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Environment and life cycles influence distribution patterns of hydromedusae in austral South America

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ABSTRACT

We analysed hydromedusa assemblages of South America (from 22°S to 56°S and from 040°W to 080°W), their association with water masses and the influence of the life cycle on medusa distributions. The geographic distribution of 130 species of hydromedusae was compiled from literature reports (62 publications between 1913 and 2012). Seven areas were defined: Atlantic Magellanic, Argentinean, Pacific intermediate zone, Pacific Magellanic, Peruvian–Chilean, South Brazilian and Oceanic. The variance of the species–environment relationship was explained by depth and temperature. Distribution patterns of Atlantic hydromedusae are associated with neritic water masses, supporting previously proposed biogeographical provinces. Assemblages on the Pacific side of South America are under the influence of the Humboldt Current system, with a break in species distribution around Chiloé Island. Only the oceanic assemblage contained the same species in both the Pacific and Atlantic zones. We found that meroplanktonic medusae contributed more to define the neritic assemblages, while the oceanic assemblage was better defined by holoplanktonic medusae. Therefore, our data suggest that meroplanktonic hydromedusae appeared to be more restricted in distribution than holoplanktonic ones.

Introduction

Important drivers of marine species distributions include circulation patterns at the basin scale and latitudinal gradients of temperature (Angel 1997). The combination of these two drivers results in apparent divisions of oceans into regions or provinces characterized by distinct species assemblages (Levinton 1995) that co-occur due to their similar or complementary ecophysiological requirements (Mazzocchi et al. 2011). These processes have led to proposals of biogeographical provinces (Longhurst 1995; Spalding et al. 2007).

Since the middle of the twentieth century, biogeographers have reported correlations between species distributions and water masses (Ekman 1953; Briggs 1974). However, boundaries between different marine faunal regions do not explain or limit the distributions of all species, and often subtle differences in species distributions may result in alternative proposals for biogeographical provinces and their boundaries. Many

species tolerate physical conditions far beyond their optimal ranges for reproduction and as a consequence, many 'boundaries' tend to consist of broad transition zones (ecotones, Angel 1997; Boltovskoy et al. 1999).

Austral South America has complex biogeographical dynamics in part due to the interaction of different water masses. In the Atlantic Ocean, the southward tropical–subtropical flow of the Brazil Current opposes the northward sub-Antarctic flow of the Malvinas (Falkland) Current, resulting in a conspicuous Confluence Zone of mixed waters. Thus, the shelf waters result from the mixing of coastal, sub-Antarctic and subtropical waters (Bisbal 1995). Similarly, the Pacific Ocean off South America has the Humboldt Current system complex. The West Wind Drift approaches southern South America from the west and branches into two flows, a northward flow called the Humboldt Current and a southward one called the Cape Horn Current. The latter influences the southernmost extreme of the continent and extends eastward to join the Malvinas (Falkland) Current. The Fjord Current arises from

the Cape Horn Current, reaching the coast near Chiloé and continuing northward (Camus 2001). In this complex physical environment, many uncertainties remain about marine biogeographic boundaries around austral South America (see Camus 2001; Balech & Ehrlich 2008). For example, the position of the northern border of the Argentinean Province is disputed (Balech 1954, 1964; Lopez 1963; Palacio 1982; Boschi 2000; Balech & Ehrlich 2008; Menni et al. 2010), with proposals ranging from Cabo Frio, Brazil (ca. 23°S) to Uruguay (30–32°S). The Argentinean Province is often considered a transitional zone with extensive mixing of warm- and cold-water organisms, with almost all species coming from neighbouring areas (Dadon & Boltovskoy 1982; Boltovskoy et al. 1999).

Proposals for marine biogeographical units may vary with the taxa used in the analysis (Bisbal 1995; Camus 2001). Although biogeographical inferences based on the distributions of hydromedusae (Cnidaria, Hydrozoa) primarily deal with planktonic communities, they indirectly also include benthic communities (cf. distribution of polyps and medusae in Mendoza-Becerríl & Marques 2013). This occurs because the basic life cycle of meroplanktonic hydromedusae has three main stages: planula, polyp and medusa. Medusae are asexual buds of polyps, which are eventually released and become sexually mature. The zygote formed through the sexual reproduction of medusae develops into a planula, which in turn will generate a new polyp. However, there are hydromedusa species with life histories lacking a benthic stage (holoplanktonic life cycle) and in some hydropolyp species the medusa stage is completely suppressed (Naumov 1969).

Over recent decades, there have been debates about the diverse species' dispersal capabilities. The long-lived planktonic stage was often considered to be the most important dispersal mode. In fact, some investigators have suggested that holoplanktonic species may often have less biogeographical structure than meroplanktonic species (Gibbons et al. 2010b), because holoplanktonic species are more widely distributed, possibly due to the homogeneity of the pelagic environment (Gibbons et al. 2010a). Paradoxically, many coastal species with a reduced or suppressed medusa stage may have wider distributions than species with a fully functional medusa stage, because they can disperse by rafting of their polyps (Cornelius 1992). Kramp (1959) had already proposed that the distribution of species was not merely dependent on the physical conditions in the region but also on the ecological habit of the species. Recently, Gibbons et al. (2010b) highlighted the importance of the interaction between oceanographic conditions and life-cycle strategies for understanding species distribution patterns.

