

Research Article

Faunal assemblages of intertidal hydroids (Hydrozoa, Cnidaria) from Argentinean Patagonia (Southwestern Atlantic Ocean)

Gabriel Genzano¹, Claudia S. Bremec¹, Luciana Diaz-Briz¹, John H. Costello²
Andre C. Morandini³, Thais P. Miranda³ & Antonio C. Marques^{3,4}

¹Estación Costera Nágera, Instituto de Investigaciones Marinas y Costeras (IIMyC)
CONICET - UNMDP, Mar del Plata, Argentina

²Biology Department, Providence College, Providence, Rhode Island, USA

³Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

⁴Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, SP, Brazil

Corresponding author: Thais P. Miranda (thaispmir@ib.usp.br)

ABSTRACT. This study provides taxonomical and ecological accounts for the poorly known diversity of hydroids distributed over ~2,000 km of Argentinean Patagonian intertidal habitats (42°-54°S). Sampling was performed in 11 sites with tidal amplitude between 6-13 m dominated by rocky outcrops, breakwaters, and salt marshes. Samples were sorted and identified up to the species level and hydroid associations were analyzed by multivariate analyses. A total of 26 species were recorded. The most frequent species were *Amphisbetia operculata*, present in 8 of the 10 sites inhabited by hydroids, followed by *Symplectoscyphus subdichotomus* and *Nemertesia ramosa*. All recorded hydroids are geographically and bathymetrically widely distributed species, common at the austral hemisphere. Seven species (*Coryne eximia*, *Bougainvillia muscus*, *Ectopleura crocea*, *Hybocodon unicus*, *Halecium delicatulum*, *Plumularia setacea*, and *Clytia gracilis*) were reported from intertidal fringes. Species richness differed according to the composition of the bottom, topographical complexity and density of mytilid communities. Some muddy intertidal fringes dominated by the glasswort *Sarcocornia perennis* had an unexpected hydroid fauna composition, never reported for salt marsh habitats, representing a remarkable novelty for the hydroid literature. The lack of studies on the hydroid fauna from these particular habitats represented a substantial gap for our biodiversity knowledge.

Keywords: hydroids community, salt marshes, rocky intertidal, Argentinean Patagonia, southwestern Atlantic.

INTRODUCTION

Organisms inhabiting intertidal ecosystems, such as barnacles, mytilids, sea anemones, live under extreme environmental conditions. Variables such as submersion, air exposure, desiccation and wave action make survival, settlement and recruitment of the intertidal zone difficult, constraining composition and spatial distribution of its community (Menge & Farrell, 1989). These extreme conditions demand a series of morphological, physiological, and behavioral adaptations. Among hydroids, few species occur intertidally, and even fewer species tolerate air exposure (e.g., *Halecium beanii*, *H. delicatulum*, *Sertularella mediterranea*; Genzano, 1994; Gili & Hughes, 1995;

Rosso & Marques, 1997; Genzano *et al.*, 2009). Hydroids at intertidal rocky fringes usually occur in sheltered microhabitats, such as tide pools or on macroalgae, that serve as natural refuges from extreme seasonal and daily temperatures and prevent hydroid colony desiccation (Genzano, 1994; Gili & Hughes, 1995). Several delicate hydroid species live under stones or in crevices where wave hydrodynamics are reduced (Boero, 1984; Hughes, 1992; Gili & Hughes, 1995). For these reasons, information on intertidal hydroids usually focuses on morphological adaptations of particular species (e.g., thickening of the hydrocaulus in species of *Leptothecata*) to specific environments, such as intertidal habitats, where the water movements are stronger (e.g., Calder, 1991;

Hughes, 1992; Rossi *et al.*, 2000; Henry, 2002). Broad ecological aspects, such as zonation and seasonality of intertidal hydroid community, as well as their interaction with other organisms, have received little attention (Genzano, 1994, 2001; Brinckmann-Voss, 1996, and information therein).

Studies on southwestern Atlantic intertidal hydroid communities are rare, but include distributional inferences for the Brazilian tropical-subtropical coast (Rosso & Marques, 1997), and ecological assessments of seasonal richness, abundance, zonation and substrata for southern temperate waters (Genzano, 1994; Genzano & Rodriguez, 1998). Knowledge on intertidal hydroids is complemented by checklists including species occurring from 0° to 54°S (Migotto *et al.*, 2002; Genzano *et al.*, 2009; Oliveira *et al.*, 2016), and biogeographic analyses (Miranda *et al.*, 2015). However, the knowledge on Patagonian intertidal hydroids, living in cold temperate waters, has been neglected. Previous knowledge for the hydroids of the area is concentrated in subtidal waters either as faunal components within an ecological study (Schwindt *et al.*, 2014) or as a source of taxonomical information from shelf areas (Vervoort, 1972; Stepanjants, 1979; Genzano *et al.*, 1991; Blanco, 1994; El Beshbeeshy & Jarms, 2011). The majority of the Patagonian records for hydroid species are still from occasional and scattered faunal surveys (see Blanco, 1994, and references therein) and from specific taxonomic studies (Rodriguez *et al.*, 2012; Cunha *et al.*, 2015).

The megatidal regime of the Patagonian coast exposes extensive coastal areas, pushing physical conditions to very extreme limits. During low tides, temperature values range seasonally from cold (in summer, with temperatures varying from 12° to 16°C) to near freezing (in winter, with temperatures varying from 6° to 12°C) (Bastida *et al.*, 2007; Bortolus *et al.*, 2009; Schwindt *et al.*, 2014). Fringe bottom is predominantly formed by sand and gravel sediments, but salt marshes and rocky outcrops are also frequent (Bastida *et al.*, 2007; Bortolus *et al.*, 2009), providing colonizable areas for hydroids. However, the lack of studies on the hydroid fauna distributed along ~2,000 km of the Patagonian coast represents a substantial gap in our biodiversity knowledge. In this study, we provide the first extensive study on Patagonian hydroids related to their taxonomy and ecology.

