although reported in Duarte *et al*. (2012), *Aurelia* sp. polyps have been never found in their natural habitat within the boundaries of the study area (see the description of *C. lactea* for explanations).

Atolla wyvillei

Atolla wyvillei (Fig. 3m) has been reported five times in the study region including the present contribution (Table 1, Fig. 4). The only new record presented here is located within the previously reported distribution (Fig. 4). There is no available information about the numbers, sizes, or state of maturity. The sparse new records and the lack of general biological information did not allow us to improve the previous knowledge about the distribution of *A. wyvillei*. This species was observed reaching intermediate frequencies but mostly at low numbers (Table 3). However, taking into account that the occurrence of this species was observed in all of the few cruises performed in the oceanic environment, it is likely that it is a common species in the Subantarctic Oceanic and the Antarctic Oceanic Domains (Larson, 1986). As an oceanic coronate species, *A. wyvillei* seems to be a deep-water species. Therefore, as for *P. periphylla*, subsequent exploration of deeper layers may result in higher frequencies and abundances in the region. Its life cycle remains unknown. As in the case of *P. periphylla*, this species was also observed northwards of the study area, along with the coast of Brazil (Morandini, 2003).

Atolla chuni

Atolla chuni has been reported four times in the study region including the present contribution (Table 1, Fig. 4). The only new record provided by this paper is located within the previously reported range (Fig. 4). This coronate medusa has been found in oceanic waters from 38°30´ to 56°25´S and from 35° to 59°W and is apparently more frequent near the Polar Front (Antarctic Convergence), separating the Subantarctic from the Antarctic Oceanic Domains. This species showed a similar pattern of spatial distribution that of *A. wyvillei* and was similarly observed reaching intermediate frequencies, mostly at low numbers (Table 3). No information about the number of specimens collected was available. Nothing is known about its life cycle or reproductive traits. Larson (1986) observed that some preserved *A. chuni* specimens had partially digested, large calanoid copepods, chaetognaths, hyperiid amphipods, and euphausiids attached to their gastric cirri, suggesting that *A. chuni* had eaten these prey items before it was captured.

Tamoya haplonema

Including this paper, there are only five reliable reports of the occurrence of *T. haplonema* (Fig. 3a) within the boundaries of the study area (Table 1, Fig. 4). The first record of a cubomedusa from the study area was made by Barattini & Ureta (1961, sometimes dated as 1960) as an uncommon occurrence of *Carybdea atlantica*. However, it has been considered that this record is dubious and possibly conspecific with *T. haplonema* (Mianzan *et al*., 1988; Mianzan & Cornelius, 1999; Pastorino, 2001; Leoni *et al*., 2016); thereby, it has been omitted in this study. Three new records (one specimen each) are reported in the present study slightly extending northwards the previously known range within the boundaries of the study area (Fig. 4). However, they were all within the previously known range of spatial distribution of the species (from 3° to 38°S, see Oliveira *et al*., 2016 and references therein). Most of the reported specimens of *T. haplonema* have been found stranded on the beach (see Table 1 in Leoni *et al*., 2016). Furthermore, in the few cases of specimens collected onboard research cruises, this medusa was always found in neritic environments (Leoni *et al*., 2016; present study) as previously reported for other regions (Nogueira Jr. & Haddad, 2006). We observed that the occurrence of this species is sporadic but always limited to the Transitional Neritic Domain (Fig. 4). This cubomedusa was always found in intermediate to low frequencies and at low numbers (Table 3), with one single specimen found most of the time (never more than 2) at each time and location. Indeed, the total number of specimens recorded is lower than 30 since its first reliable record in 1961 published by Goy (1979). The low frequency of occurrence and their low abundance confirmed that the Argentine and Uruguayan coasts are the southernmost limit of the distribution of this species. Furthermore, only one of the 26 recorded medusae was found south of the Río de la Plata Estuary (Fig. 4).

Information on its biology and ecology is very limited probably due to its sporadic occurrence and the relatively few specimens available for study. Some observations on their diet have been published for Brazilian specimens (Nogueira Jr. & Haddad, 2008) but not for specimens collected within the boundaries of the study area. Bell height of the few available data ranged between 6 and 16 cm (Leoni *et al*., 2016). The life cycle has not been described yet.