A recent review of the species richness of hydromedusae in South America made an extensive database for that area available (Genzano et al. 2008; Rodriguez 2012; Oliveira et al. 2016). We used that database to analyse hydromedusa assemblages in South America and their association with water masses, in comparison with previous marine biogeographical proposals. Additionally, we discuss the influence of the life cycle on potential medusa distributions.

Material and methods

Hydromedusa distributional information from the Atlantic and Pacific Oceans of southern South America, from 22°S to 56°S and 40°W to 80°W, was compiled from literature reports (65 publications between 1913 and 2012) (Supplementary material Table SI). These primary data generated a databank of the distributions of 130 accurately identified hydromedusa species (58 Anthoathecata, 37 Leptothecata, six Limnomedusae, 12 Narcomedusae and 17 Trachymedusae). Medusae not identified to species level were not used.

The study area was divided into $2° \times 2°$ cells ($n = 131$) and, in each cell, the presence (1) or absence (0) was scored for each of the 130 species. Any species based on one or two specimens or recorded at only one point of latitude and longitude, as well as all cells with only one species, were excluded. The final data matrix contained 104 cells with 116 species (Table SII).

Assemblages were inferred using a hierarchical agglomerative method that links cells that have mutually high levels of species similarity. The resulting hierarchical clustering arranges samples according to their similarity level and is represented by a tree diagram or dendrogram (CLUSTER analysis, Clarke & Warwick 2001). This hierarchical clustering with group-average linking was based on a similarity matrix constructed with the Bray–Curtis coefficient. In order to objectively identify groups and subgroups displayed by the dendrogram, a similarity profile test (SIMPROF, Clarke et al. 2008) was performed. This permutation test is based on the null hypothesis that a specified set of samples do not differ from each other in a multivariate structure. As a result, the 'true' groups found in the SIMPROF test are identified by the continuous lines in the dendrogram. Similarity percentages analysis (SIMPER, Clarke & Warwick 2001) was used to identify those species which contributed most to similarities within groups. This analysis calculates the

'internal similarity', the contribution that each species makes to the average similarity within each group (Software PRIMER v6, Clarke & Warwick 2001).

In order to test whether the life cycles of hydromedusae and their distributions are closely related, the original data matrix was separated into two matrices, one containing the presence (1) or absence (0) of meroplanktonic species per cell and the second containing the presence–absence of holoplanktonic species per cell. The RELATE routine was used to test if the among-sample relationships agreed exactly in the same way in both data sets when comparing the two similarity matrices (based on the Bray–Curtis similarity index). The null hypothesis of this permutation test is that the matching coefficient $P = 0$ if there is no relationship whatsoever between the two similarity matrices. Its null distribution can be obtained by randomly permutating both sets of sample labels and recalculating P to construct a frequency histogram with which the true value of P can be compared (Software PRIMER v6, Clarke & Warwick 2001). The relationship between life-cycle patterns and hydromedusa distributions was inferred based on the results of this routine and the contribution of meroplanktonic and holoplanktonic hydromedusae to the similarity within each group obtained with CLUSTER (SIMPER analysis results, see above).

The environmental influence on hydromedusa spatial distribution was tested using Canonical Correspondence Analysis (CCA). The CCA forms a linear combination of environmental variables that maximally separates the niches of the species, and the primary result is an ordination diagram (Leps & Smilauer

2003). The statistical significance of the effect of each variable is tested by a Monte Carlo permutation test (Software CANOCO Version 4.5). Depth and mean annual sea-surface temperature and salinity for each cell were obtained from the Aquamaps Environmental Dataset (Kaschner et al. 2016; Table SII). The 200 m bathymetric contour was chosen as the line separating the neritic and oceanic zones.

Results

The dendrogram obtained with CLUSTER and SIMPROF displayed 12 groups defining seven different areas (Figure 1): (1) Atlantic Magellanic, (2) Argentinean, (3) Pacific intermediate zone, (4) Pacific Magellanic, (5) Peruvian–Chilean, (6) South Brazilian and (7) Oceanic. Three areas (1, 2 and 6) were found to have internal differentiation.

The Atlantic Magellanic province covered sub-Antarctic waters of the southern Patagonian Shelf, from 46°S on the Atlantic side to 52°S on the Pacific side (Figure 2). It was composed of three groups (Figures 1 and 2): 1a was located in the coastal waters of Argentinean Patagonia, from 46°S to 52°S, with low temperature and salinity levels; 1b covered the outer waters of Argentinean Patagonia, deeper than 100 m and with low temperatures; and 1c was located in the cold waters of the Strait of Magellan and Malvinas (Falkland) Islands (Table I). The Argentinean province was located on shelf waters from Uruguay (~34°S) to the San Jorge Gulf (~46°S) (Figure 2) and two groups within it could be differentiated, the Uruguayan (2a) and Rionegrensis (2b) districts. The Uruguayan district covered the northern part, with depths shallower than 200 m (except for one cell), low salinity and intermediate temperatures, and the Rionegrensis district covered the southern part at depths shallower than 100 m (Table I). The two districts mixed between 36°S and 40°S. Area 3 was located around Chiloé Island (Pacific coast) between 40°S and 44°S and was an intermediate zone between the Peruvian–Chilean province (area 5) to the north and the Pacific Magellanic province (area 4) to the south (Figure 2). The South Brazilian province covered the subtropical waters of the south-southeastern Brazilian coast up to the Río de la Plata estuarine zone (~35°S) (Figure 2). It was composed of three groups: 6a and 6b covered the southeast Brazilian shelf between 22°S and 26°S, characterized by high salinity and high temperature, and group 6c covered the south Brazilian shelf between 26°S and 35°S and also had high temperature and salinity, although some zones had low salinity (Table I). The Oceanic assemblage was deeper than 200 m and close to the shelf