MATERIALS AND METHODS

Study area

We sampled different rocky outcrops, breakwaters and salt marshes along ~2,000 km of the Argentinean

Patagonia coast, between 42°-54°S (Fig. 1, Table 1). A general description of benthic communities inhabiting the sampling sites is found in Bastida *et al.* (2007) and Bortolus *et al.* (2009).

Sampling sites were grouped according to tidal amplitude, topography and benthic communities. Northern sites at Puerto Madryn (PM, 42°46'S, 65°02'W), Rada Tilly (RT, 45°55'S, 67°34'W), Caleta Olivia (CO, 46°26'S, 67°31'W) and Puerto Deseado (PD, 47°44'S, 65°53'W) had tidal amplitudes up to 6 m, intertidal areas with large rocky boulders, deep crevices, and wide tidal pools. Mollusks were dominant on these outcrops, and were primarily colonized by the mytilid *Brachidontes purpuratus* (Lamarck, 1819), but the kelp *Macrocystis pyrifera* (Linnaeus, 1758) was occasionally present (Fig. 2).

Southern sites had intertidal fringes with particular topographies. In San Julián (SJ, 49°18'S, 67°43'W), rocky boulders up to 2 m formed a complex topographic landscape, with tidal amplitudes up to 9 m. These areas were mainly colonized by patches of mytilids (*B. purpuratus*). Puerto Santa Cruz (PS, 50°11'S, 68°31'W) and Río Gallegos (RG, 51°37'S, 69°13'W) had tidal amplitudes up to 13 m, extensive muddy intertidal zones with scattered rocks (up to ~0.6 m wide) in PS and wood/concrete breakwaters in RG, and small mytilid patches (*B. purpuratus*) in both areas. The Río Grande (RGr, 53°47'S, 67°42'W) intertidal zone had a large rock platform with wide tidal pools and deep crevices. Mytilids covered most of the available substrate, although some denuded areas were also present. The kelp *M. pyrifera* developed on rocky bottoms at the lower intertidal level of SJ and RGr (Fig. 3).

Four sites (PDm, SJm, PSm, RGrm; "m" indicating "marsh") had muddy marshes dominated by the glasswort *Sarcocornia perennis* (Mills.) that reached 0.5 m in height. These sites were characterized by scattered, wide, tidal pools and large tidal channels (Fig. 4).

Finally, Ushuaia (U, 54°48'S, 68°18'W), the southernmost intertidal area, was distinguished from other sites by its small tidal amplitude (2 m) and narrow tidal fringe dominated by the mussel *Mytilus edulis* (Linnaeus, 1758) (Fig. 5).

Sampling and ecological analysis

Hydroids were collected in austral spring (November 2010) and summer (February 2012) seasons, periods in which most species would likely be present in the cold waters at the area. Hydroid colonies were collected during low tide, individually labeled, and preserved in 4% formaldehyde seawater solution. Samples were sor-

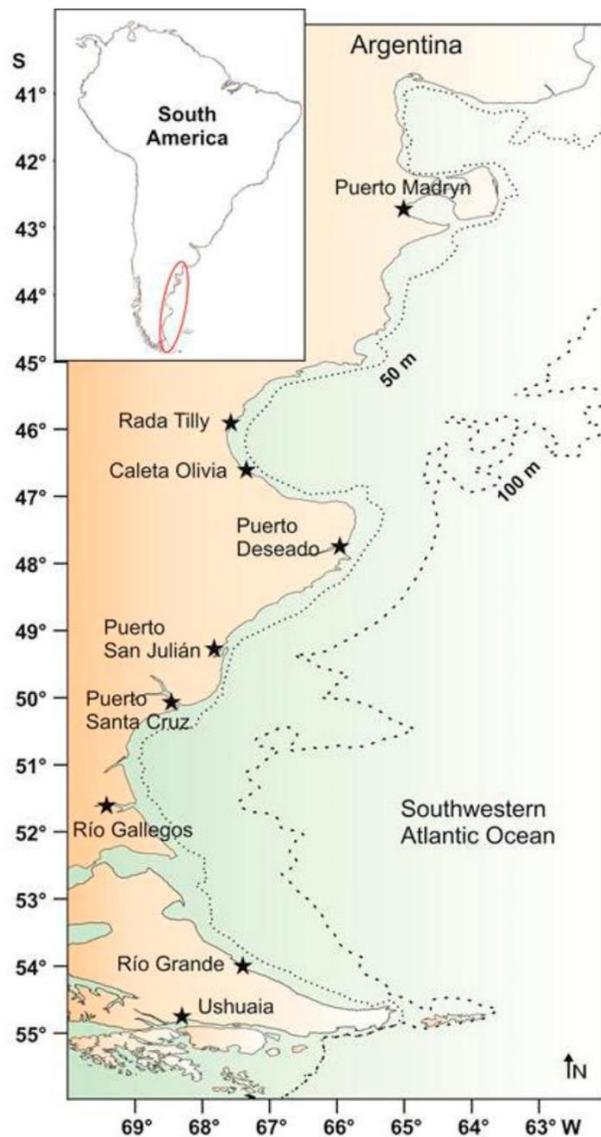


Figure 1. Intertidal sampled sites at Argentinean Patagonia shelf. Stars: rocky outcrops; Circles: salt marshes.

ted and identified in the laboratory down to the species level. Vouchers are deposited in the collections of the UNMDP and MZUSP.

