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Parasitism (Trematoda, Digenea) in medusae from the southwestern Atlantic Ocean: medusa hosts, parasite prevalences, and ecological implications

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Abstract Digenean are important endoparasites of fish with complex life cycles; some genera include medusae as secondary hosts. Their transmission to fish occurs when fish prey on these jelly hosts. Fish predation on jellyfish is a widespread phenomenon, even though predation by fish on jellyfish has not been determined through parasitism yet. We hypothesized that medusae with high prevalences of digeneans could be important for their transmission to fish. A

total of 48,900 specimens of 50 medusa species were analyzed; 2,181 harbored digeneans. *Opechona* sp. and *Monascus filiformis* were the most frequent and abundant parasites with the widest range of hosts. Hemiuridae gen. sp. and *Bacciger* sp. were found in few specimens of some medusa species. Prevalences were unevenly distributed in the region. Three groups with high prevalence values were identified mainly related to frontal areas: Río de la Plata, Bahía Blanca, and North Patagonian tidal front. *Eucheilota ventricularis*, *Clytia hemisphaerica*, *Proboscoidactyla mutabilis*, *Liriope tetraphylla*, and *Aequorea* spp. were the medusae that contributed the most as secondary hosts to *M. filiformis* and *Opechona* sp. The high prevalences found in these medusae suggest that may be a fundamental part of the life cycles of both parasites in these areas.

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Introduction

Helminths are common parasites that occur in the marine environment. Among these, the digeneans are considered an important endoparasitic group of vertebrates (mostly fish). Digeneans have complex life cycles, during which several groups of marine animals are used as intermediate hosts that harbor their larval

stages to insure the transmission toward the final hosts. The transmission of these parasites often involves different predator–prey interactions between the hosts (Rohde, 1993; Marcogliese, 1995, 2004; Martorelli, 2001).

Zooplankters, including copepods, amphipods, and chaetognaths, are considered important intermediate or paratenic hosts of many digenean parasites of marine fish (Marcogliese, 1995; Daponte et al., 2008); however, some genera of these parasites, such as *Monascus* Looss, 1907 and *Opechona* Looss, 1907, include medusae and ctenophores as secondary hosts. Their transmission to fish, in which they culminate their life cycles, occurs when fish consume the jellyfish hosts (Lauckner, 1980; Girola et al., 1992; Marcogliese, 1995; Cremonte & Sardella, 1997; Martorelli & Cremonte, 1998; Martorelli, 2001).

Few complete life cycles are described for these parasites that involve medusae or ctenophores as secondary intermediate hosts, and only a limited number of fish species are known to be final hosts of these parasites (Cremonte & Sardella, 1997; Martorelli & Cremonte, 1998; Kohn et al., 2007; Averbuj & Cremonte, 2010; Diaz Briz personal observations). Most of the fish species are not documented as “jellyfish eaters”.

The number of fish species that feed exclusively on jellies is small (see Arai, 2005). However, direct observations of fish stomach contents have shown that predation on jelly organisms is more common and frequent than previously thought. Many fish species with broad diets (i.e., spiny dogfish *Squalus acanthias* Linnaeus, 1758, chum salmon *Oncorhynchus keta* (Walbaum, 1792), and Atlantic mackerel *Scomber scombrus* Linnaeus, 1758) feed at times on jelly organisms (Arai, 1988, 2005; Ates, 1988, 1991; Mianzan et al., 1996; Arai et al., 2003). This behavior, named “feeding on survival food” (Mianzan et al., 2001), may occur when other prey are not available, which implies a complex, and adaptive food web.

Analysis of stomach contents provides an overall picture of the number of fish that consume jelly organisms (Mianzan et al., 1996), but the identity of the prey may be difficult to obtain. These fragile organisms are rapidly digested in the fish gut, thus identification usually refers to broad “jelly groups” (e.g., ctenophores, medusae, etc.). Even though predation by fish on jellyfish has not yet been determined through parasitism (Arai, 2005), a high prevalence of

digenean parasites in medusae or ctenophores allows us to infer that jellies may have an important role in the transmission of parasites to their final fish hosts (Lauckner, 1980; Marcogliese, 2002). In particular, knowledge of species richness of medusae as hosts of digenean parasites of fish can be useful to suggest feeding interactions between medusae and fish (Mianzan et al., 1996).

Although several studies have reported on parasite–host interactions in the Northern Hemisphere (Lebour, 1916; Stunkard, 1967, 1969; Kjøie, 1975; Lauckner, 1980), such information from the Southern Hemisphere is scarce. In the southwestern Atlantic Ocean, the few records available only described the morphology of the metacercariae found in one ctenophore and several medusa hosts, usually collected by hand (Martorelli, 1991, 2001; Girola et al., 1992; Martorelli & Cremonte, 1998; Morandini et al., 2005). Only one digenean life cycle is known from this area (Martorelli & Cremonte, 1998). Because fish predation on jellyfish is a widespread phenomenon in the southwestern Atlantic Ocean (up to 35% of fish consume jelly prey; Mianzan et al., 1996), it is hypothesized that medusae with high prevalences of parasitism could be important for the transmission of digenean to fish.