Table I. Mean depth and mean annual sea-surface temperature and salinity for each South American hydromedusa group obtained with the CLUSTER analysis: Atlantic Magellanic (groups 1a, 1b and 1c), Argentinean (groups 2a and 2b), Pacific intermediate zone (3), Pacific Magellanic (4), Peruvian–Chilean (5), South Brazilian (groups 6a, 6b and 6c) and Oceanic (7).

| Group | Environmental variables | | |
	Temperature (°C)	Salinity	Depth (m)
1a	9.2 (8.4–10.9)	33 (32.6–33.3)	64.8 (33.7–88.2)
1b	7.6 (6–9.1)	33.8 (33.6–34.0)	1266.8 (138.9–2394.7)
1c	7.2 (6.7–7.7)	33.6 (33.4–34.0)	322.1 (36.37–1323.9)
2a	16.6 (15.6–17.4)	31 (27.1–34.1)	653.6 (9.7–2366.6)
2b	14 (12.2–15.7)	33.4 (31.4–33.9)	42.4 (16.2–77.4)
3	12.8 (12.6–13.1)	33.4 (33.3–33.5)	530 (49.5–1498.1)
4	11.6 (11.1–12)	33 (32.9–33.2)	10.7 (3.3–18.1)
5	14.6 (13.9–15.5)	33.9 (33.6–34.1)	688 (68.4–2184.2)
6a	23.4 (23–23.7)	35.7 (35.1–36.0)	272 (35.4–720.4)
6b	23.3 (22.5–24.1)	35.7 (35.4–36.0)	68.8 (12.5–125.1)
6c	21.1 (19.3–23)	32.9 (26.9–35.9)	776.4 (32.6–2566.7)
7	13.8 (3.8–24.7)	34.4 (33.5–36.6)	2214.2 (81.5–4542.8)

In parentheses, minimum and maximum values for each environmental variable are provided.
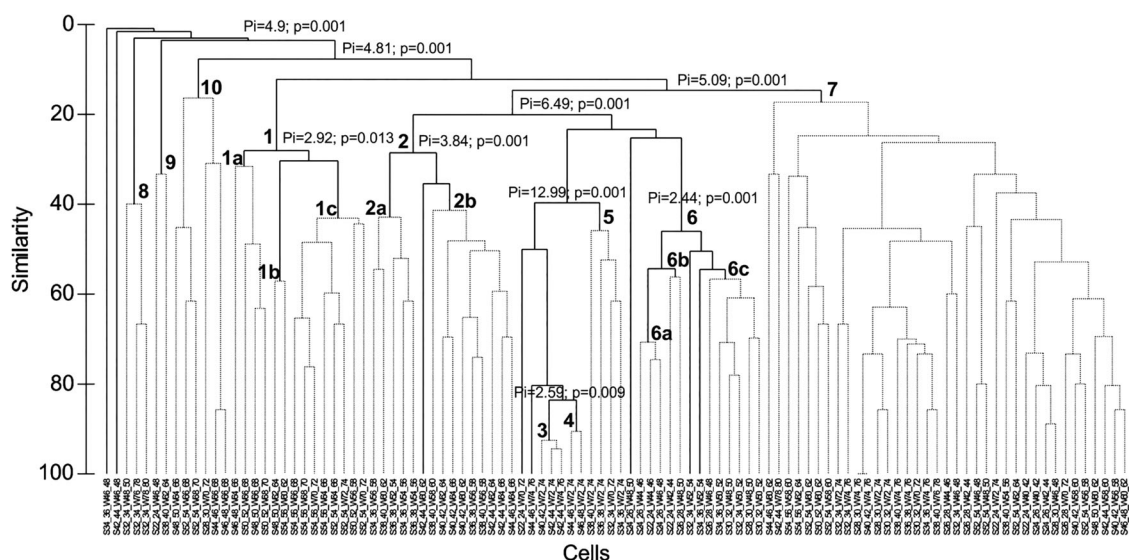
Figure 1. Dendrogram obtained with CLUSTER analysis; the 'true' groups found by the SIMPROF test are identified by the solid lines, and the dashed lines indicate groups of samples not separated (at $P < 0.05$). Values in the dendrogram show the significance of the formation of groups. Twelve groups defined seven different areas: 1, Atlantic Magellanic (groups 1a, 1b and 1c); 2, Argentinean (groups 2a and 2b); 3, Pacific intermediate zone; 4, Pacific Magellanic; 5, Peruvian–Chilean; 6, South Brazilian (groups 6a, 6b and 6c); and 7, Oceanic. Three additional groups (8, 9 and 10) did not define any area. The code labels of the dendrogram represent each cell of the study area in South America with data for presence–absence of each hydromedusa species.

break (Figure 2). Three additional small groups obtained with CLUSTER (8, 9 and 10) (Figure 1) included a few cells ($N = 11$) that were irregularly distributed (Figure 2).

The analysis of the holoplanktonic and meroplanktonic matrices showed that the two were independent (RELATE, $P = 0.187$) and that they were distributed differently throughout the cells. The SIMPER analysis results (Table II) showed that only holoplanktonic species contributed to the similarity in the Oceanic group. Meroplanktonic medusae contributed to the within-group similarity to define neritic areas, except for the South Brazilian province and the Uruguayan district, for which holoplanktonic species were also important (Figure 3).