Hydroid associations were analyzed by multivariate analyses (Clarke, 1993; Clarke & Warwick, 2001) using PRIMER 6.0. First, we performed a cluster analysis using the Bray-Curtis similarity index based on presence/absence data of each species. SIMPROF analysis was used to test whether the groups resulted from cluster analysis were significantly different. Subsequently, a test of similarity percentage (SIMPER) was performed to determine the contribution of each species to the similarity/dissimilarity within the groups resulted from the cluster analysis. Finally, we carried

out ANOSIM analysis among (a) Patagonian intertidal heavily colonized by mytilids (*B. purpuratus*), (b) rocky outcrops with conspicuous patchy mytilid beds (*B. purpuratus*) and denude areas, and (c) muddy intertidal fringes dominated by glasswort, in order to test the null hypothesis of the absence of difference in species composition between these three different intertidal habitats.

RESULTS

A total of 26 species of hydroids were found at different intertidal habitats at the Argentinean Patagonia coast (Fig. 1), with 22 leptothecate and 4 anthothecate species (Table 2). SJ and RGr rocky intertidal areas presented high species richness, with 21 and 15 hydroid species, respectively, followed by PS (7 species), then all other sites showed with variable and lower number of species. Remarkably, no hydroids were found at PM and U. Intertidal areas dominated by salt marshes also had lower number of species (RG with 7 species, SJ and PS with 2 species) and PDM also had no hydroid species recorded, as in some rocky intertidal areas (SJ, RGr).

The most frequent hydroid species was *Amphisbetia operculata*, present in 8 of the 10 sites, followed by *Symplectoscyphus subdichotomus* and *Nemertesia ramosa* (5 sites). Some less frequent species occurred in high abundances in each site, such as *Orthopyxis integra*, *Obelia geniculata* and *Ectopleura crocea*. Other less frequent species were usually represented by few colonies (Table 2).

Nine epizoic species were colonizing at least 12 other hydroid species (Table 2). Fronds of the giant kelp *M. pyrifera* were also used as substrate by four epiphytic hydroids, two of them (*Silicularia rosea* and *O. geniculata*) found exclusively on this algae. Sites with low species richness (RT, CO, PD) had all hydroids species we sampled exclusively on *M. pyrifera*. Four species were found attached to rocks and occasionally on other substrata, such as mussel shells (Table 2).

SIMPROF analysis resulted in three significant groups, all with internal similarity higher than 40% (Fig. 6). Group 1 (G1) comprises the northern sampling sites (RT, CO, PD) and five species, and two of them contributed for the internal similarity (*O. geniculata*, 80.6%; *Plumularia setacea*, 19.4%). Group 2 (G2) comprises intertidal muddy salt marshes (SJm, PSm, RGr) or breakwaters (RG), including 7 species, from which 3 mostly contributed for the internal similarity (*A. operculata*, 52.0%; *N. ramosa*, 21.4%; *Hartlaubella gelatinosa*, 21.4%). Group 3 (G3), comprising rocky

Table 1. Habitats and location of samplings along the Argentinean Patagonia coast with respective tidal amplitude and topographic characterization. Information on the coordinates of each site is in Figure 1 and Material and Methods section. Code of sites: RT (Rada Tilly), CO (Caleta Olivia), PD (Puerto Deseado), SJ (San Julián), SJm (San Julián salt marsh), PS (Puerto Santa Cruz), PSm (Puerto Santa Cruz salt marsh), RG (Río Gallegos), RGM (Río Gallegos salt marsh), RGr (Río Grande).

Habitat	Sites	Tidal amplitude	Topography
Rocky outcrops and break waters	PM, RT, CO, PD	Up to 6 m	Rocky boulders, deep crevices and wide tidal pools; colonized by the mytilid <i>Brachidontes purpuratus</i> and by the kelp <i>Macrocystis pyrifera</i> .
	SJ	Up to 9 m	Rocky boulders up to 2 m wide; colonized by patches of mytilids (<i>B. purpuratus</i>).
	PS, RG, RGr	Up to 13 m	Muddy intertidal zones with scattered rocks up to 0.6 m wide, large rock platform with wide tidal pools and deep crevices, wood/concrete breakwaters; colonized by small mytilid patches (<i>B. purpuratus</i>) and by the kelp <i>Macrocystis pyrifera</i> .
Salt marshes	U	2 m	Narrow tidal fringe dominated by the mussel <i>Mytilus edulis</i> .
	PDm, SJm, PSm, RGM		Scattered, wide, tidal pools and large tidal channels; muddy marshes dominated by the glasswort <i>Sarcocornia perennis</i> .