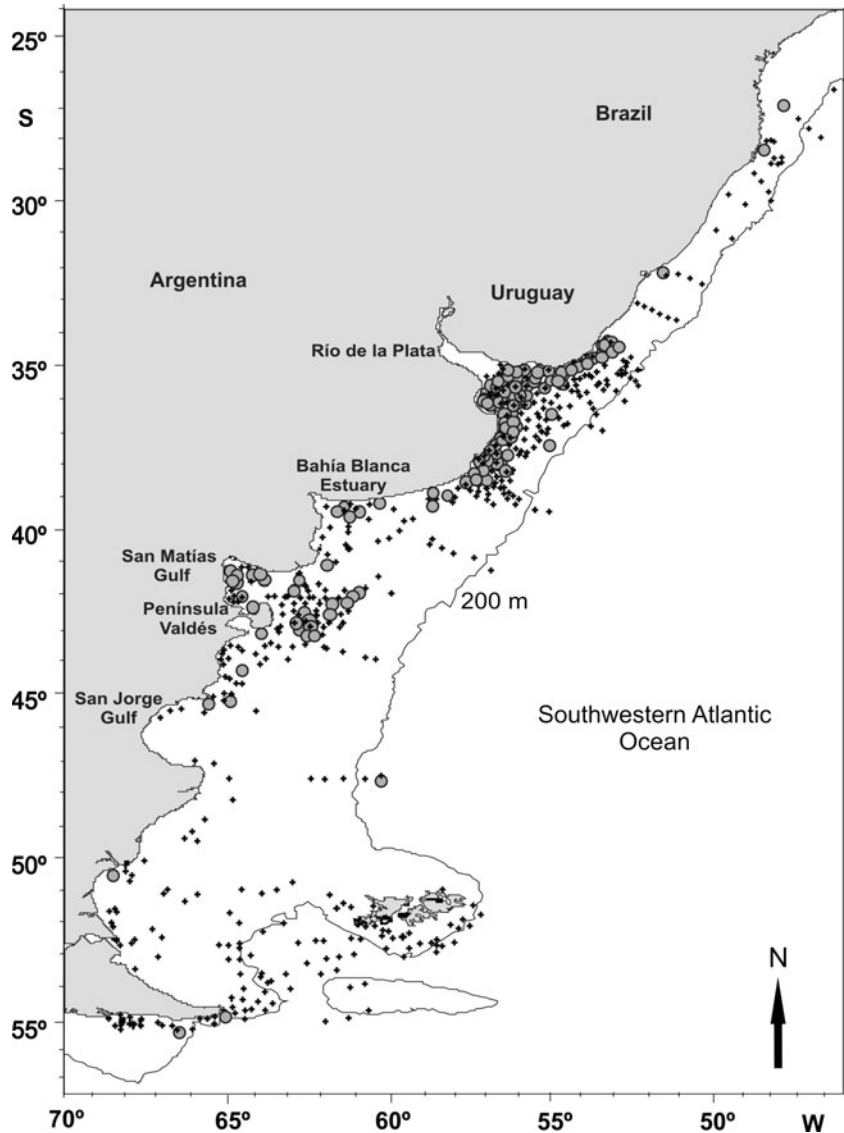
To test this hypothesis several medusae species from an extensive geographical area of the southwestern Atlantic Ocean (26–55°S) were analyzed for first time, with the objectives to (1) expand the knowledge about different medusa species hosts of digenean parasites of fish, (2) establish the geographic distribution of the parasitized medusae and determine which zones have the highest parasite prevalences, and (3) indicate which of these parasitized species of medusae may transmit the parasites to fish.

Materials and methods

Data collection

The study area comprised the southern Brazilian, Uruguayan, and Argentine Continental Shelf (26–55°S; Fig. 1). Zooplankton samples were collected during 115 cruises carried out by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) between 1987 and 2010. Hensen and Bongo plankton nets were used mostly and Calvet, Biomoc,

Fig. 1 Geographic distributions of all zooplankton samples collected in the southwestern Atlantic Ocean between 1987 and 2010 that contained medusae (shaded circle samples with medusae parasitized by digenean metacercariae; plus samples with medusae without parasites)



and Multired nets were used occasionally (see Wiebe & Benfield, 2003 for descriptions of nets). All samples were preserved in a 5% formalin-seawater solution. The resulting database is unique for the study area and contains all available biological and ecological information on medusae species.

A total of 3,335 zooplankton samples were analyzed. All medusa specimens were separated, identified with the aid of a stereomicroscope, and quantified. The larval stages (metacercariae) of the digenean parasites were removed with dissection needles from the mesoglea of the medusae. These parasites then were stained with Gill's Hematoxylin, dehydrated in

an ethanol series, cleared in clove oil, and mounted in natural Canada balsam to be identified at the lowest taxonomical level possible. To corroborate the taxonomic identification, measurements of 10 specimens from each metacercariae group were taken by use of an ocular micrometer in the stereomicroscope. The morphological features and measurements of these metacercariae agreed with those previously reported by Martorelli & Cremonte (1998) and Martorelli (2001). Prevalence values were calculated according to Bush et al. (1997). Medusa specimens and mounted digeneans were kept in the collection of the UNMdP-INIDEP.