The CCA ordination showed that 91% of the variance of the species–environment relationship was explained by the first two axes (Figure 4). The first axis explained 58% of the variance and was associated with depth (eigenvalue = 0.439; $P = 0.002$). The second axis, associated with temperature, explained 33% of the variance (eigenvalue = 0.251; $P = 0.002$). Along axis 1, the Oceanic assemblage found in deep waters was separated from the Rionegrensis district at low depths, except *Clytia simplex* (Browne, 1902). Two provinces were separated along axis 2: species contributing to the three groups of Atlantic Magellanic provinces were associated with lower temperatures, except the species *Solmundella bitentaculata* (Quoy & Gaimard, 1833) and *Rhopalonema velatum* Gegenbaur,

1857, and species of the three groups of the South Brazilian provinces were associated with higher temperatures, except *Coryne eximia* Allman, 1859 and *R. velatum* (Figure 4). The set of species that contributed to the Uruguayan district and Pacific areas (Magellanic, Intermediate zone and Peruvian–Chilean) were not associated with any axis.

Discussion

Biogeographical provinces

The biogeographical provinces resulting from our analyses are ecologically defined by water depth and temperature. Indeed, the distribution patterns of Atlantic hydromedusae are associated with neritic water masses, supporting previously proposed biogeographical provinces, such as the South Brazilian, Argentinean and Magellanic. In the Magellanic province (sub-Antarctic neritic after Dadon & Boltovskoy 1982; but see Marques & Peña Cantero 2010 and Miranda et al. 2013 for hydrozoan polyp analyses) the hydromedusae are associated with the cold sub-Antarctic waters of the Patagonian shelf (6.8–10.7°C) (Hubold 1980). Although salinity was not statistically associated with the internal differentiation of biogeographical provinces in the CCA analysis, group 1a corresponds to coastal low-salinity waters (~32.5) related to the discharge from melting ice near the Strait of Magellan, and groups 1b and 1c
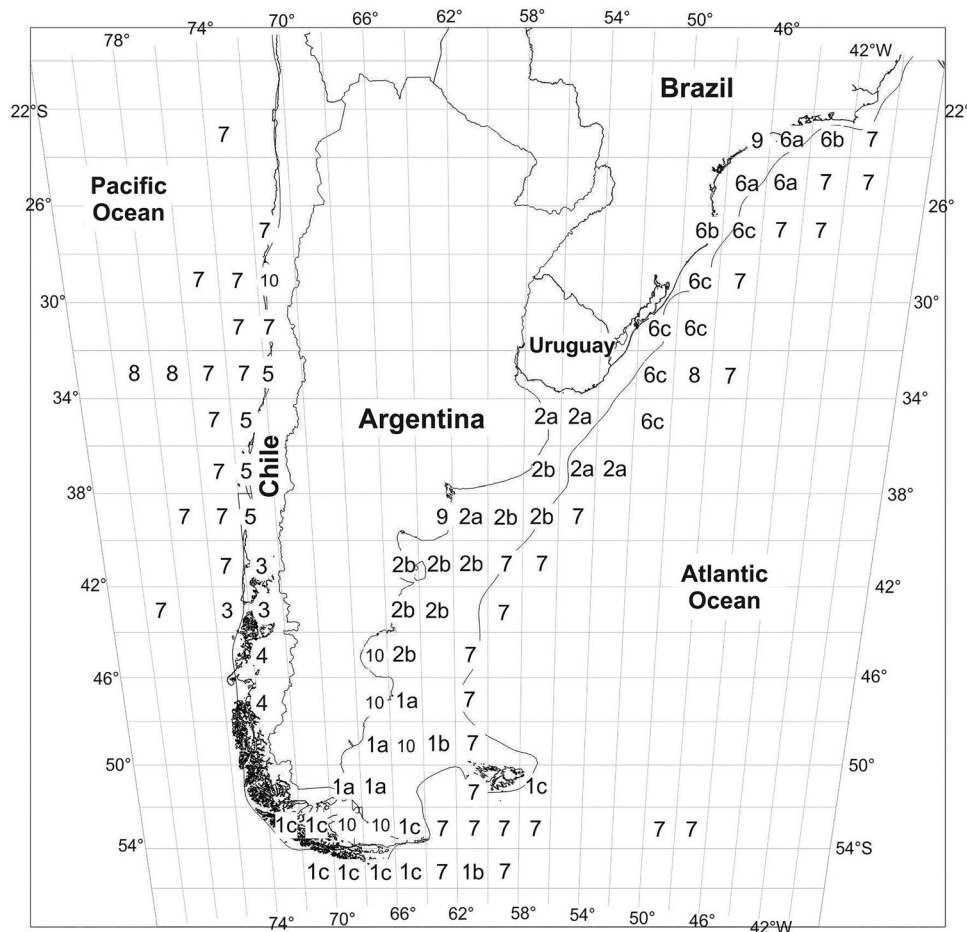
Figure 2. Spatial distribution of each hydromedusa assemblage obtained with the CLUSTER analysis. 1, Atlantic Magellanic (groups 1a, 1b and 1c); 2, Argentinean (groups 2a and 2b, Uruguayan and Rionegrensis, respectively); 3, Pacific intermediate zone; 4, Pacific Magellanic; 5, Peruvian–Chilean; 6, South Brazilian (groups 6a, 6b and 6c); and 7, Oceanic. The irregularly distributed groups 8, 9 and 10 did not define any biogeographical area. The Albers projection was employed for the map.

with middle- and outer-shelf waters with variable salinity from 33.4 to 34.1 (Hubold 1980; Guerrero & Piola 1997; Piola & Rivas 1997).