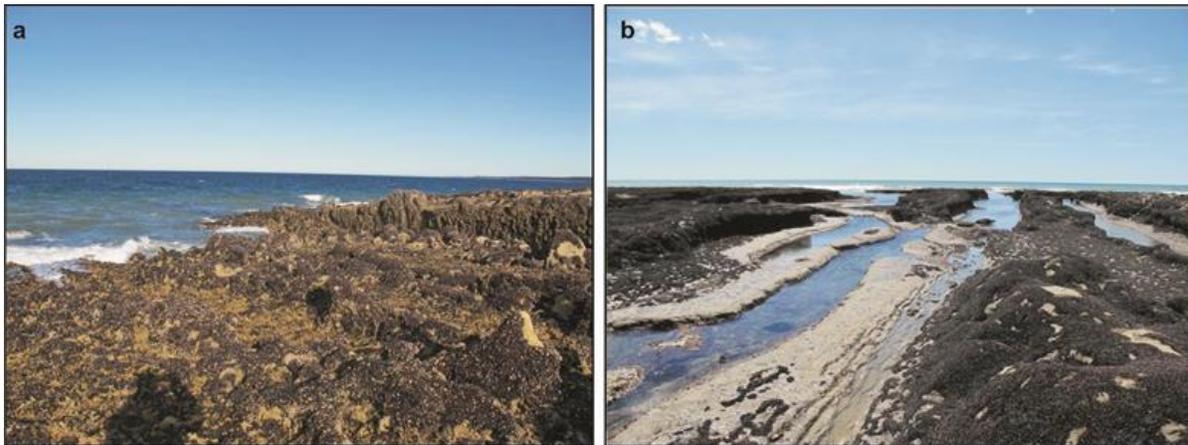


Figure 2. General view of rocky intertidal areas with mussel beds at a) Puerto Madryn, and b) Caleta Olivia.

intertidal outcrops (PS, SJ, RGr), is the richest group (26 species), with 4 species mostly collaborating for their internal similarity (*Amphisbetia operculata*, *S. subdichotomus*, *Clytia gracilis* and *P. setacea*, with 14.6% each). ANOSIM analysis rejected the null hypothesis of absence of difference between the hydroid composition among the intertidal fringes, showing significant differences between them (global $R = 0.927$; $P = 0.2$).

DISCUSSION

We listed 26 hydroids typical of intertidal habitats distributed along the ~2,000 km of the Argentinean Patagonia coast, and inferred their ecological distribution among the different sites. This corresponds

to ~9% (26 of 295 species recorded) and less than 1% (26 of 3,428 species recorded) of the hydrozoan species recorded for the Argentinean Patagonia and worldwide, respectively (Oliveira *et al.*, 2016; Schuchert, 2016), showing that the knowledge on the biodiversity of hydroids at intertidal habitats of Argentinean Patagonia is still scarce. Most of the 26 species were already reported for adjacent subtidal communities, but *Bougainvillia muscus* and *Phialella belgicae* were previously reported only for the Buenos Aires coast and the northern Patagonia (Genzano *et al.*, 2009), and *N. ramosa* is firstly reported for the Argentinean Continental Shelf. Previous records of *N. ramosa* for the Southwestern Atlantic Ocean were from depths greater than 400 and 800 m (Vervoort, 1972; Blanco, 1976), referred as *Plumularia insignis* (Allman, 1883) (see Stepanjants, 1979; Ramil & Vervoort, 1992).



Figure 3. General view of intertidal zone at a) Puerto Santa Cruz, and b) detailed view of boulders with colonies of *Amphisbetia operculata* (yellow arrow). Rocky outcrops at c-d) San Julián, and e-f) Río Grande f) with areas covered by *Macrocystis pyrifera* fronds.

All hydroids herein recorded have wide bathymetrical ranges, commonly found at the austral hemisphere as well as worldwide. Seven species (*Coryne eximia*, *B. muscus*, *E. crocea*, *Hybocodon unicus*, *Halecium delicatulum*, *P. setacea* and *C. gracilis*), however, were also reported at intertidal fringes (Genzano & Zamponi, 2003; Genzano *et al.*, 2009).

Species richness differed according to the type of sea bottom and to the biotic community of the different sites. Intertidal rocky fringes heavily colonized by

mytilids had none (PM and U) or few hydroid species (RT, CO, PD; Group 1 in the cluster analysis). When present in these habitats, hydroids were growing over large kelp fronds. Conversely, southern outcrops with patchy mytilid beds and denuded areas (SJ, PS and RGr, Group 3 of the cluster analysis; Fig. 6) had higher hydroid richness, most likely because of their diverse topographical complexity. The hydroids colonized different microhabitats of these areas (tide pools, crevices, rocky joints, fractures, and others cryptic



Figure 4. a) General view of salt marsh community dominated by the glasswort *Sarcocornia perennis* at Río Gallegos intertidal fringe, b) Detail of marsh pool, and c) *Amphisbetia operculata* (yellow arrow) colony attached on glasswort.



Figure 5. Narrow intertidal fringe at Ushuaia.

surfaces), as well as other hydroid clumps and kelps. The only intertidal outcrop from northern temperate waters of the southwestern Atlantic richer than these areas are the quartzite rocks of Mar del Plata (38°S, with 10 species). Both regions possess a high habitat heterogeneity given by crevices, small caves, and channels (Genzano, 1994; Genzano & Zamponi, 2003).

Most of the hydroid species we sampled were attached to other organisms. Fronds of *M. pyrifera* were a frequent substrate and two hydroid species, *O. geniculata* and *S. rosea*, were found exclusively on this alga. Even previous records from the same area report these hydroids in association with *M. pyrifera* (Blanco, 1964; Blanco & Morris, 1977; G. Genzano, *pers. observ.*), indicating a specialized epiphytic/basibiont relationship (see Oliveira & Marques, 2007, 2011).

Table 2. Hydroid species collected at Argentinean Patagonian intertidal shelf. Code of sites: RT (Rada Tilly), CO (Caleta Olivia), PD (Puerto Deseado), SJ (San Julián), SJm (San Julián salt marsh), PS (Puerto Santa Cruz), PSm (Puerto Santa Cruz salt marsh), RG (Río Gallegos), RGm (Río Gallegos salt marsh), RGr (Río Grande). Classification follows recent phylogenetic updates (Maronna *et al.*, 2016; Cunha *et al.*, 2017).