Data analysis

To identify areas with similar parasitic prevalences, the study area was divided into 33 one-degree grid squares. In each square, the mean prevalence of each parasite species per species of medusa host was calculated. Medusae present in just one square were excluded from the analysis (e.g., *Coryne eximia* Allman, 1859 and *Leuckartiara octona* (Fleming, 1823)). Classification methods (group average sorting of the Bray–Curtis similarity measures based on $\log(X + 1)$ transformed prevalence data) were carried out using the PRIMER 5 software package (Clarke & Warwick, 2001). A one-way, non-parametric, multivariate analysis of similarity (ANOSIM) was implemented to evaluate differences among groups obtained by the cluster analysis. ANOSIM was used to test the null hypothesis that there was no difference in the composition of medusa species and their parasites between the groups. ANOSIM is an analogue of one-factor analysis of variance based on multispecies data (Chapman & Underwood, 1999), and it calculated the statistic R (Clarke & Warwick, 2001). SIMPER analysis (similarity percentages) was used to identify the medusa species that contributed most to (dis)similarities among and within groups. This analysis calculates the “average similarity” (contribution of the *i*th species to the overall dissimilarity between the groups considered) and the “internal similarity” (contribution each species makes to the average similarity within each group considered) (see Clarke & Warwick, 2001 for details).

Results

Approximately 30% of the analyzed zooplankton samples contained medusae, and of those, about 20% had parasitized medusae (Fig. 1). A total of 48,900 medusa specimens were analyzed including 50 species (Table 1). Of those, 2,181 (16 species of hydromedusae and 1 scyphomedusa) harbored the larval stage of digenean parasites in their mesoglea (Fig. 2a, b). The total prevalence was approximately 5%. Almost all the parasitized medusae species (16) were new records of secondary hosts to at least one taxon of digenean parasite (Table 1).

Four species of digenean metacercariae were found in the medusae: *Monascus filiformis* (Rudolphi, 1819)

Table 1 Taxonomic list of analyzed medusae following the classification of Marques & Collins (2004), Cartwright et al. (2008) and Collins et al. (2008)

Medusa species analyzed	Number of analyzed specimens
Phylum Cnidaria	
Subphylum Medusozoa	
Class Hydrozoa	
Subclass Hydroidolina	
Order Anthoathecata	
<i>Amphinema dinema</i> (Péron & Lesueur, 1810)	9
<i>Amphinema rugosum</i> (Mayer, 1900)	3
<i>Bougainvillia frondosa</i> Mayer, 1900	1
<i>Bougainvillia macloviana</i> (Lesson, 1830)	130
<i>Bougainvillia muscus</i> Allman, 1863	23
<i>Bougainvillia</i> sp. ^a	361
<i>Corymorpha gracilis</i> (Brooks, 1882)	11
<i>Corymorpha januarii</i> Steenstrup, 1854	6
<i>Coryne eximia</i> Allman, 1859 ^a	421
<i>Dipurena reesi</i> Vannucci, 1956	1
<i>Euphysa aurata</i> Forbes, 1848	342
<i>Hybocodon</i> spp.	40
<i>Hydractinia</i> spp.	13
<i>Rathkea formosissima</i> (Browne, 1902)	1
<i>Tiaricodon coeruleus</i> Browne, 1902	5
<i>Turritopsis nutricula</i> McCrady, 1859	11
<i>Leuckartiara octona</i> (Fleming, 1823) ^a	17
<i>Proboscidactyla mutabilis</i> (Browne, 1902) ^a	3,589
Order Leptothecata	
<i>Aequorea</i> spp. ^a	60
<i>Blackfordia virginica</i> Mayer, 1910	8,975
<i>Clytia gracilis</i> (Sars, 1851)	15
<i>Clytia hemisphaerica</i> (Linnaeus, 1767) ^a	956
<i>Clytia lomae</i> (Torrey, 1909) ^a	8
<i>Clytia simplex</i> (Browne, 1902) ^a	20
<i>Cosmetirella davisi</i> (Browne, 1902) ^a	39
<i>Euceilota ventricularis</i> McCrady, 1859 ^a	9,861
<i>Eutonina scintillans</i> (Bigelow, 1909)	2
<i>Halopsis ocellata</i> A. Agassiz, 1863 ^a	6
<i>Laodicea pulchra</i> Browne, 1902	3
<i>Laodicea undulata</i> (Forbes and Goodsir, 1851)	193
<i>Mitrocomella brownnei</i> (Kramp, 1930) ^a	229
<i>Mitrocomella frigida</i> (Browne, 1910)	5
<i>Modeeria rotunda</i> (Quoy and Gaimard, 1827)	1
<i>Obelia</i> spp.	4,864
<i>Phialella falklandica</i> Browne, 1905 ^a	99

Table 1 continued

Medusa species analyzed	Number of analyzed specimens
<i>Rhacostoma atlanticum</i> L. Agassiz, 1850	1
Subclass Trachylina	
Order Limnomedusae	
<i>Aglauropsis conanti</i> Browne, 1902	1
<i>Aglauropsis kawarii</i> Moreira and Yamashita, 1972	10
<i>Gossea brachymera</i> Bigelow, 1909 ^a	25
<i>Olindias sambaquiensis</i> Müller, 1861 ^b	18
Olindiidae indet.	2
<i>Liriope tetraphylla</i> (Chamisso and Eysenhardt, 1821) ^a	17,152
Order Narcomedusae	
<i>Cunina octonaria</i> McCrady, 1859	11
<i>Pegantha laevis</i> H. B. Bigelow, 1909	79
<i>Solmundella bitentaculata</i> (Quoy and Gaimard, 1833)	9
Order Trachymedusae	
<i>Amphogona apicata</i> Kramp, 1957	1
<i>Aglaura hemistoma</i> Pèron and Lesueur, 1810	58
<i>Rhopalonema velatum</i> Gegenbaur, 1857	1,116
<i>Sminthea eurygaster</i> Gegenbaur, 1857	1
Class Scyphozoa	
Subclass Discomedusae	
Order Semaestomeae	
<i>Chrysaora lactea</i> Eschscholtz, 1829 ^a	96
Total number of analyzed specimens	48,900
Total number of analyzed species	50