Hydromedusae of the South Brazilian province (subtropical neritic after Dadon & Boltovskoy 1982) are associated with the high temperatures of the Brazilian coastal waters from Cabo Frio to the Río de la Plata (Balech 1954, 1964; Palacio 1982; Balech & Ehrlich 2008). The relatively narrow southern Brazilian continental shelf (Acha et al. 2004) is influenced by the tropical waters of the Brazil Current, by the cold South Atlantic Central Water and by freshwater discharge from land into these coastal waters, mainly from the Lagoa dos Patos and the Río de la Plata (Emílsson 1961; Bisbal 1995; Castro & de Miranda 1998). This province tends to have high temperatures (18–25°C) (Hubold 1980, see also CCA analysis) and variable salinity (33–36.5) (Emílsson 1961). The internal differentiation might be related to the hydrographic features dividing the southern Brazilian coast into two

latitudinal areas: southern Brazilian Bight (22–28°S, groups 6a and 6b) and southern Subtropical Shelf (28–35°S, group 6c). The main contrast between these two areas derives from the stronger influence of waters of the Southern Subtropical Shelf derived from the La Plata outflow and the seasonal changes in the latitudinal position of the northern border of the Subtropical Convergence between the Brazil and Malvinas (Falkland) currents (see Lopes et al. 2006).

Endemism is expected to occur to varying degrees in biogeographical provinces (Spalding et al. 2007), but this may not be true for transitional zones. The Argentinean province is a transitional neritic zone between the South Brazilian and Atlantic Magellanic provinces (~34–46°S) (cf. Dadon & Boltovskoy 1982; Boltovskoy et al. 1999), with which it shares several species of hydromedusae, as well as many other species that are found throughout the study area. The only species exclusively in the Argentinean province, *Eutima mira* McCrady, 1859, is not endemic to

Table II. SIMPER analysis results for the data of presence/absence of hydromedusae species per cell.

Code	Species	Contribution to similarity within group											
		1A	1B	1C	2A	2B	3	4	5	6A	6B	6C	7
1	*Bougainvillia macloviana* Lesson, 1830 (M)	15.84	50	18.80			3.13	4.17					
2	*Bougainvillia muscus* (Allman, 1863) (M)					3.18		4.17		1.85			
3	*Bougainvillia frondosa* Mayer, 1900 (M)											5.64	
4	*Bougainvillia muscoides* (Sars, 1846) (M)					3.13		4.17					
5	*Bougainvillia pyramidata* (Forbes & Goodsir, 1853) (M)					3.13							
6	*Bougainvillia involuta* Uchida, 1947 (M)								5.02				
7	*Bougainvillia fulva* Agassiz & Mayer, 1899 (M)								1.46				
8	*Turritopsis nutricula* McCrady, 1857 (M)									5.31	11.11	5.36	
9	*Hydractinia borealis* (Mayer, 1900) (M)						3.13	4.17					
10	*Hydractinia carica* Bergh, 1887 (M)			2.86			3.13	4.17					
11	*Amphinema dinema* (Perón & Lesueur, 1809) (M)					3.13				5.31			
12	*Amphinema rugosum* (Mayer, 1900) (M)						3.13	4.17					
13	*Leuckartiara octona* (Fleming, 1823) (M)					3.38	3.13	4.17	10.45				
14	*Leuckartiara zacae* Bigelow, 1940 (M)								1.53				
15	*Proboscidactyla mutabilis* (Browne, 1902) (M)	32.51		5.17	19.95	13.83	3.13						
16	*Proboscidactyla ornata* (McCrady, 1859) (M)						3.13	4.17	2.43	5.31	11.11	8.71	
17	*Proboscidactyla stellata* (Forbes, 1846) (M)						3.13	4.17					
18	*Coryne eximia* Allman, 1859 (M)					13.83	3.13	4.17	10.45	5.31			
19	*Sphaerocoryne coccometra* (Bigelow, 1909) (M)							4.17					
20	*Corymorpha gracilis* (Brooks, 1883) (M)									5.31	11.11	8.71	
21	*Corymorpha januarii* Steenstrup, 1855 (M)										11.11		
22	*Euphysa aurata* Forbes, 1848 (M)					10.28	3.13	4.17	10.45				
23	*Hybocodon chilensis* Hartlaub, 1905 (M)					2.15	3.13	4.17					
24	*Hybocodon unicus* (Browne, 1902) (M)						3.13						
25	*Tiaricodon coeruleus* Browne, 1902 (M)	6.52											
26	*Niobia dendrotentaculata* Mayer, 1900 (M)									5.31			
27	*Eucodonium brownei* Hartlaub, 1907 (M)									1.85			
28	*Heterotiara minor* Vanhöffen, 1911 (M)						3.13						
29	*Ectopleura dumortierii* (Van Beneden, 1844) (M)						3.13	4.17	4.25	5.31			
30	*Cytaeis tetrastyla* Eschscholtz, 1829 (M)									5.31			
31	*Podocorynoides minima* (Trinci, 1903) (M)						3.13			5.31			
32	*Aequorea coerulescens* (Brandt, 1838) (M)						3.13						
33	*Aequorea globosa* Eschscholtz, 1829 (M)						3.13						
34	*Rhacostoma atlanticum* L. Agassiz, 1851 (M)									1.89			
35	*Eucheilota duodecimalis* A. Agassiz, 1862 (M)										11.11		
36	*Eucheilota paradoxica* Mayer, 1900 (M)									5.31			
37	*Eucheilota ventricularis* McCrady, 1859 (M)				19.95	3.26				5.31			
38	*Laodicea pulchra* Browne, 1902 (M)	4.34	50	6.02			3.13	4.17					
39	*Laodicea undulata* (Forbes & Goodsir, 1853) (M)					7.54	3.13	4.17					
40	*Cosmetirella davisii* (Browne, 1902) (M)	5.21		18.80	6.07								
41	*Halopsis ocellata* Agassiz, 1865 (M)			10.94			3.13	4.17					
42	*Mitrocomella frigida* (Browne, 1910) (M)			7.12	1.90								
43	*Mitrocomella brownei* (Kramp, 1930) (M)					10.28							
44	*Phialella quadrata* (Forbes, 1848) (M)						3.13		5.02				
45	*Phialella falklandica* Browne, 1902 (M)	13.67											
46	*Modeeria rotunda* (Quoy & Gaimard, 1827) (M)						3.13	4.17					
47	*Clytia lomae* (Torrey, 1909) (M)					1.75							
48	*Clytia simplex* (Browne, 1902) (M)			13.23		5.09	3.13	4.17	5.9				
49	*Clytia gracilis* (Sars, 1850) (M)					2.12							
50	*Clytia hemisphaerica* (Linnaeus, 1767) (M)				10.55							3.05	
51	*Aglauropsis conanti* Browne, 1902 (M)	13.67											
52	*Gossea brachymera* Bigelow, 1909 (M)							4.17					
53	*Olindias sambaquiensis* Müller, 1861 (M)					3.44							
54	*Aegina citrea* Eschscholtz, 1829 (H)											1.83	
55	*Solmundella bitentaculata* (Quoy & Gaimard, 1833) (H)			3.13	1.99		3.13	4.17		5.31	11.11	8.71	19.55
56	*Cunina peregrina* Bigelow, 1909 (H)						3.13	4.17				3.05	
57	*Cunina octonaria* McCrady, 1859 (H)			5.28						5.31	11.11	8.71	
58	*Cunina globosa* Eschscholtz, 1829 (H)								1.53				
59	*Solmissus marshalli* Agassiz & Mayer, 1902 (H)								4.25				
60	*Pegantha clara* R.P. Bigelow, 1909 (H)								1.53				
61	*Solmaris corona* (Keferstein & Ehlers, 1861) (H)									5.31		8.71	
62	*Liriope tetraphylla* (Chamisso & Eysenhardt, 1821) (H)				19.95		3.13		10.45			8.71	9.25
63	*Haliscera conica* Vanhöffen, 1902 (H)								1.53				
64	*Halitrephes maasi* Bigelow, 1909 (H)					7.54							