Taxa	Occurrence	Remarks
Class Hydrozoa Owen, 1843 “Superorder Anthoathecata” Cornelius, 1992 “Order Filifera” Kühn, 1913 Family Bougainvilliidae Lütken, 1850 <i>Bougainvillia muscus</i> (Allman, 1863)	RG	Immature colonies, epizoic on <i>H. chilensis</i> .
Order Capitata Kühn, 1913 <i>sensu stricto</i> Family Corynidae Johnston, 1836 <i>Coryne eximia</i> Allman, 1859	SJ; RG	Abundant mature colonies with small gonophores, commonly settled on <i>E. crocea</i> hydrocauli.
Order Aplanulata Collins, Winkelman, Hadrys, Schierwater, 2005 Family Tubulariidae Fleming, 1828 <i>Ectopleura crocea</i> (L. Agassiz, 1862)	SJ; PS	Large clumps of mature colonies mainly attached to rocks, sometimes on mussel valves.
<i>Hybocodon chilensis</i> Hartlaub, 1905	RG	Mature colonies on rocks. Species status clarified by Rodriguez <i>et al.</i> (2012).
Superorder Leptothecata Cornelius, 1992 Order Lafoeida Bouillon, 1984 Family Lafoeidae A. Agassiz, 1865 <i>Filellum</i> sp.	RGr	Stolonial, immature colonies commonly on <i>S. tenella</i> and <i>G. abietina</i> . Colonies without gonophores prevent identification (viz. Marques <i>et al.</i> , 2011).
<i>Grammaria abietina</i> (M. Sars, 1851)	PS, RGr	Large, immature colonies detached from substrate, but presumably on rocks.
Order Statocysta Leclère, Schuchert, Cruaud, Couloux, Manuel, 2009 Family Phialellidae Russell, 1953 <i>Phialella belgicae</i> (Hartlaub, 1904)	SJ; RGr	Small colonies without gonophores, epizoic on <i>E. crocea</i> , <i>C. eximia</i> and <i>H. chilensis</i> .
Family Campanulariidae Johnston, 1836 <i>Campanularia subantarctica</i> Millard, 1971	SJ; RG	Scarce and immature colonies, epizoic on <i>P. setacea</i> (SJ) and <i>N. ramosa</i> (RGm salt marsh).
<i>Orthopyxis integra</i> (McGillivray, 1842)	CO; SJ; RGr	Mature colonies mainly on <i>M. pyrifer</i> , <i>E. crocea</i> , <i>S. tenella</i> , <i>S. subdichotomus</i> . Frequently reported in Patagonia under different names (status clarified by Cunha <i>et al.</i> , 2015).
<i>Silicularia rosea</i> Meyen, 1834 Family Obeliidae Haeckel, 1879	SJ; RGr	Colonies epiphytic on <i>M. pyrifer</i> .
<i>Hartlaubella gelatinosa</i> (Pallas, 1766)	PS; RG	Large colonies with gonothecae, mostly in salt marshes (tide pools of PSm and RGm), sometimes on wood breakwaters (RG).
<i>Obelia dichotoma</i> (Linnaeus, 1758)	SJ; RG	Immature colonies on mytilid shells and rock (SJ), or in salt marsh tide pools (RGm).
<i>Obelia geniculata</i> (Linnaeus, 1758)	RT, CO, PD, SJ	Many colonies found exclusively on <i>M. pyrifer</i> , some with small gonothecae.
Family Clytiidae Maronna, Miranda, Peña Cantero, Barbeitos, Marques, 2016 <i>Clytia gracilis</i> (M. Sars, 1851)	SJ; PS; RGr	Immature colonies epizoic on <i>N. ramosa</i> and <i>E. crocea</i> .
Order Macrocolonia Leclère, Schuchert, Cruaud, Couloux, Manuel, 2009 Family Haleciidae Hincks, 1868 <i>Halecium delicatum</i> Coughtrey, 1876	SJ	Small, immature colonies attached on colonies of <i>A. operculata</i> .
<i>Halecium</i> sp.	SJ	Fragments of colonies detached from rocks, with few and immature gonophores different from <i>H. delicatum</i> ; poor condition of colonies prevents species identification.

Continuation

Taxa	Occurrence	Remarks
Family Sertulariidae Lamouroux, 1812 <i>Amphisbetia operculata</i> (Linnaeus, 1758)	PD; SJ; PS; RG; RGr	Large clumps of mature colonies common in most of intertidal zones studied herein, mainly attached on rocks, less frequently on mussel bivalves, rarely on algae. Living colonies in salt marsh tide pools (SJm, PSm, RGr) and numerous dead fragments common among stems of <i>Sarcocornia perennis</i> . Species on wood breakwaters in PS, completely exposed during low tide, several meters above bottom; other colonies attached on small pebbles lying on muddy bottom.
Family Sertularellidae Maronna, Miranda, Peña Cantero, Barbeitos, Marques, 2016 <i>Sertularella antarctica</i> Hartlaub, 1900	SJ; RGr	Small, immature colony on algae.
<i>Sertularella picta</i> (Meyen, 1834)	SJ	Mature colonies epiphytic or on rocks.
<i>Sertularella tenella</i> (Alder, 1856)	CO; SJ; RGr	Immature colonies usually associated to <i>A. operculata</i> .
Family Symplectoscyphidae Maronna, Miranda, Peña Cantero, Barbeitos, Marques, 2016 <i>Symplectoscyphus milneanus</i> (d'Orbigny, 1839)	SJ; RGr	Few immature colonies usually associated to <i>A. operculata</i> .
<i>Symplectoscyphus subdichotomus</i> (Kirchenpauer, 1884)	SJ; PS; RG; RGr	Abundant colonies, most with gonothecae. Predominantly on rocks, some on <i>G. abietina</i> and wood breakwaters. Few colonies in salt marsh tide pools (RGr).
<i>Symplectoscyphus</i> sp.	SJ; RG	Immature colonial fragment, distinct from <i>S. subdichotomus</i> , on rocky intertidal zone detached from substrate (S), or in salt marsh tide pool associated with <i>A. operculata</i> (RGr).
Family Thyrosocyphidae Stechow, 1920 <i>Parascyphus repens</i> (Jäderholm, 1904)	SJ	Large, immature colonies detached from substrate.
Family Plumulariidae McCrady, 1859 <i>Nemertesia ramosa</i> (Lamarck, 1816)	SJ; PS; RG	Abundant, most colonies with gonothecae. Frequent at areas with soft muddy sediments, on rocks, wood breakwaters, or tidal pools; numerous dead fragments among stems of <i>Sarcocornia perennis</i> in salt marshes (SJm; RGr).
<i>Plumularia setacea</i> (Linnaeus, 1758)	CO; PD; SJ; PS; RGr	Mature and immature colonies attached on rocks or sponges in southern areas, but epiphytic on <i>M. pyrifer</i> in northern areas dominated by mussels (CO and PD).