^a New records of secondary medusa hosts of at least one digenean parasite

^b Secondary medusa hosts previously reported for the study area. The total numbers of specimens analyzed per medusa are given

Looss, 1907, *Opechona* sp., *Bacciger* sp. Nicoll, 1914, and Hemiuridae gen. sp. (Fig. 2c–f). *Opechona* sp. and *M. filiformis* were the most frequent parasites and occurred in 13 and 11 of the 17 parasitized species of medusae, respectively. Moreover, the total prevalences of both species were high, with *M. filiformis* found in 68.2% of the parasitized medusae and *Opechona* sp. in 39.7%. In general, the prevalence values of *Monascus filiformis* were higher than of those observed for *Opechona* sp. (Table 2). Hemiuridae gen. sp. and *Bacciger* sp. infected only 1.4 and

1.0% of the specimens, respectively, of three species of medusae (Table 2).

Most of the parasitized species of medusae only hosted *M. filiformis* and *Opechona* sp. By contrast, *Liriope tetraphylla* and *Eucheilota ventricularis* were parasitized by four taxa of metacercariae, and *Proboscoidactyla mutabilis* and *Clytia simplex* were parasitized by three taxa (Table 2). Usually, a single medusa specimen harbored more than one parasite species. *L. tetraphylla*, *E. ventricularis*, *C. hemisphaerica*, *Aequorea* spp., and *P. mutabilis* medusae were often infested by both *M. filiformis* and *Opechona* sp. Three parasite species (*M. filiformis*, *Opechona* sp., and Hemiuridae gen. sp.) were found in only one *P. mutabilis* medusa. *Eucheilota ventricularis* medusa had the highest frequency of infection on the total of parasitized medusa specimens (54.6%), followed by *L. tetraphylla* (29.0%), and *C. hemisphaerica* (7.3%). The remaining species had infection frequencies less than 3.9%.

Parasitized medusae were unevenly distributed within the study area (Fig. 1). Some zones had a high concentration of medusa species and parasitized specimens. In semi-enclosed areas such as the Río de La Plata Estuary, Bahía Blanca Estuary, San Matías Gulf, and the North Patagonia tidal front (Península Valdés), the prevalences of *Opechona* sp. and *M. filiformis* were high. By comparison, *Bacciger* sp. and Hemiuridae gen. sp. had relatively low prevalences even though both usually occurred in the same zones as *Opechona* sp. and *M. filiformis* (Fig. 3a–d).

Prevalence indexes varied considerably among the different groups defined by the cluster analysis (ANOSIM, global $R = 0.598$, $P < 0.001$). Group 1 (33.4% internal similarity SIMPER analysis) cluster samples were mainly from the Río de La Plata and Bahía Blanca estuaries. Parasitized medusa hosts more important were *Eucheilota ventricularis* and *Clytia hemisphaerica* with *M. filiformis* (26.9 and 23.5%, cumulative contribution respectively, SIMPER analysis), *E. ventricularis*, and *C. hemisphaerica* with *Opechona* sp. (21.2 and 9.7%, respectively), and *Liriope tetraphylla* with *M. filiformis* (7.4%) and with *Opechona* sp. (6.1%) (Fig. 4a–c). Group 2 (29.1% average similarity) mostly corresponded to the San Matías Gulf, Peninsula Valdés and surrounding areas (tidal front of Patagonia), and the south coast of Buenos Aires. Only *P. mutabilis* medusae with *M. filiformis* and *Opechona* sp. contributed to this group (71.1 and 25.9%, respectively, SIMPER analysis)