(Continued)

Table II. Continued.

							Contribution to similarity within group					
Code	Species	1A	1B	1C	2A	2B	3	4	5	6A	6B	6C	7
65	*Aglaura hemistoma* Péron & Lesueur, 1809 (H)						3.13			5.31	11.11	8.71	
66	*Rhopalonema velatum* Gegenbaur, 1857 (H)			5.72	5.87				10.45	5.31	11.11	8.71	55.33
67	*Sminthea eurygaster* Gegenbaur, 1857 (H)								4.25			1.83	5.91
	Meroplanktonic	100	100	90	64	92	86	91	63	71	56	65	–
	Holoplanktonic	–	–	10	36	8	14	9	37	29	44	35	100

The contribution of each hydromedusae species (%) to similarity within each group obtained with CLUSTER analysis and the total contribution of meroplanktonic and holoplanktonic species to each group (%) are indicated. The species are listed following the code used in Figure 4 and the life cycle type of each one is indicated in parentheses: holoplanktonic (H) and meroplanktonic (M).

that region and has been reported in the tropical waters of northeastern Brazil (Vannucci 1957; Goy 1979). Although the immense discharge of the Río de la Plata is considered a zoogeographical barrier to the distribution of various marine groups (Boltovskoy et al. 1999; López Gappa et al. 2006), it acts only as an intermittent barrier, because in periods of low flow and prevailing NE winds, planktonic species and fishes of the South Brazilian province can reach up to 38°S (Mianzan et al. 2001; Mianzan & Acha 2008).

Species of the Argentinean province were associated with intermediate water temperatures as well, and not with low or high temperatures, as were the Magellanic (sub-Antarctic) and Brazilian (subtropical) provinces, respectively. The internal differentiation of the province into two districts was suggested to be related to a predominance of 'more sub-Antarctic' and 'more subtropical' species in the Rionegrensis and Uruguayan districts, respectively (see Balech & Ehrlich 2008), but this was not corroborated by the hydromedusa distribution.