Drymonema gorgo

Drymonema gorgo (Fig. 3i) was previously reported by Mianzan (1986, 1989a, 1989b) and Dutto *et al*. (2017) who found specimens stranded on the beach at two different locations at the Buenos Aires Province coast (Table 1, Fig. 4). In the present review we added six more findings of medusae stranded in the same region and at the Uruguayan coast (Fig. 4). Therefore, the occurrence of this species is restricted to the Transitional Neritic Domain (Fig. 4). This species has been observed reaching intermediate frequencies but always at low numbers (mostly one single medusa was found in each case, and never more than three at the same position) (Table 3). *Drymonema gorgo* has been observed at the Río de la Plata Estuary (Argentina-Uruguay), and over the Buenos Aires Province coast at Mar del Plata and Bahía Blanca (Fig. 4). Although few specimens were collected, they were found over a wide temporal period (February, March, April, May, and August) suggesting a wide temporal occurrence. The only six specimens measured ranged from 5.2 to 18.3 cm in bell diameter (Mianzan, 1986). Only the presence of “juveniles and adults” has been recorded (H. Mianzan, *pers. comm.*). Feeding strategies or diet of *D. gorgo* has not been studied. However, an experimental observation in the laboratory based on a single medusa indicated that this species can catch and consume other medusae like *Olindias sambaquiensis* (Mianzan, 1986). Such medusivorous diet is shared with other species of the genus (Larson, 1987; Bayha & Dawson, 2010).

Stygiomedusa gigantea

Stygiomedusa gigantea (Fig. 3j) has been reported in seven geographical positions in the Subantarctic Oceanic Domain, six of them south of 50°S near the boundary with the Antarctic Domain (Table 1, Fig. 4). It is a rare species that has been reported only a few times (literature and new records) and mostly as single specimens (Table 3). The two medusae measured in this study had bell diameters of 33 and 39 cm. This species is the only scyphomedusa supposed to be viviparous. A detailed description of this unique reproductive feature is given by Russell & Rees (1960) and our observations agreed with them. The observed specimens agreed with the description of the species; the only point to mention is that the network of anastomosing canals is less complex (probably due to the size of the specimens).The absence of tentacles and the extreme development of its oral arms suggest that the arms capture prey while the medusa is swimming (Larson, 1986). However, no empirical evidence has been found.

Phacellophora camtschatica

Phacellophora camtschatica (Fig. 3k) has been reported for the study region only in three cases including the present contribution totalizing six locations (Table 1, Fig. 4). With the exception of Browne (1908), who reported one specimen found at the northern limit of the Transitional Oceanic Domain, the remaining five findings corresponded exclusively to the Transitional (subantarctic), the transitional area in between the Transitional Neritic and the Subantarctic Neritic domains (Fig. 4). It is a rare species that has been reported only a few times (literature and new records) and mostly as single specimens (Table 3). The life cycle of *P. camtschatica* has been described as metagenetic (Widmer, 2006). Adults, juveniles, and metephyrae have been found always in low numbers (<5 specimens) but the location of polyps in the wild remains unknown. Bell diameter of the few measured specimens (n = 6) ranged between 13.9 and 22.0 cm. No observations about the diet of this species were made for the specimens collected in the study area. However, *P. camtschatica* was observed feeding on medusae, ctenophores, and fish larvae (Larson, 1986). Specific tests were performed on humans but no stinging effects have been observed (Mianzan, 1986).

Poralia rufescens

This species has been reported only by Larson (1986) who found them in eight geographical positions, mostly in the Subantarctic Oceanic Domain around 55°S and near the Polar Front over the border between this and the Antarctic Domain (Table 1, Fig. 4). Only one report has been located northwards at 47°S corresponding to the southern part of the Transitional Oceanic Domain (Table 3, Fig. 4). No information about numbers and bell diameter was found. The presence of filiform tentacles and small oral arms suggests that it feeds on small prey most likely swallowed whole (Larson, 1986).

Desmonema comatum

This species has been reported for the study region by Vannucci & Tundisi (1962) and Larson (1986) at three different locations, two of them located over the border between the Neritic and Oceanic Subantarctic Domains (over the 200 m isobath between 52° and 55°S), and the third one about 20° northwards at the Transitional Neritic (35°S) over the coast of the Buenos Aires Province (Table 1; Figs. 3g, 4). No information about the number of specimens collected was given. Vannucci & Tundisi (1962) reported bell diameters of three specimens captured off Isla de Los Estados (Tierra del Fuego, Argentina) (10, 19 and 21 cm). Although the diet of *D. comatum* is unknown, the existence of its thin, threadlike tentacles suggests that it probably catches small or weakly swimming prey (Larson, 1986).

Atolla gigantea

As for the previous two species, *A. gigantea* (Fig. 3l) has been reported only by Larson (1986) (Table 1, Fig. 4). This species has been found only at three sampling stations, in the Subantarctic Oceanic Domain around the 55°S (Fig. 4). No information about the number of specimens collected not their sizes were given.