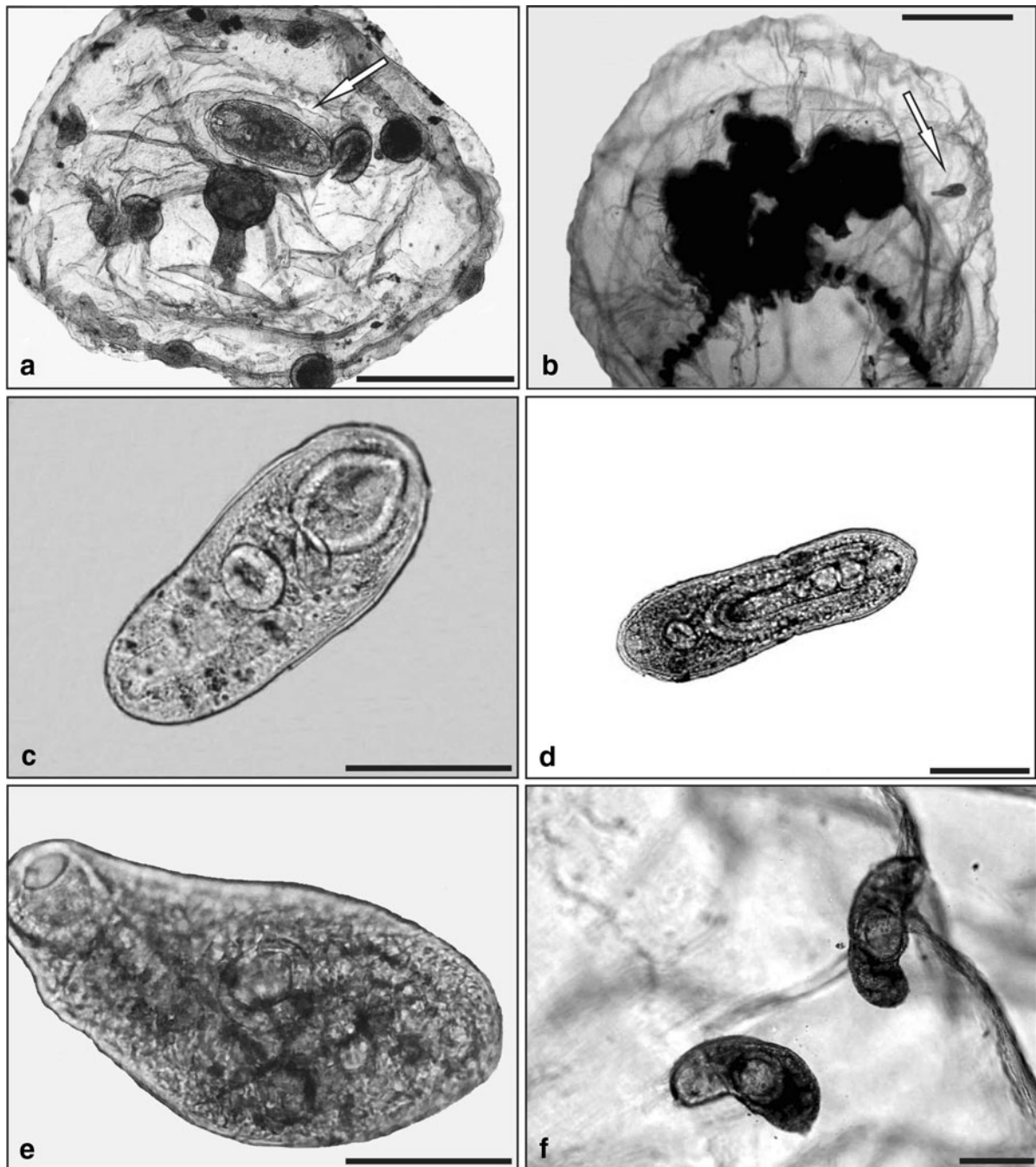


Fig. 2 Metacercariae of **a** *Monascus filiformis* in a *Eucheilota ventricularis* medusa, **b** *Opechona* sp. in a *Proboscicactyla mutabilis* medusa, and **c** *M. filiformis*, **d** *Opechona* sp., **e** *Bacciger* sp., **f** Hemiuridae gen. sp. Scale bars 1 mm (a, b), 200 μ m (c, f), 100 μ m (d, e)

(Fig. 4a–c). Group 3 (55.6% average similarity) was heterogeneous and clustered samples from distal sectors, such as the tidal front of Patagonia, Samborombón Bay, and Laguna dos Patos (south of Brazil). Only one medusa contributed in this group,

Aequorea spp., which was parasitized by *Opechona* sp. and *M. filiformis* (50.45 and 49.5%, respectively) (Fig. 4a–c). Thus, we rejected the null hypothesis that there was no difference in the composition of medusa species and their parasites between the groups.

Table 2 List of parasitized medusae by species for the study area (26–55°S), including the total numbers of specimens examined and parasitized per species, and total numbers of medusae parasitized by different digenean metacercariae

Medusae	Total number examined	Total number parasitized and prevalence	Total number of medusae parasitized by			
			<i>Monascus filiformis</i> and prevalence	<i>Opechona</i> sp. and prevalence	Hemiuridae and prevalence	<i>Bacciger</i> sp. and prevalence
<i>Liriope tetraphylla</i>	17,163	633 (3.7)	508 (80.2)	120 (18.9)	28 (4.4)	1 (0.1)
<i>Eucheilota ventricularis</i>	9,861	1,193 (12.1)	772 (64.7)	559 (46.8)	2 (0.2)	20 (1.7)
<i>Clytia simplex</i>	20	3 (15.0)	1 (33.3)	1 (33.3)	0	1 (33.3)
<i>Proboscidactyla mutabilis</i>	3,589	85 (2.4)	83 (97.6)	6 (7.0)	1 (1.2)	0
<i>Clytia hemisphaerica</i>	956	161 (16.8)	105 (65.2)	84 (52.2)	0	0
<i>Aequorea</i> spp.	60	13 (21.7)	12 (92.3)	10 (76.9)	0	0
<i>Cosmetirella davisii</i>	39	2 (5.1)	2 (100)	0	0	0
<i>Clytia lomae</i>	8	3 (37.5)	2 (66.7)	1 (33.3)	0	0
<i>Mitrocomella browni</i>	229	2 (0.9)	2 (100)	0	0	0
<i>Halopsis ocellata</i>	6	1 (16.7)	1 (100)	0	0	0
<i>Leuckartiara octona</i>	17	1 (5.9)	1 (100)	0	0	0
<i>Coryne eximia</i>	421	5 (1.2)	0	5 (100)	0	0
<i>Bougainvillia</i> sp.	361	21 (5.8)	0	21 (100)	0	0
<i>Phialella falklandica</i>	99	1 (1.0)	0	1 (100)	0	0
<i>Chrysaora lactea</i>	96	53 (55.2)	0	53 (100)	0	0
<i>Gossea brachymera</i>	25	1 (4.0)	0	1 (100)	0	0
<i>Olindias sambaquiensis</i>	18	3 (16.7)	0	3 (100)	0	0
Total	32,968	2,181	1,489 (68.2)	865 (39.7)	31 (1.4)	22 (1.0)