Assemblages on the Pacific side of South America are under the influence of the Humboldt Current system complex. A break in species distribution occurs around Chiloé Island (~40–44°S). From Chiloé northward, cold (11–19°C), nutrient-rich waters (Boschi 2000) run along the Peruvian–Chilean Province; from Chiloé southward, the Cape Horn Current influences the southernmost Magellanic Province and extends eastward to join the Malvinas (Falkland) Current (Camus 2001). Indeed, several authors suggested an association between the faunas of the southernmost regions of Chile and Argentina and with this view, a single Magellanic Province would extend from Chiloé Island to the southern limits of Golfo Nuevo (43–44°S), passing through Cape Horn at Tierra del Fuego (Carcelles & Williamson 1951; Balech 1954; Lopez 1963; Stuardo 1964; Boschi 2000). However, we found two separate assemblages and no evidence supporting this connection, perhaps because of the lack of more thorough sampling of hydromedusae between 46°S and 52°S (cf. Camus 2001).

Finally, the Oceanic assemblage is clearly uniform; the same species were found in the southern Pacific and Atlantic off South America, as much in subtropical as in sub-Antarctic waters. Consequently, we found no support for associations between species assemblages and oceanic water masses that would suggest the existence of three biogeographical areas: subtropical oceanic, transitional oceanic and sub-Antarctic oceanic (cf. Dadon & Boltovskoy 1982; Tarling et al. 1995; Thompson & Alder 2005; Berasategui et al. 2006). Oceanic pelagic species are usually widespread, often cosmopolitan (Pierrot-Bults 1997) and therefore endemic oceanic species appear to be rare or non-existent (Pierrot-Bults 2003), due either to the absence of ecological barriers (Boltovskoy 1999) or to their ecophysiological tolerance (physiological plasticity or adaptive behaviours, Van der Spoel 1994). However, recent studies using molecular techniques have also indicated that presumed 'cosmopolitan' oceanic species are often a composite of genetically distinct entities, representing geographically isolated populations or many cryptic species (see Bucklin et al. 2010, for medusozoans see Dawson 2003; Pontin & Cruickshank 2012; Aglieri et al. 2014).

Life cycle and distribution pattern

For a long time it has been proposed that free-living stages (i.e. those not attached to the bottom) would decisively contribute to dispersal (Mackie 1974). Therefore, a medusa stage, traditionally considered dispersive, would promote both interpopulation genetic mixing and range extension, and this seems to occur for holoplanktonic medusae. However, hydroids with a reduced or suppressed medusa stage would have similar geographical distributions to species with a long-lived planktonic medusa stage. Some hydrozoans without a medusa are efficient dispersers as well, and can reach remote areas (Cornelius 1992; Miranda et al. 2013) or may be cosmopolitan (Boero & Bouillon 1993), although those species have generally not yet undergone thorough taxonomic analyses (cf. Cunha et al. 2015). Sessile hydroids (and fragments of colonies and polyps as well) could drift attached to algae, driftwood and other floating debris, thereby effectively
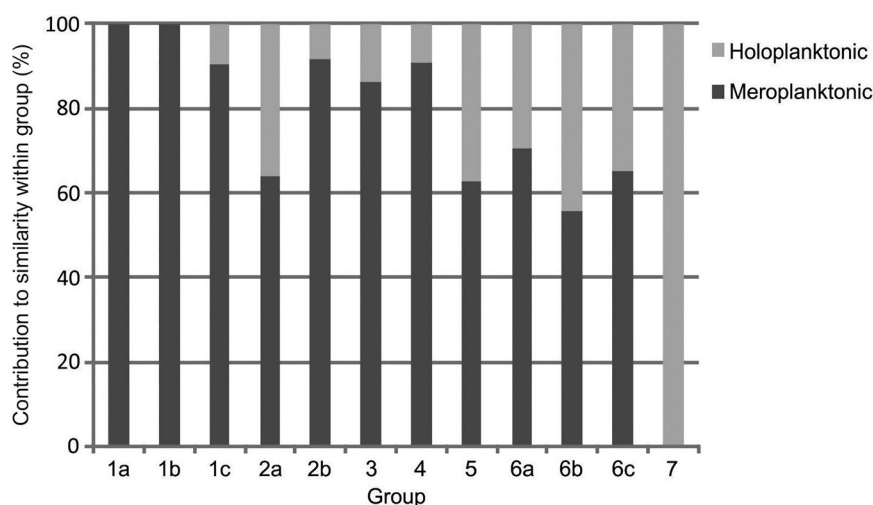
Figure 3. Histogram showing the contributions of meroplanktonic and holoplanktonic hydromedusa species in South America to the average similarity within each group (SIMPER analysis): Atlantic Magellanic (1a, 1b and 1c); Argentinean (2a and 2b); Pacific intermediate zone (3); Pacific Magellanic (4); Peruvian–Chilean (5); South Brazilian (6a, 6b and 6c); Oceanic (7).

reaching remote areas (Mackie 1974; Cornelius 1992; Calder et al. 2014). Some hydroids have the capacity to become temporarily dormant in response to unfavourable environmental conditions (Calder 1990) and this enhances the survivability of hydroids across vast distances. Dispersal by rafting is also present in at least some meroplanktonic medusozoans (Cornelius

1992). So, the long-range dispersal of meroplanktonic hydrozoan species may also be attributable to passive transport of hydroids compared to their mostly short-lived and less physiologically tolerant medusae.