This association might be related to the important role played by kelps as humid substrates for initial settlement and recruitment of delicate species, such as *O. integra* (cf. Cunha *et al.*, 2015). The use of stems of hydroids as substrata for other hydroid species is also a common phenomenon for the temperate southwestern Atlantic (*e.g.*, stems of *Amphisbetia operculata*, *Plumularia setacea*; Genzano, 1994; Genzano *et al.*, 2009; Meretta & Genzano, 2015). Species with bushy habits or grouped in clumps, such as large colonies of *A. operculata*, *N. ramosa*, *Hybocodon chilensis* and *E. crocea*, were frequently used as substrata by smaller hydroid species (*e.g.*, *P. belgicae*, *Filellum* sp., *C. gracilis*, *O. integra*). This epizoic pattern is known to be a strategy to avoid the negative effect of sediment deposition and the competition for space, also providing better water flow conditions for suspension feeders, such as hydroids (Gili & Hughes, 1995; Genzano *et al.*, 2009; Meretta & Genzano, 2015).

Some intertidal fringes dominated by mud, scattered pebbles, and cobbles embedded in the sediment were colonized by relatively few hydroid species, most commonly *A. operculata* and *N. ramosa*. These species formed clumps laid on mud during the low tide, indicating a high tolerance to the negative effects of the deposition of fine sediments, as well as extreme daily temperature changes when exposed. Some clumps of *A. operculata* were attached to breakwaters ~0.6 m above sea level, completely exposed to the air during low tide, demonstrating a remarkable tolerance to desiccation stress.

Finally, some muddy intertidal fringes dominated by the *S. perennis* had an unexpectedly rich hydroid fauna composition (Group 2 in the cluster analysis; Fig. 6). This is a remarkable novelty for the hydroid literature, never reported before for salt marshes. Even a specific revision of Patagonian salt marsh communities (Bortolus *et al.*, 2009) did not report cnidarians

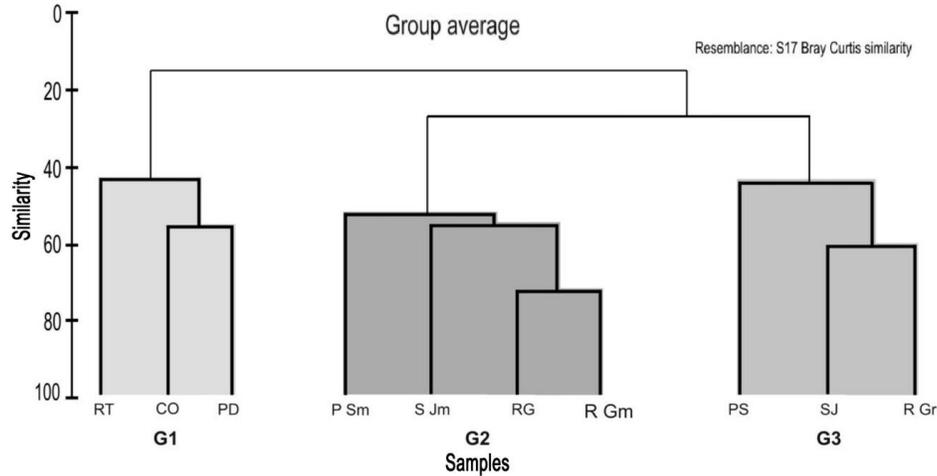


Figure 6. Dendrogram showing significant faunal groups (G1, G2, G3) resulted from cluster and SIMPROF analyses among the sampled sites. Code of sites: RT (Rada Tilly), CO (Caleta Olivia), PD (Puerto Deseado), SJ (San Julián), SJm (San Julián salt marsh), PS (Puerto Santa Cruz), PSm (Puerto Santa Cruz salt marsh), RG (Río Gallegos), RGm (Río Gallegos salt marsh), RGr (Río Grande).

among the marine invertebrates inhabiting these extensive areas. We found only few specimens of microcrustaceans and polychaetes in the studied austral Patagonian pool marshes. But, remarkably, there were up to seven hydroid species living in pristine waters at marsh pools, usually settled on pebbles. These microhabitats also retain water during the low tide periods, and provide favorable and almost continuously protected areas for the development of colonies (Bastida *et al.*, 2007). Glasswort stems had no epiphytic hydroid and only hydrocauli fragments were present on the macrophyte. This pattern might be related with predation, competition, seasonality or other intrinsic factor concerning the species' preference. Whatever the process is, this is out of the scope of this study and would be better investigated and discussed under an ecological/physiological approach.