Prevalence (%) is in parentheses

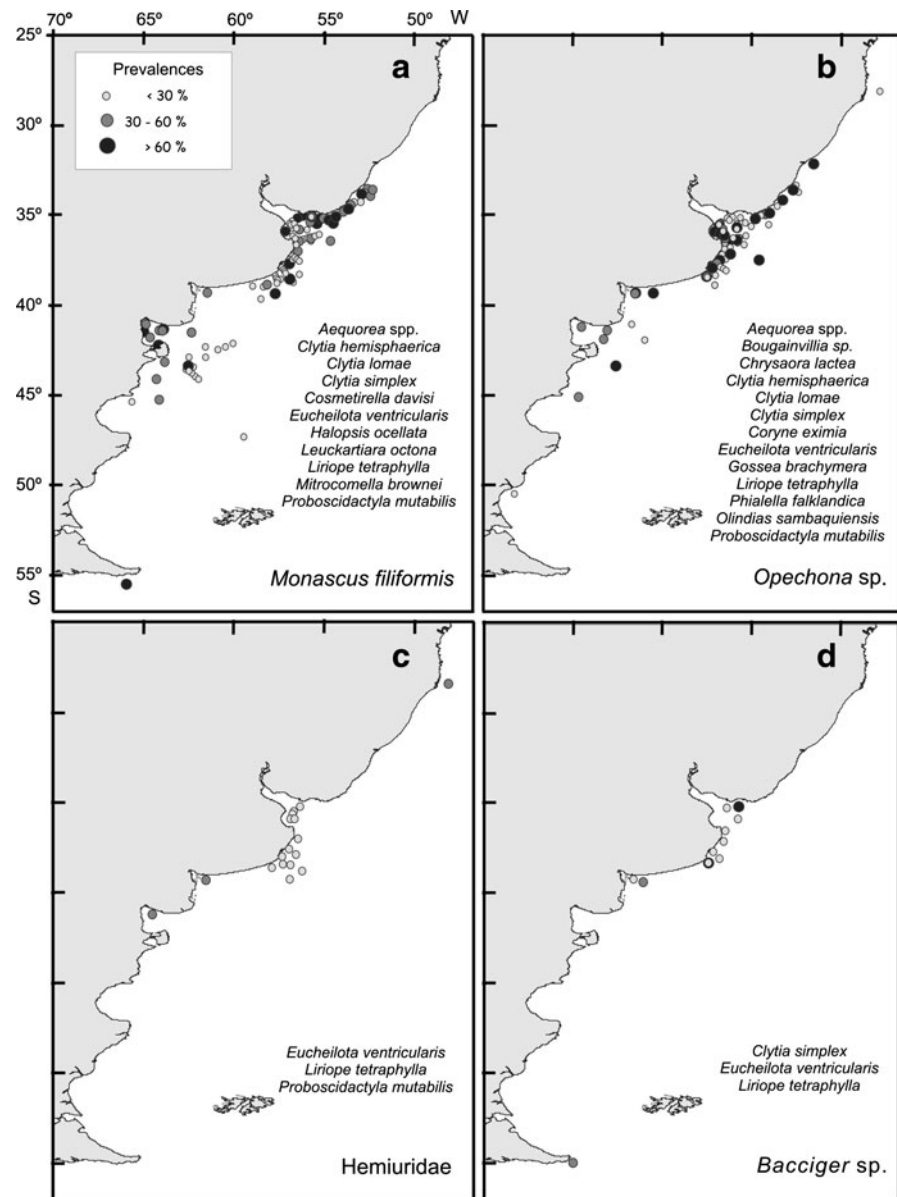
Discussion

In this study, 16 of the 17 parasitized species of medusae were reported as new records of intermediate hosts of digenean parasites of fish: *Monascus filiformis*, *Opechona* sp., *Bacciger* sp., and Hemiuridae gen. sp. (Tables 1, 2). Although previous studies pointed to the presence of these parasites in some medusae and ctenophores as well as their prevalence values for the area (see Martorelli, 1991, 1996, 2001; Girola et al., 1992; Martorelli & Cremonese, 1998; Morandini et al., 2005), our finding triples the number of medusa hosts

known previously. Our results indicate that the interaction between digenean parasites and their jellyfish hosts is more common than previously thought. In addition, the parasite prevalences were higher than those previously recorded for the region.

It is well known that parasites use predator–prey relationships among their hosts to insure their transmission (Marcogliese, 1995). Their presence in a host population provides information on the host diet and predators of the host, as well as the trophic role of the host in the marine trophic web (see Marcogliese, 2004, 2005). Marcogliese (2002) proposed that a high