Our analyses showed that meroplanktonic medusae contributed more to defining neritic assemblages, while the single oceanic assemblage was defined by
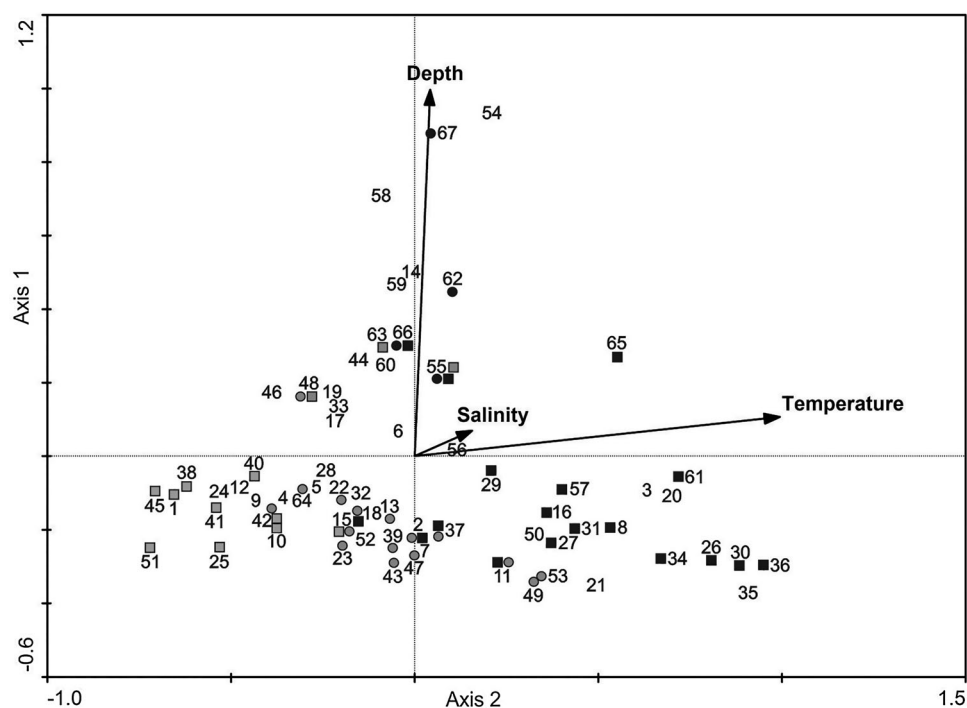

Figure 4. CCA ordination diagram showing the environmental variables and spatial distributions of hydromedusa species in South America that contributed to similarity within groups obtained with the CLUSTER analysis. The numbers refer to the species codes in Table II. Symbols represent species that contributed to the Rionegrensis district (group 2b) (grey circles), Oceanic assemblage (group 7) (black circles), Atlantic Magellanic province (groups 1a, 1b and 1c) (grey squares) and South Brazilian province (groups 6a, 6b and 6c) (black squares).

holoplanktonic medusae (Figure 3). Therefore, our results corroborated the supposition that meroplanktonic hydromedusae would be more restricted in distribution than would holoplanktonic ones. Some biological aspects may explain the distribution of meroplanktonic hydromedusae. First, the discontinuous presence of medusae in the plankton may be compensated by the long-term presence of polyps in the benthos (Boero et al. 1996), even though recruitment may occur seasonally in the tropical and subtropical areas studied (Migotto et al. 2001; Fernandez et al. 2014, 2015). Second, medusa reproduction may be compromised after long-distance dispersal, because successful fertilization and planula recruitment are less likely (see also Boero 1984). Meroplanktonic hydromedusae also may drift to areas without suitable substrates for larval settlement, constraining the distribution of polyps to coastal areas (cf. maps of niche modelling by Mendoza-Becerríl & Marques 2013). Thus, the presence of medusae of a particular species in a given area does not indicate that the organisms complete their entire life cycle there. Also, some hydromedusae may remain in the plankton through asexual reproduction (e.g. *Hydractinia carica* Bergh, 1887, *Niobia dendrotentaculata* Mayer, 1900, *Proboscidactyla ornata* (McCrady, 1859) and *Rathkea formosissima* (Browne, 1902)) (Browne & Kramp 1939; Schuchert 2009) and therefore they could remain longer in the plankton and also disperse over larger areas.

Importantly, holoplanktonic hydromedusae also contributed to define the South Brazilian provinces. In this region, the intrusion of South Atlantic Central Water transports eggs and fish larvae (along with these oceanic hydromedusae) from the oceanic to the neritic realm (Lopes et al. 2006), so it is not surprising that the holoplanktonic species *R. velatum* and *S. bitentaculata* were present in these neritic provinces (cf. also Navas-Pereira 1981; Tronolone 2007). Also, *Liriope tetraphylla* (Chamisso & Eysenhardt, 1821), a holoplanktonic species, is very abundant in the Río de la Plata estuarine zone (Gaitán 2004), contributing to define the Uruguayan district of the Argentinean province.

Future directions

Recent studies carried out in different areas also show that the diversity of medusae varied mainly in relation to different water masses (Lindsay et al. 2014; Licandro et al. 2015). However, the distribution of plankton stages is apparently not limited only by physical mechanisms. They can also be mediated by species behaviour (cf. Prairie et al. 2012) and phylogenetic history (cf. Morandini & Marques 2010). Holoplanktonic

groups such as Trachymedusae and Narcomedusae are more liable to be transported out of their 'home' ranges, and this is expected to be less likely for meroplanktonic species because the origin of their medusa stage is from benthic polyps (Lindsay et al. 2014). Therefore, the distribution of hydromedusae and, consequently, the delimitation of biogeographic provinces may also vary depending on the life cycles of the species involved. However, our hypothesis concerning the influence of the life cycle on medusa distribution patterns should be tested in several situations, including benthic species, as well as by molecular and population-genetics techniques (cf. Gibbons et al. 2010a).

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