Stomolophus meleagris

Only one medusa of this species has been found within the limits of the study area (Table 1; Figs. 3c, 4). This unique finding, firstly reported by Mianzan (1986) and later by Mianzan (1989a), corresponded to a medusa of 3.8 cm collected in September 1925 in Mar del Plata (Buenos Aires, Argentina) (specimen deposited in the MACN, collection Nº22807).

CONCLUSIONS

Our study provides the first review of the species composition, spatial distribution patterns, life history and interaction with human enterprises of the Scypho- and Cubozoan fauna from a vast study region in the southwestern Atlantic Ocean. The new records of scyphozoan species from Argentine and Uruguayan continental shelves and their adjacent oceanic waters presented in this study exceeded by 3.4 times the total number of previously reported data collected for the same area during the last 137 years (1880 to 2017) and represents the largest scyphozoan data-base from Latin America in terms of the sampling effort (temporal and spatial coverage) and biological and ecological information.

There are particular important regions within the study area where fisheries and other socio-economical activities take place. In some of these regions, scyphozoan can form frequent accumulations. The Río de la Plata Estuary and adjacent marine waters, where intense fishing activity take place involving resources shared by Argentina and Uruguay, is the most important region within the boundaries of the study area as evidenced by common and intense occurrences of *L. lucerna* and *C. lactea*. On the other hand, *D. gaudichaudi* frequently reaches high numbers over the southern Patagonian coasts and the continental shelf break throughout most of the latitudinal range covered in this study, and overlap with another important fishing resource of Argentina such as the squid *Illex argentinus* (Brunetti *et al*., 1998). In contrast, jellyfish fauna from one of the most important fishing grounds of Argentina (San Jorge Gulf and adjacent waters in northern Patagonia), where the fisheries of the Argentine hake (*Merluccius hubbsi*) and the Patagonian shrimp (*Pleoticus muelleri*) are caught (Bezzi *et al*., 2004; Moriondo-Danovaro *et al*., 2016), seemed to be dominated by non-scyphozoan gelatinous species including the ctenophores *Mnemiopsis leidyi* and *Pleurobrachia pileus* and the hydromedusae *Aequorea* sp. (Schiariti *et al*., 2015). The only scyphomedusae species observed in this particular area are *C. plocamia* and *P. camtschatica* and, despite of some sporadic massive occurrences of *C. plocamia* (see also Mianzan *et al*., 2014), seems to occur in low numbers (Table 3).

Guidelines for the future

Although the dataset utilized in our study has been useful in improving our knowledge about scypho- and cubomedusa from the region, there is a clear bias given by the spatio-temporal heterogeneous sampling effort and the methodologies utilized. This is a consequence of the fact that none of the surveys from which the dataset arises targeted jellyfish, and indeed often ignored them. Thus, there are a number of improvements that can be made to the collection of jellyfish data in Argentina and Uruguay that would provide more reliable information not only about scypho- and cubomedusae, but also about macro hydromedusae such as *Aequorea* or *Rhacostoma* (A. Schiariti, *unpubl. data*). As recommended by Flynn *et al*. (2012) for Namibian waters, all catches of jellyfish (by species) in fishery research cruises performed by Argentine and Uruguayan institutions should be routinely recorded. Specimens should be photographed against a scale bar, DNA samples should be taken, and then preserved for future species identification. Bell diameter, weight, and number of specimens collected from a subsample should be registered on board. All these activities have recently begun to take place in Argentina by technical and scientific personnel of the INIDEP (National

Institute for Fishery Research and Development, Argentina), enabling them to do the job through technical reports and specific courses (Schiariti *et al*., 2013). We expect to incorporate the aforementioned tasks as part of the "Observers on Board" INIDEP's program in commercial operations.

In our view, Argentina and Uruguay are far behind other regions of the world (*e.g.*, Mediterranean, North Sea, Baltic Sea) in jellyfish research. Specialists in the region are still too few to cover such a vast region; thereby, MSc and PhD students should be attracted to this field. An understanding of baseline information, such as jellyfish diversity, relative abundance of each species, and taxon-specific distributional patterns in this area will facilitate other research areas, including the role of jellyfish species in marine ecosystems, their incorporation in ecological modeling, their economic exploitation as fishing resources, or potential usefulness in pharmacology and biomedical research. Through the implementation of the recently described programs over long-term periods, we expect to reduce the gap in our knowledge of the life history and population dynamics of jellyfish species in the marine ecosystems of in the area covered by this study. Only when interdisciplinary research starts across a number of areas, including the interaction of fishery scientists and academic marine biologists will be in a better position to address the current concerns about the role of jellyfish in marine ecosystems and their potential impact on human activities.

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