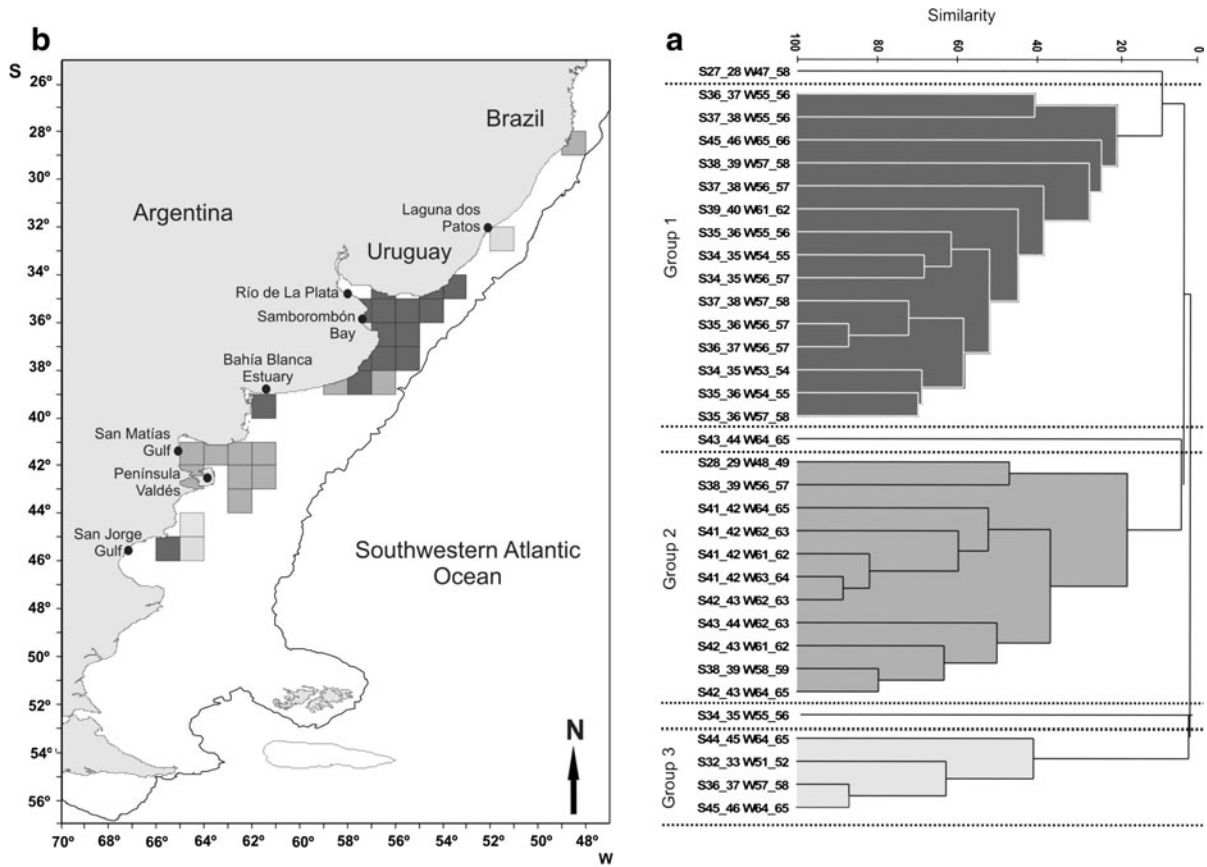
Fig. 3 Spatial distribution of the prevalence of each digenean parasite species on their medusa hosts in the southwestern Atlantic Ocean. **a** *Monascus filiformis*, **b** *Opechona* sp., **c** Hemiuridae gen. sp., and **d** *Bacciger* sp.



increment in number of some parasites in a host species may reflect more predation upon that species. Therefore, if one medusa species is commonly used as secondary host by a digenean parasite of fish and it has a high prevalence, then we can assume that fish predation on the jellies increases the probability of parasite transmission. Thus, it seems unlikely that the many parasitized medusae are “dead ends” for these parasites, especially considering that many fish species consume jelly organisms in the area (Mianzan et al., 1996, 2001). The high percentage of parasitized

species of medusae found in this study (34% of the total analyzed) and the high parasite prevalences observed in the majority of these medusae (Table 2) suggest that many of them are important in the transmission of digenean parasites to their final fish hosts in the southwestern Atlantic Ocean, supporting our hypothesis.

Opechona sp. and *Monascus filiformis* were the most frequent and abundant parasite species, with the widest range of medusae hosts (occurring in 13 and 11 species of medusae, respectively). Adults of genus



c

SIMPER analysis

Group 1		Group 2	
<i>Euceilota ventricularis</i> (<i>Monascus filiformis</i>)	26.97 %	<i>Proboscidactyla mutabilis</i> (<i>Monascus filiformis</i>)	1.66 %
<i>Clytia hemisphaerica</i> (<i>Monascus filiformis</i>)	23.52 %	<i>Euceilota ventricularis</i> (<i>Bacciger</i> sp.)	1.38 %
<i>Euceilota ventricularis</i> (<i>Opechona</i> sp.)	21.25 %	<i>Cosmetirella davisii</i> (<i>Monascus filiformis</i>)	0.66 %
<i>Clytia hemisphaerica</i> (<i>Opechona</i> sp.)	9.75 %	<i>Liriope tetraphylla</i> (Hemiuridae)	0.61 %
<i>Liriope tetraphylla</i> (<i>Monascus filiformis</i>)	7.37 %	<i>Chrysaora lactea</i> (<i>Opechona</i> sp.)	0.50 %
<i>Liriope tetraphylla</i> (<i>Opechona</i> sp.)	6.13 %	<i>Euceilota ventricularis</i> (Hemiuridae)	0.19 %
		Group 3	
		<i>Aequorea</i> spp. (<i>Opechona</i> sp.)	50.45 %
		<i>Aequorea</i> spp. (<i>Monascus filiformis</i>)	49.55 %

Fig. 4 a Cluster groups of mean prevalence for the four parasites found across all parasitized medusae by species, b spatial distribution of the three groups obtained in the cluster

Opechona and *M. filiformis* were found in eight and six fish species of the region, respectively (Travassos et al., 1965, 1967; Amato, 1982, 1983; Fernandes

analysis, and c results of the SIMPER analysis. Percentage (%) of parasitized medusae contribution for each digenean parasite is indicated for each group

et al., 1985; Wallet & Kohn, 1987; Girola et al., 1992; Cremonte & Sardella, 1997; Martorelli & Cremonte, 1998; Pereira et al., 2000; Abdallah et al., 2002; Kohn

et al., 2007). The fact that nearly 70% of the parasitized medusae harbored *M. filiformis* and 40% had *Opechona* sp. metacercariae (Table 2) indicates the importance of these medusae as secondary hosts for these parasites.