This study provides a list of hydroid species, their distributions, richness and ecological associations between salt marshes and intertidal outcrops of the SW Atlantic Patagonia. We found three main faunal clusters along the studied area. Each cluster was characterized by a particular hydroid composition and a series of biotic associations unique to those habitats. The picture presented here of the composition and richness of hydroids species from SW Atlantic Patagonia provides a small outline of the high marine benthic biodiversity within this region that is little-studied and faces an increasing range of environmental threats.

ACKNOWLEDGMENTS

The authors thank to Mr. B. Vera who provided logistic support and assistance during field works and Miss Paula Genzano for help during field surveys in Río Grande. This work was supported by CONICET (Grant PIP 0152), UNMdP (Grant EXA 734/15), FAPESP (grants 2010/52324-6, 2010/06927-0, 2011/50242-5, 2013/50484-4, 2014/24407-5), CAPES PROEX, and CNPq (142269/2010-7, 474672/2007-7, 562143/2010-6, 477156/2011-8, 301039/2013-5, 305805/2013-4, 445444/2014-2).

REFERENCES

- Bastida, R., M.O. Zamponi, A. Roux, C. Bremec, G.N. Genzano & R. Elias. 2007. Las comunidades bentónicas. In: J.I. Carreto & C. Bremec (eds.). El mar Argentino y sus recursos pesqueros. Volumen 5. El ecosistema marino. INIDEP, Mar del Plata, pp. 89-123.
- Blanco, O.M. 1964. Algunos campanularidos argentinos. *Rev. Mus. La Plata*, 7: 149-171.
- Blanco, O.M. 1976. Hidrozoos de la expedición Walther Herwig. *Rev. Mus. La Plata*, 12: 27-74.
- Blanco, O.M. 1994. Enumeración sistemática y distribución geográfica preliminar de los hidroides de la República Argentina. Suborden Athecata (Gymnoblastera, Anthomedusae), Thecata (Calyptoblastea, Leptomedusae) y Limnomedusae. *Rev. Mus. La Plata*, 14: 181-216.

- Blanco, O.M. & M.R. Morris 1977. Nueva cita para *Obelia geniculata* (L.) (Hydroida Campanulariidae). *Neotropica*, 23: 91-93.
- Brinckmann-Voss, A. 1996. Seasonality of hydroids (Hydrozoa, Cnidaria) from an intertidal pool and adjacent subtidal habitats at Race Rocks, off Vancouver Island, Canada. *Sci. Mar.*, 60: 89-97.
- Boero, F. 1984. The ecology of marine hydroids and effects of environmental factors: a review. *Mar. Ecol.*, 5: 93-118.
- Bortolus, A., E. Schwindt, P. Bouza & Y. Idaszkin. 2009. A characterization of the Patagonian salt marshes. *Wetlands*, 29: 772-780.
- Calder, D.R. 1991. Vertical zonation of the hydroid *Dynamena crisioides* (Hydrozoa, Sertulariidae) in a mangrove ecosystem at Twin Cays, Belize. *Can. J. Zool.*, 69: 2993-2999.
- Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.*, 18: 117-143.
- Clarke, K.R. & R.M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation.. PRIMER-E Ltd, Plymouth Marine Laboratory, Plymouth, 172 pp.
- Cunha, A.F., G.N. Genzano & A.C. Marques. 2015. Reassessment of morphological diagnostic characters and species boundaries requires taxonomical changes for the genus *Orthopyxis* L. Agassiz, 1862 (Campanulariidae, Hydrozoa) and some related campanulariids. *PLoS ONE*, 10(2): e0117553.
- Cunha, A.F., A.G. Collins & A.C. Marques. 2017. Phylogenetic relationships of Proboscoida Broch, 1910 (Cnidaria, Hydrozoa): are traditional morphological diagnostic characters relevant for the delimitation of lineages at the species, genus, and family levels? *Mol. Phyl. Evol.*, 106: 118-135.
- El Beshbeeshy, M. & G. Jarms. 2011. Thekate Hydroiden vom Patagonischen Schelf (Cnidaria, Hydrozoa, Thecata). *Verh. Naturwiss. Ver. Hamburg*, 46: 19-233.
- Genzano, G.N. 1994. La comunidad hidroide del intermareal rocoso de Mar del Plata (Argentina). I. Estacionalidad, abundancia y períodos reproductivos. *Cah. Biol. Mar.*, 35: 289-303.
- Genzano, G.N. 2001. Associated fauna and sediment trapped by colonies of *Tubularia crocea* (Cnidaria, Hydrozoa) from the rocky intertidal of Mar del Plata, Argentina. *Biociencias*, 9: 105-119.
- Genzano, G.N., E.I. Cuartas & A.C. Excoffon. 1991. Porifera y Cnidaria de la Campaña Oca Balda 05/88. *Thalassas*, 9: 63-78.
- Genzano, G.N., D. Giberto, L. Schejter, C. Bremec & P. Meretta. 2009. Hydroids assemblages in SW Atlantic (34-42°S): richness and settlement substrata. *Mar. Ecol.*, 30: 33-46.
- Genzano, G.N. & G.M. Rodriguez. 1998. Associations between hydroid species and their substrates from intertidal of Mar del Plata (Argentina). *Misc. Zool.*, 21: 21-29.
- Genzano, G.N. & M. Zamponi. 2003. Hydroid assemblages from Mar del Plata, Argentina, at depths between 0 and 500 m. Distribution and biological substrata. *Oceanol. Acta*, 25: 303-313.
- Gili, J.-M. & R.G. Hughes. 1995. The ecology of marine benthic hydroids. In: A.D. Ansell & M. Barnes (eds.). *Oceanography and marine biology: an annual review* 33. UCL Press, London, pp. 351-426.
- Henry, L.-A. 2002. Intertidal zonation and seasonality of the marine hydroid *Dynamena pumila* (Cnidaria: Hydrozoa). *Can. J. Zool.*, 80: 1526-1536.
- Hughes, R.G. 1992. Morphological adaptations of the perisarc of the intertidal hydroid *Dynamena pumila* to reduce damage and enhance feeding efficiency. *Sci. Mar.*, 56: 269-277.
- Maronna, M.M., T.P. Miranda, A.L. Peña Cantero, M.S. Barbeitos & A.C. Marques. 2016. Towards a phylogenetic classification of Leptothecata (Cnidaria, Hydrozoa). *Sci. Rep.*, 6: 18075.
- Marques, A.C., A.L. Peña-Cantero, T.P. Miranda & A.E. Migotto. 2011. Revision of the genus *Filellum* Hincks, 1868 (Lafoeidae, Leptothecata, Hydrozoa). *Zootaxa*, 3129: 1-28.
- Menge, B.A. & T.M. Farrell. 1989. Community structure and interaction webs in shallow marine hard-bottom communities: tests of an environmental stress model. *Adv. Ecol. Res.*, 18: 189-262.
- Meretta, P.E. & G.N. Genzano. 2015. Epibiont community variation on two morphologically different hydroid colonies: *Amphisbetia operculata* and *Plumularia setacea* (Cnidaria, Hydrozoa). *Mar. Biol. Res.*, 11: 294-303.
- Migotto, A.E., A.C. Marques, A.C. Morandini & F.L. Silveira. 2002. Checklist of the Cnidaria Medusozoa of Brazil. *Biota Neotrop.*, 2: 1-31.
- Miranda, T.P., G.N. Genzano, A.C. Marques. 2015. Areas of endemism in the Southwestern Atlantic Ocean based on the distribution of benthic hydroids (Cnidaria: Hydrozoa). *Zootaxa*, 4033: 484-506.
- Oliveira, O.M.P. & A.C. Marques. 2007. Epiphytic hydroids (Hydrozoa: Anthoathecata and Leptothecata) of the world. *Check List*, 3: 21-38.
- Oliveira, O.M.P. & A.C. Marques. 2011. Global and local patterns in the use of macrophytes as substrata by hydroids (Hydrozoa: Anthoathecata and Leptothecata). *Mar. Biol. Res.*, 7: 786-795.
- Oliveira, O.M.P., T.P. Miranda, E.M. Araujo, P. Ayón, C.M. Cedeño-Posso, A.A. Cepeda-Mercado, P. Córdova, A.F. Cunha, G.N. Genzano, M.A. Haddad, H.W. Mianzan, A.E. Migotto, L.S. Miranda, A.C.