Bacciger sp. and Hemiuridae gen. sp. were found in only three species of medusae at low prevalences (Table 2). These metacercariae are known to utilize several marine invertebrates and vertebrates (primarily crustaceans and fish) as second intermediate hosts, in addition to medusae and ctenophores (Marcogliese, 1995; Martorelli, 2001; Daponte et al., 2006, 2008; Rocka, 2006). Several fish species act as their final hosts (Rocka, 2006; Kohn et al., 2007; Alarcos et al., 2008; Guagliardo et al., 2010). The use of a wide range of secondary hosts and the low prevalences found in this study (Table 2) suggests that parasitized medusae may act as paratenic hosts (see Marcogliese, 2005) for both parasites.

Digenean parasites were found in several species of medusae that covered a vast area but were not evenly distributed (Fig. 1). High prevalences of digeneans were concentrated in two major areas, the temperate estuarine zones of the Río de La Plata and Bahía Blanca, and the North Patagonian tidal front (Península Valdés) zone (Acha et al., 2004 and references therein) (Fig. 4b). In these zones, high prevalences (up to 100%) were observed mostly for *M. filiformis* and *Opechona* sp. (Fig. 3a, b).

Infection rates of parasites are extremely low in the pelagic realm due to its dilute nature (Marcogliese, 1995, 2002); however, certain areas like fronts may be paramount in parasites' success. In these zones, exceptionally high primary production provides adequate feeding or reproductive habitats for nektonic species, such as fish and squids, and act as retention areas for larvae of benthic species, which promotes establishment of adult beds (Acha et al., 2004). Gelatinous organisms also are very abundant in these frontal zones (Mianzan & Guerrero, 2000). Therefore, parasites may be aided by retention in frontal zones, maximizing their encounters with secondary and final hosts. The digenean parasites of this study have life cycles that usually involve a benthic mollusk as a primary intermediate host, a gelatinous zooplankton as a secondary or paratenic host, and a fish as a final definitive host. In these frontal areas, the primary hosts are the gastropods *Buccinanops monilifer* (Kiener, 1834) and *Buccinanops cochlidium* (Dillwyn, 1817) for *Opechona* sp., and the bivalve

Nucula obliqua Lamarck, 1819 for *Monascus filiformis* (Martorelli, 1991; Martorelli & Cremonte, 1998; Averbuj & Cremonte, 2010).

Marine front areas favor the aggregation of prey organisms as well as their predators and can increase the transmission of parasites. It is unclear, however, how small cercaria finds a secondary host after leaving the first intermediate host, which is usually a benthic mollusk. Cercaria may use behavioral traits of the next host species. The infestation mechanisms (active penetration or by eating free-swimming cercariae) used by cercariae when infesting their jellyfish hosts (Stunkard, 1969; Martorelli, 1991; Martorelli & Cremonte, 1998; Morandini et al., 2005) could be enhanced by vertical migration of many medusae and ctenophores. The aggregation of some jellyfish species near the seafloor (Alvarez Colombo et al., 2003; Costello & Mianzan, 2003; Mianzan et al., 2010) may facilitate encounters between cercariae released from a benthic mollusk with medusae and between medusae and fish. The potential trophic importance of jellyfish near the seafloor is indicated by the presence of gelatinous prey in the gut contents of a variety of demersal fishes from the Argentine continental shelf (Mianzan et al., 1996). The vertical movements of medusae create trophic linkages between zones and opportunities for parasites to traverse different habitats (Marcogliese, 2002).

On the other hand, the southern Patagonian region had very few parasitized medusae and the prevalences were quite low (Fig. 3c, d). This may be related to fewer hydromedusa species being observed in high than in low latitudes (Genzano et al., 2008); however, large hydromedusae like *Aequorea* spp. that typically inhabit the pelagic zone showed high prevalences of infestation (Table 2). The fact that these large medusae are poorly sampled by traditional plankton nets makes the study of their parasitosis difficult. Also, prevalences of *Opechona* sp. in their first intermediate hosts (mollusks) are generally lower when the water temperature decreases (Averbuj & Cremonte, 2010), which could potentially limit the infection of medusae in high latitudes.

The high number of species and specimens of medusae parasitized by *M. filiformis* and *Opechona* sp. allowed us to increase knowledge about the use of medusae as secondary hosts in the southwestern Atlantic Ocean. The high prevalence values found indicate that medusae species parasitized by these

digeneans may be a fundamental part of the life cycles of these parasites. It is proposed that the temperate estuarine zones and the North Patagonian tidal fronts above mentioned would provide ideal environments for *M. filiformis* and *Opechona* sp. to thrive.

Future studies about the life cycles of these digeneans, seasonality in medusae hosts, and distribution of their first intermediate and final fish hosts will allow us to achieve a better understanding of the role that gelatinous plankton have in local pelagic food webs.

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