- Morandini, R.M. Nagata, K.B. Nascimento, M. Nogueira Jr., S. Palma, J. Quiñones, C.S. Rodriguez, F. Scarabino, A. Schiariti, S.N. Stampar, V.B. Tronolone & A.C. Marques. 2016. Census of Cnidaria (Medusozoa) and Ctenophora from South American marine waters. *Zootaxa*, 4194: 1-256.
- Ramil, F. & W. Vervoort. 1992. Some consideration concerning the genus *Cladocarpus* (Cnidaria: Hydrozoa). In: J. Bouillon, F. Boero, F. Cicogna, J.-M. Gili & R.G. Hughes (eds.). Aspects of hydrozoan biology. *Sci. Mar.*, 56: 171-176.
- Rodriguez, C.S., T.P. Miranda, A.C. Marques, H. Mianzan & G. Genzano. 2012. The genus *Hybocodon* (Cnidaria, Hydrozoa) in the southwestern Atlantic Ocean, with a revision of *Hybocodon* species recorded in the area. *Zootaxa*, 3523: 39-48.
- Rossi, S., J.-M. Gili & R.G. Hughes. 2000. The effects of exposure to wave action on the distribution and morphology of the epiphytic hydrozoans *Clava multicornis* and *Dynamena pumila*. *Sci. Mar.*, 64: 135-140.
- Rosso, S. & A.C. Marques. 1997. Pattern in intertidal hydrozoan distribution along the coast of São Paulo State, Southeastern Brazil. Proceedings of the VI International Conference on Coelenterate Biology. The Netherlands, Leiden, 8 pp.
- Schuchert, P. 2016. Hydrozoa. World Register of Marine Species [<http://www.marinespecies.org/aphia.php?p=taxdetails&id=1337>]. Reviewed: 23 Nov 2016.
- Schwindt, E., J. López-Gappa, M.P. Raffo, M. Tatián, A. Bortolus, J.M. Orensanz, G. Alonso, M.E. Diez, B. Doti, G.N. Genzano, C. Lagger, G. Lovrich, M.L. Piriz, M.M. Mendez, V. Savoya & M.C. Sueiro. 2014. Marine fouling invasions in ports of Patagonia (Argentina) with implications for legislation and monitoring programs. *Mar. Environ. Res.*, 99: 60-68.
- Stepanjants, S. 1979. Hydroids of the Antarctic and Subantarctic waters. *Biol. Res. Soviet Antarct. Exped.*, ed. Isslad Fauny Morei, 20: 1-200 (in Russian).
- Vervoort, W. 1972. Hydroids from “Theta”, “Vema” and “Yelcho” cruises of the Lamont Doherty Geological observatory. *Zool. Verh.*, 120: 1-249.

Received: 15 March 2016; Accepted: 30 November 2016